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Blacklegged Tick (*Ixodes scapularis*) Distribution in Maine, USA, as Related to Climate Change, White-tailed Deer, and the Landscape

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BLACKLEGGED TICK (*IXODES SCAPULARIS*) DISTRIBUTION IN MAINE, USA, AS RELATED TO CLIMATE CHANGE, WHITE-TAILED DEER, AND THE LANDSCAPE

By

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A DISSERTATION

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Earth and Climate Sciences)

The Graduate School

The University of Maine

May 2019

Advisory Committee:

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by Susan P. Elias

Dissertation Advisor: Dr. Kirk A. Maasch

An Abstract of the Dissertation Presented
in Partial Fulfillment of the Requirements for the
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Lyme disease is caused by the bacterial spirochete *Borrelia burgdorferi*, which is transmitted through the bite of an infected blacklegged (deer) tick (*Ixodes scapularis*). Geographic invasion of *I. scapularis* in North America has been attributed to causes including 20th century reforestation and suburbanization, burgeoning populations of the white-tailed deer (*Odocoileus virginianus*) which is the primary reproductive host of *I. scapularis*, tick-associated non-native plant invasions, and climate change. Maine, USA, is a high Lyme disease incidence state, with a history of increasing *I. scapularis* abundance and northward range expansion. This thesis addresses the question: “To what extent has the range expansion of blacklegged ticks in Maine been associated with climate change, deer, and other factors?” using a long-term, passive surveillance dataset (1990-2013) of *I. scapularis* in Maine.

Chapter 1 characterized temporal trends in *I. scapularis* submissions rate (an index of abundance) and phenology, in Maine’s northern (7 counties) versus southern (9 counties) tier. In the northern tier the *I. scapularis* submission rate and season duration increased throughout the duration of the time series, indicating *I. scapularis* was emergent but not established. By contrast, in the southern tier, submissions rate and season duration increased initially but after

about 13 years leveled off, indicating *I. scapularis* was established by the mid-2000s. Winter and fall average minimum temperatures increased in the northern tier and summer relative humidity in both tiers increased. *I. scapularis* submission rates and phenological changes were correlated with relative humidity statewide. Generally, *I. scapularis* submission rates and phenological changes were correlated with winter warming, but predominantly in the northern tier and only the early half of the time series for the southern tier. Though northern tier climate appears to have become more permissive over time, current ecological suitability for *I. scapularis* in the northern tier may be limited due to low deer densities, which averaged ~5/mi^2. In the southern tier, deer densities were higher and correlated with *I. scapularis* submissions rate. However, a number of other, unknown population-limiting mechanisms could have been operating to keep *I. scapularis* in the southern tier at a dynamic equilibrium since the mid-2000s. Also observed was a correlation between Lyme incidence and *I. scapularis* in the northern but not southern tier. This may represent decoupling of reported disease incidence and entomological risk as measured simply by tick abundance and Borrelial infection prevalence. This discrepancy suggested that disease discovery had increased through greater clinician and patient awareness and testing effort, and/or that acarological risk may be a more nuanced function of diverse, variously virulent strain types in multiple pathogens borne by *I. scapularis*.

Chapter 2 used a generalized additive mixed model (GAMM) to model linear and nonlinear relationships between nymphal *I. scapularis* abundance and predictors, while allowing for spatiotemporal dependencies within and among wildlife management districts. *I. scapularis* nymphs increased with increasing deer densities up to ~13 deer/mi^2, but beyond this threshold tick abundance did not vary with deer density. This result corroborated the idea of a saturating relationship between *I. scapularis* and deer density. It was also consistent with empirical studies suggesting deer density must be lowered below ~8-13/mi^2 to lower *I. scapularis* abundance enough to lower Lyme disease. The model also indicated that more ticks were associated with higher relative humidity, warmer minimum winter temperatures and more degree-day accumulation, and that without deer >4/mi^2 warmer winters would not increase nymphal abundance. The Maine Department of Inland Fisheries and Wildlife northern tier goals range from 10-15/mi^2 and southern tier goals from 15-20/mi^2 for 2030 (MEIFW 2017). We recommended deer densities be kept to ≤10/mi^2 in all of Maine's northern tier to mitigate likely increases in ticks due to future warming. Suburbanization and presence of tick-associated non-native plants did not enter the model because they co-occurred with deer.

Chapter 3 ascertained that Lyme incidences on the off-shore, unbridged islands of Maine have been above the statewide average and at least on par with those seen on other offshore islands in Massachusetts and Rhode Island. Increasing *I. scapularis* abundance and Lyme incidence have been attributed to high deer densities by some residents of these island communities. Burgeoning deer densities on some of these islands have led to various deer management histories along with a good deal of conflict on how to manage deer populations. We summarized the burden of Lyme disease, entomological risk, and deer management histories on these islands. We also polled island residents in 2016 to quantify the level of concern about the Lyme disease problem and assess the level of support for deer herd reduction on their islands. A 2016 survey of island residents indicated that other deer-related problems, namely vehicle collisions and garden and forest damage, motivated support for deer reduction as much as Lyme disease. We recommended efforts to keep deer density ≤15/mi^2 and to remove invasive plant species--particular Japanese barberry—from the landscape. The benefits of these measures will extend beyond vector tick control to improved deer and forest health.

DEDICATION

I dedicate this dissertation to my father, Merrill Francis Elias, PhD, MPH, Professor Emeritus, University of Maine. Dad's scientific scholarship has inspired me from day one. I further dedicate this dissertation to my mother, Sandra Bernice Horsman Leonard, who passed down to me her scholarship, especially her love of the English language. I dedicate this work to my stepparents, David Albert Leonard, and Penelope Lee Kelly Elias, PhD, who have unendingly supported and inspired me. I also dedicate this work to Samuel Frederick Gerken and David Henry Gerken, who have encouraged me every step of the way, and who have become high scholars in their own right and make their mother very proud. I dedicate this effort to Scott Robert Cyr, who has a heart of gold. I dedicate this work also to my major advisor, Kirk Allen Maasch, PhD. Finally, I dedicate this work to the people of the State of Maine.

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CHAPTER 1.

TRENDS IN QUESTING BLACKLEGGED TICK ABUNDANCE AND PHENOLOGY IN NORTHERN VERSUS SOUTHERN MAINE, USA

1.1 Abstract

Lyme disease is caused by the bacterial spirochete *Borrelia burgdorferi*, which is transmitted through the bite of an infected blacklegged tick (*Ixodes scapularis*). Maine, USA, is a high Lyme disease incidence state, with rising incidence of Lyme and other tick-borne illnesses associated with a history of increasing *I. scapularis* abundance, including range expansion to the north. Using a passive surveillance dataset (1990-2013), we characterized temporal trends in *I. scapularis* submissions rate (an index of abundance) and phenology, in Maine's northern (7 counties) versus southern (9 counties) tier. We also determined whether questing *I. scapularis* submissions rate and phenology were correlated with climatological variables and white-tailed deer (*Odocoileus virginianus*) density. In the northern tier the *I. scapularis* submissions rate and season duration increased throughout the duration of the time series, indicating *I. scapularis* was emergent but not established. By contrast, in the southern tier, submission rate and season duration increased initially but after about 13 years leveled off, indicating *I. scapularis* was established by the mid-2000s. Winter and fall average minimum temperatures in the northern tier, and fall average temperatures and summer relative humidity in both tiers increased. *I. scapularis* submission rates and phenological changes were correlated with relative humidity statewide. Generally, *I. scapularis* submission rates and phenological changes were correlated with winter warming, but predominantly in the northern tier and only the early half of the time series for the southern tier. Though northern tier climate appears to have become more

permissive over time, current ecological suitability for *I. scapularis* in the northern tier may be limited due to low deer densities, which averaged ~5/mi^2. In the southern tier, deer densities were higher and correlated with *I. scapularis* submissions rate. However, a number of other, unknown population-limiting mechanisms could have been operating to keep *I. scapularis* in the southern tier at a dynamic equilibrium since the mid-2000s. Also observed was a correlation between Lyme incidence and *I. scapularis* in the northern but not southern tier. This may represent decoupling of reported disease incidence and entomological risk as measured simply by tick abundance and Borrelial infection prevalence. This discrepancy suggested that disease discovery had increased through greater clinician and patient awareness and testing effort, and/or that acarological risk may be a more nuanced function of diverse, variously virulent strain types in multiple pathogens borne by *I. scapularis*.

1.2 Introduction

1.2.1 Expansion of Lyme Disease

Lyme disease is the most common tick-borne disease in the US, accounting for 69% of all tick- and mosquito-borne illness (Adams et al. 2016). Lyme disease is caused by the bacterial spirochete *Borrelia burgdorferi*, which is transmitted through the bite of an infected blacklegged tick (*Ixodes scapularis*) (Mead et al. 2015, Rosenberg et al. 2018). With >37,000 cases reported to the Centers for Disease Control and Prevention (CDC) during 2013, Lyme disease ranks fifth among all nationally notifiable conditions (Mead et al. 2015). The number of reported Lyme disease cases has roughly tripled from 1992 to 2015 (Adams et al. 2016) and its geographic range has expanded (Fig. 1.1, CDC 2018a) in both the northeast and upper Midwest.

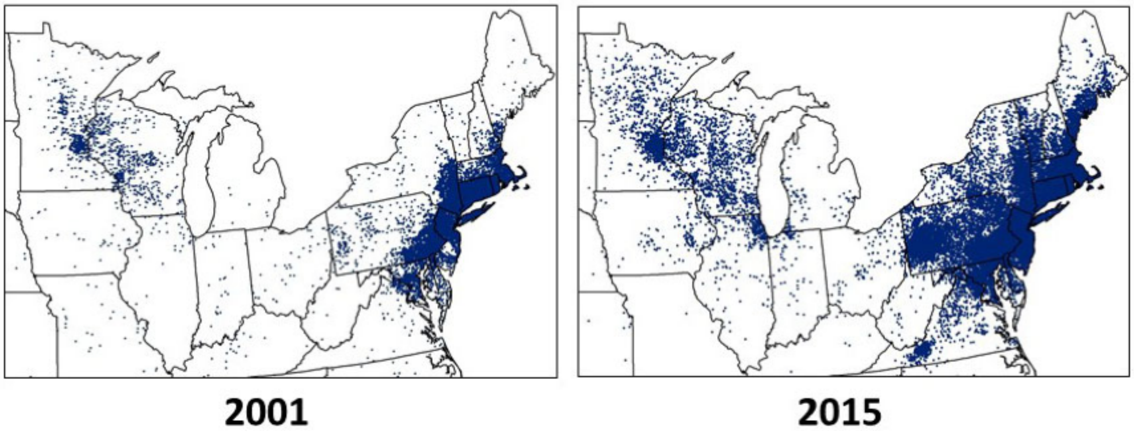

Figure 1.1 Range expansion of Lyme disease cases in the US, 2001 versus 2015.

The first known case of Lyme disease in Maine was in 1986 (Rand et al. 2007) and the first reports of *I. scapularis* in Maine were published in the late 1980s (Anderson et al. 1987, Ginsberg and Ewing 1988). Maine has ranked among the top five states for Lyme incidence since 2008, with the highest 3-year average (2015-2017) incidence in the nation at 89.2 cases per 100,000 people (CDC 2018b). Case-counting is inexact (Cartter et al. 2018), but Maine is consistently a high-incidence state for reported Lyme disease with increases over time in every county (Fig. 1.2, MECDC 2018a). Incidence is the rate of occurrence of new cases and conveys information about the risk of contracting the disease. Lyme incidence has been above the statewide average in the southern coastal and interior counties (Androscoggin, Cumberland, Hancock, Kennebec, Knox, Lincoln, Sagadahoc, Waldo, and York), and below average in the more western and northern counties (Aroostook, Franklin, Oxford, Penobscot, Piscataquis, Somerset) and the easternmost county, Washington County, which includes what is known as the Downeast coast.

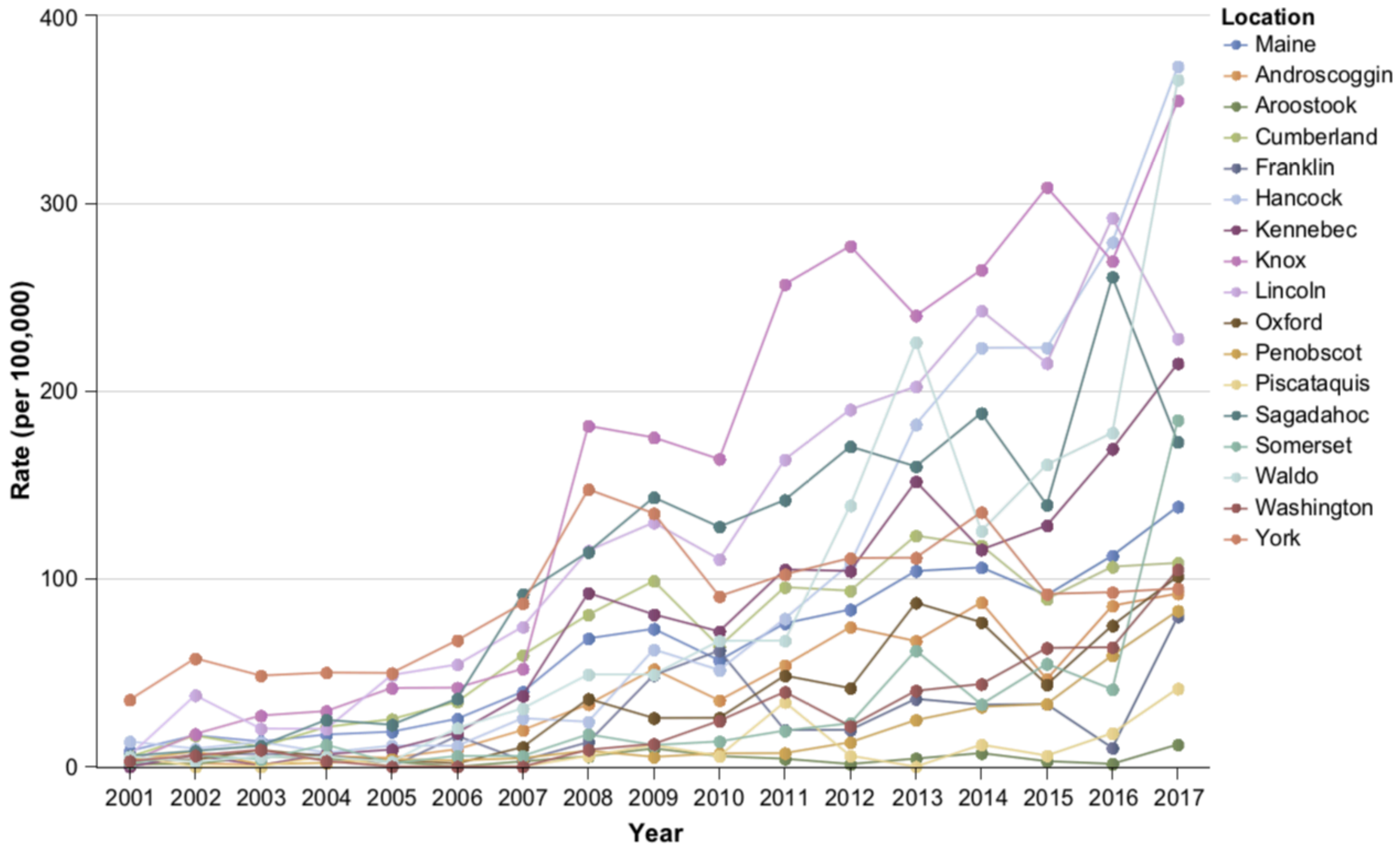

Figure 1.2 Statewide increases in incidence of Lyme disease in Maine by county, 2001-2017. e: Maine Center for Disease Control and Prevention (MECDC 2018a).

Based on whether counties have been above or below the statewide average for Lyme incidence from 2001 through 2017), we can define the southern tier as including nine counties: Androscoggin, Cumberland, Hancock, Kennebec, Knox, Lincoln, Sagadahoc, Waldo, and York and the northern tier as including the remaining seven (Fig. 1.3). The geographic expansion of Lyme incidence (cases/100,000) in Maine shown in Figure 1.4 (MECDC 2018a) allows a visual comparison of county-level incidence in 2008-2012 versus 2013-2017. Clearly, Lyme incidence has increased in the southern tier of the state and expanded into the northern tier.

Figure 1.3 Maine divided into northern and southern tiers by county groupings.

1.2.2 Expansion of *Ixodes scapularis*

Using data from a statewide tick identification program that began in 1989, Rand et al. (2007) demonstrated for Maine a strong spatial relationship between Lyme disease incidence and nymphal *I. scapularis* (n = 16 counties, R^2 = 0.77) as well as a moderate temporal relationship over the years of the study (1989-2006, n = 18 years, R^2 = 0.52). The study showed that *I. scapularis* emerged first along the coast, then advanced inland and northwards in Maine. Increases over time were clear for the south coastal portions of the state as well as inland. Comparison with macroscopically similar *I. cookei* (woodchuck tick) indicated a true increase in abundance over time of questing *I. scapularis*, not just increased activity on the part of blacklegged ticks or tick submitters.

This statewide tick identification program, henceforth referred to as passive tick surveillance, continued through most of 2013. Appending the data collected since Rand et al. (2007) and it can be seen that the geographic range of *I. scapularis* in Maine continued to expand north and west (Fig. 1.5a,b) through the end of the passive surveillance program. Viewed as time series at the county level (Fig 1.6), *I. scapularis* submissions increased over time in the northern tier counties, especially Penobscot County. Meanwhile, submissions decreased in the southern tier, except for Hancock, which borders the northern tier. Given the universal increase in Lyme incidence in every county (Fig. 1.2), the decrease in *I. scapularis* in southern tier counties was counterintuitive. We thought that both the northward range expansion and the southern tier declines in *I. scapularis* submissions since Rand et al. (2007) merited investigation.

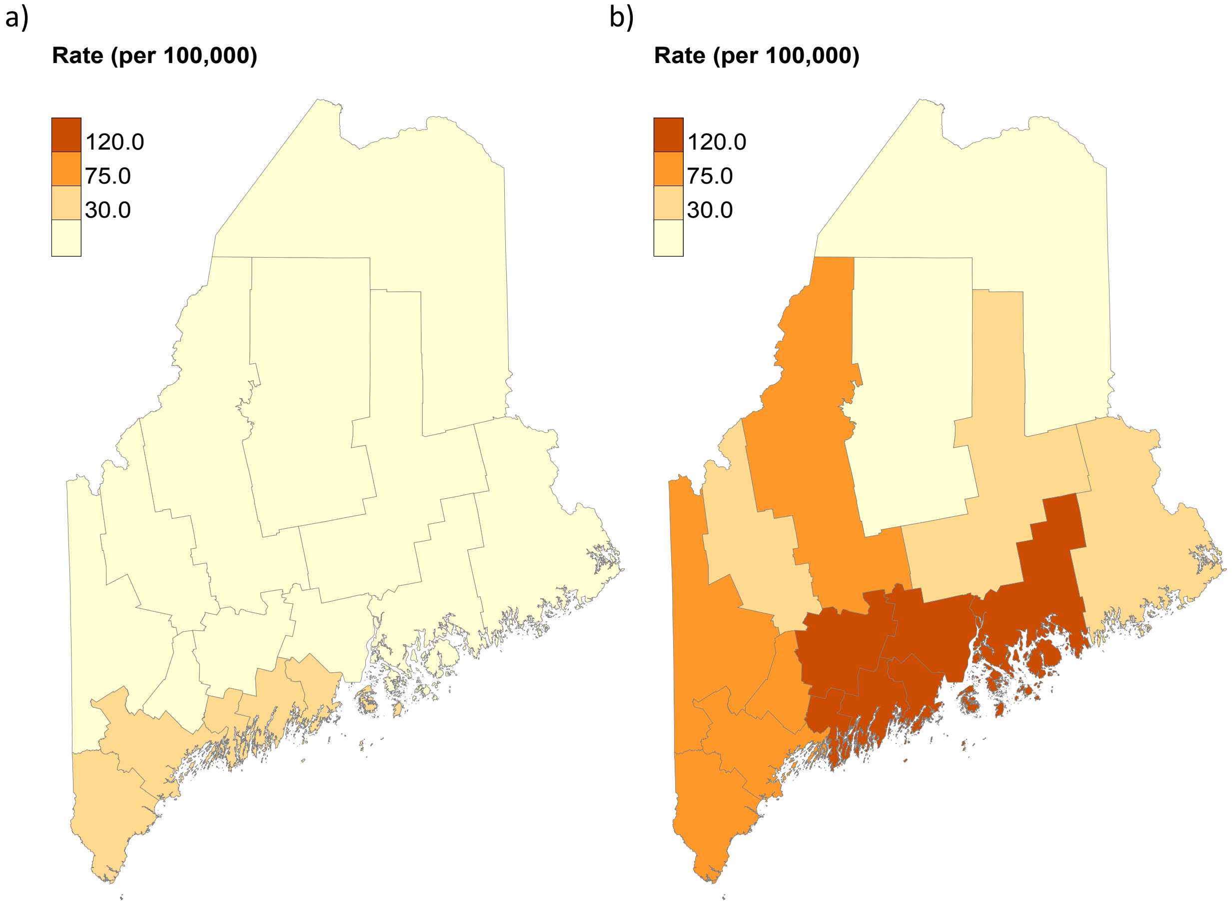

Figure 1.4 Lyme disease incidence (confirmed and probable cases per 100,000 people) by county in Maine, (a) 2003-2007 versus (b) 2013-2017. Maine CDC's Infectious Disease Program obtained these data through notifiable conditions surveillance based upon reports from healthcare providers, laboratories, and other healthcare partners. Source: Maine Tracking Network (MECDC 2018a).

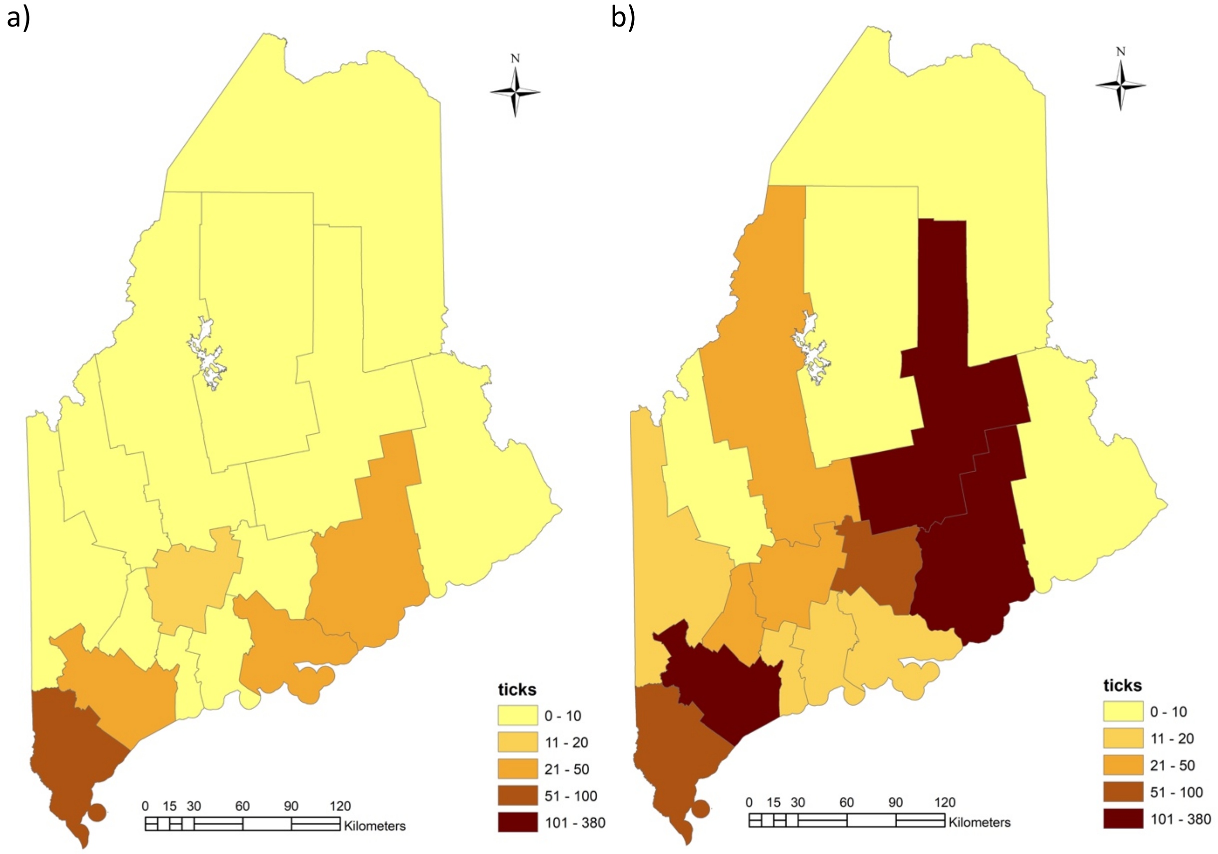

Figure 1.5 By-county counts of *I. scapularis* submitted to Maine Medical Center's tick identification program; select years represented (a) 2000, (b) 2012. Source: Vector-borne Disease Laboratory, Maine Medical Center Research Institute, Scarborough, Maine.

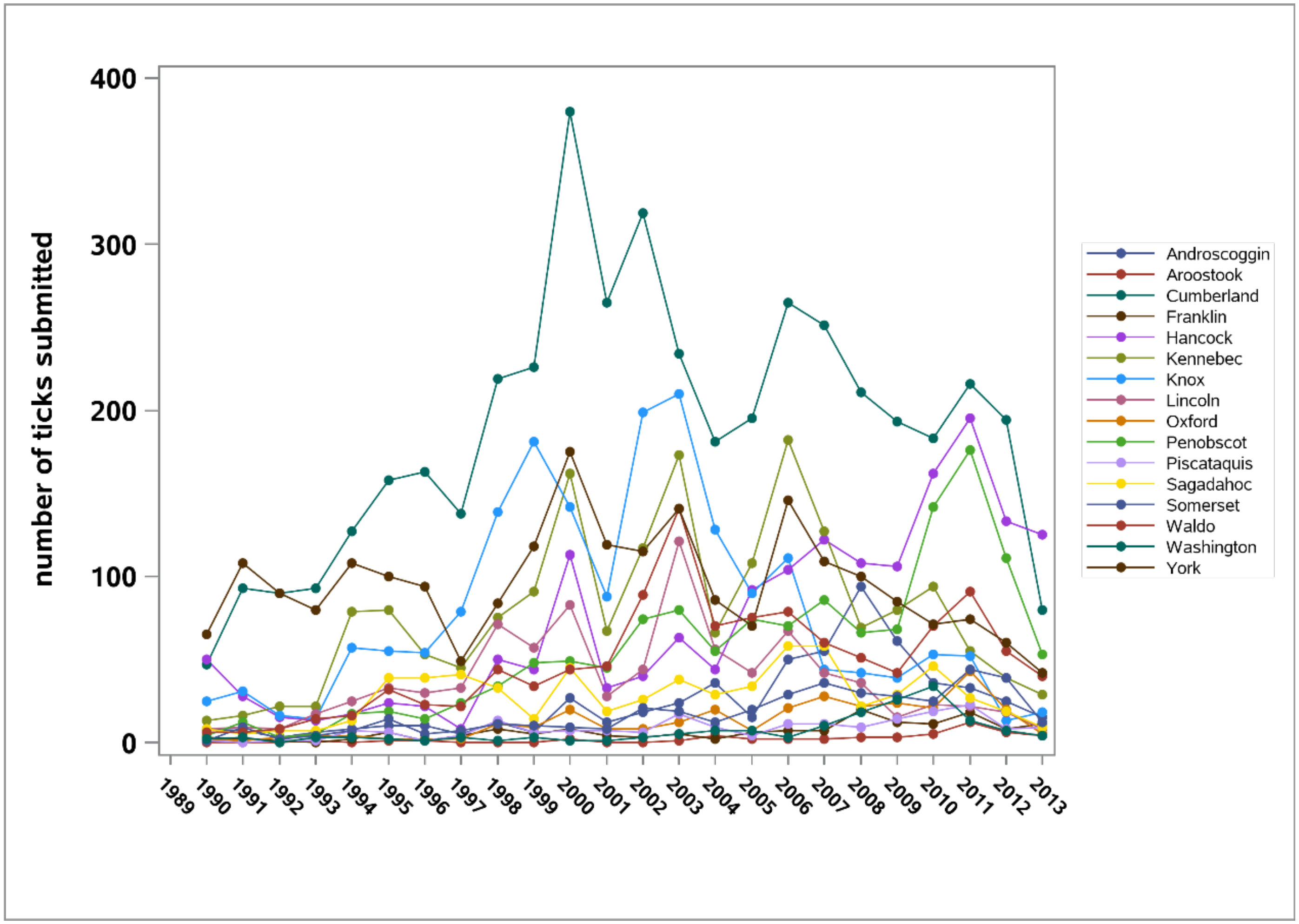

Figure 1.6 *I. scapularis* submitted to Maine Medical Center's tick identification program by county. Source: Vector-borne Disease Laboratory, Maine Medical Center Research Institute, Scarborough, Maine, USA.

1.2.3 The Life Cycle of *I. scapularis*

To understand how climate and weather may affect *I. scapularis* in Maine, it is helpful to know its life cycle and the seasonality of life stage events in Maine. In northern New England, blood-fed, gravid, female *I. scapularis* lay eggs (oviposit) generally in May of Year 1 (Fig. 1.7). These eggs hatch in August to become questing larvae which are “naïve”, that is, not infected by the agent of Lyme disease, *Borrelia burgdorferi*. Larvae that find blood meals, typically from small mammal hosts such as white-footed mice (*Peromyscus leucopus*) or birds, will be nourished and molt to the nymphal stage. These nymphs will diapause, overwinter, and become active the following spring and summer of Year 2. July is the peak nymphal blood meal questing month for nymphs in Maine. Nymphs that find blood meals, typically from white-footed mice and other rodents, as well as birds, will molt to become questing adults, with peak adult questing activity in Maine in late October into November (Year 2, Fig. 1.7). Those questing adults that find a blood meal—typically a white-tailed deer--in fall of Year 2 will diapause, overwinter, and lay eggs in May. Those adults that did not find a blood meal in fall of Year 2 will diapause, overwinter, and quest in the month of April and, if fed, lay eggs in May. Of course, through extended diapause, ticks may extend their life cycle across three or four years (Lindsay et al. 1998, Ogden et al. 2018). Thus, *I. scapularis* spends most of its time off-host, where survival, development, and questing (blood-meal seeking) are constrained by temperature and humidity (e.g., Ogden 2006, Ogden 2008, Parham et al. 2015, Ostfeld et al. 2015) at all stages of the two-year tick life cycle (Fig. 1.7).

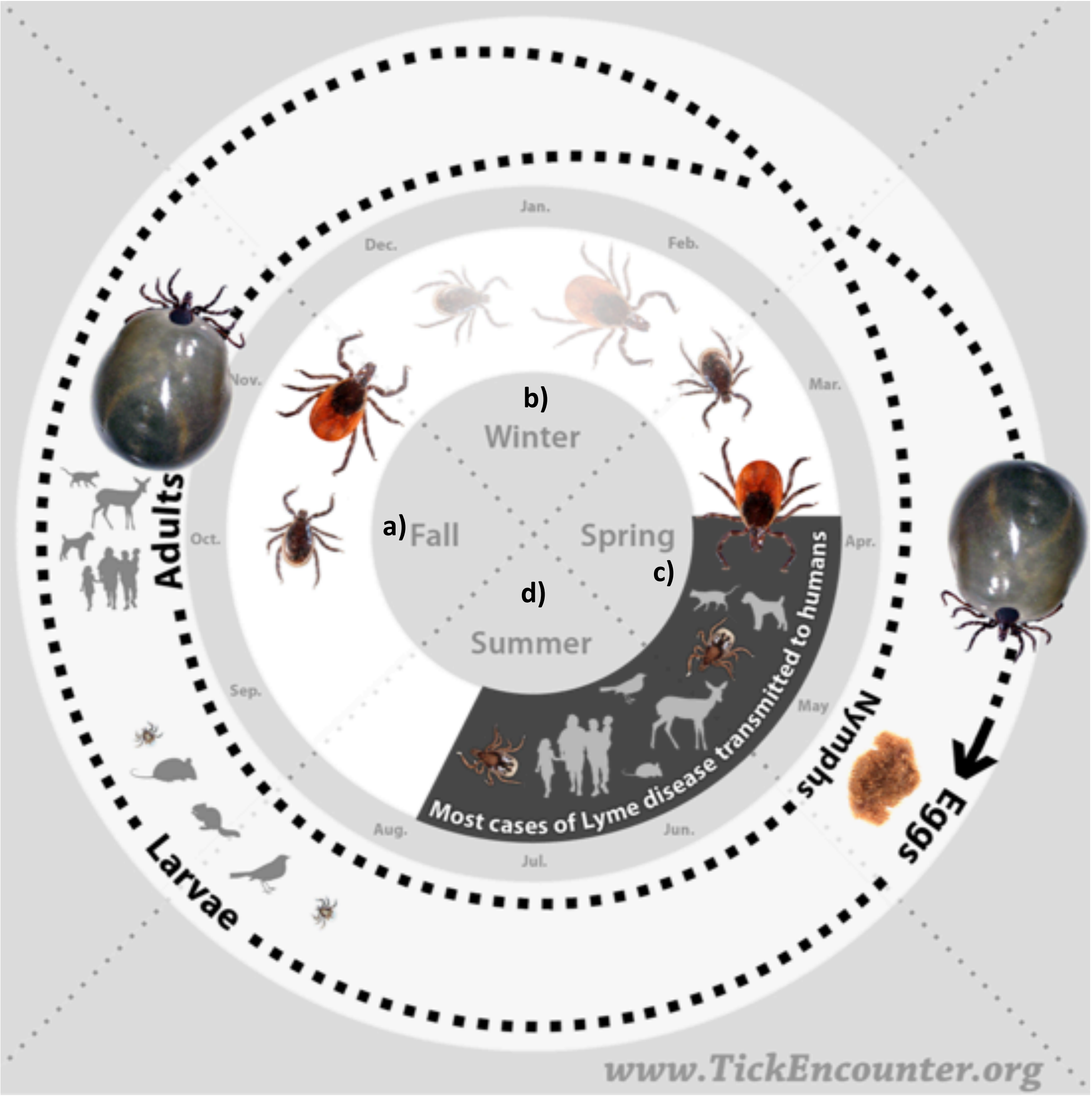

Figure 1.7 Life cycle of the blacklegged tick. Warmer, longer falls would allow for longer questing seasons for larvae and adults (a), warmer/shorter winters would enhance overwinter survival of all stages (b), earlier, warmer springs would allow earlier questing of all stages, especially adults, and earlier accumulation of degree-days would lead to earlier egg-laying and larval hatch (c), and sufficient humidity would rescue ticks from desiccation in summer (d). Life cycle figure used with permission from the University of Rhode Island TickEncounter Resource Center (www.TickEncounter.org).

1.2.4 Climate, Temperature, and Humidity Constraints on *I. scapularis*

Eisen et al. (2016) summarized the expectation that there should be stronger linkages between *Ixodes* abundance and climate near the margins of their range where populations are emergent (southern Canada and US northeast and upper Midwest states) or receding (US southeast), as opposed to core areas where temperature and humidity are optimal and *Ixodes* are established. The northward range expansion of *I. scapularis* in Canadian provinces (Leighton et al. 2012, Clow et al. 2017) including and east of Ontario is likely driven in part by climate change (Ogden et al. 2006a, Ogden et al. 2008a) and this may be the case for all or part of Maine as well. Climate change has been accelerating in Maine during the 2000s and 2010s (Fernandez et al. 2015, Birkel and Mayewski 2018), manifesting as a shorter cold season (daily average ≤0°C), with warmer winters and falls, less snow and earlier ice-out, more hot, humid summer days, i.e., heat index >35°C (95°F), and more extreme rainfall events (>5cm within 24hr) (Fernandez et al. 2015). Relative humidity has been increasing (Dai 2006, Lyon and Barnston 2017), and over the last decade, sea surface temperatures in the Gulf of Maine increased faster than 99% of the global ocean (Pershing et al. 2015). These changes are linked to global-scale changes such as more frequent moderate to strong El Niños and rapid decline of Arctic sea ice (e.g., Birkel and Mayewski 2018).

Temperature and humidity are the key elements defining the climate suitability envelope of *I. scapularis* (Eisen et al. 2016). Both high and low temperature thresholds constrain questing activity, development duration, and survival of *Ixodes* ticks (e.g., Lindsay et al. 1995, Ogden et al. 2006a, Ogden et al. 2008a, Parham et al. 2015, Ostfeld et al. 2015, Linske et al. 2019) at all stages of the two-year tick life cycle: egg, larva, nymph, and adult, and especially in summer and winter.

Chilling injury and mortality in all stages of *I. scapularis* occur in the range of -18°C to -10°C (Burks et al. 1996, VanDyk et al. 1996, Brunner et al. 2012). Brunner et al. (2012) found that hazard of mortality in nymphs in soil core enclosures increased rapidly at temperatures below -13°C. Burks et al. (1996) found the threshold for direct chilling injury ranged from -10 to -14°C for all stages of three tick species examined, including *I. scapularis*. VanDyk et al. (1996) found for unengorged *I. scapularis* that LT50 (lethal temperature for 50% of ticks) at 2 hours exposure was -18°C for nymphs, -12°C for adults, and -11°C for larvae. This range (-18°C to -10°C) is common in northern Maine winters, at least in terms of air temperature above leaf litter and snow. But average winter temperatures have been rising in Maine, and relatively faster in the northern than southern tier (Fernandez et al. 2015, Fig. 1.8). Extended falls and earlier springs attend shorter, or “compressed” winters, which should allow adult ticks to quest longer into the fall before snow blankets the landscape, and begin questing earlier in spring upon snowmelt, leading to increased questing season duration for fall and spring adults. Temperatures >30°C increase direct mortality rates (Ogden et al. 2004) and indirect *I. scapularis* mortality rates through reduced host seeking (Vail and Smith 1998). Thus, high summer temperatures regulate *I. scapularis* at the southern edges of its US range, and low winter temperatures regulate *I. scapularis* at the northern edges and higher altitudes (Ogden et al. 2004, Diuk-Wasser et al. 2010) by delaying development and decreasing survival.

In addition to cold winters, *I. scapularis* is constrained at the northern margins of its range via insufficient accumulation of degree-days for eclosion (egg laying) and oviposition (egg

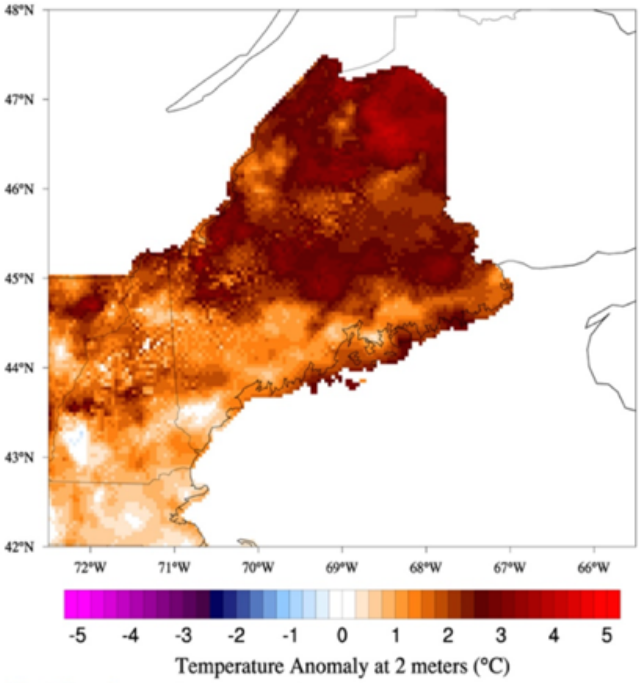

Figure 1.8. Difference map showing the increase in average winter temperature for 1990-1994 vs. 2010-2014, Maine, USA. Source: Climate Reanalyzer Climate Change

hatching) (Lindsay et al. 1995, Estrada-Pena 2002, Rand et al. 2004a, Ogden et al. 2005, Ogden et al. 2006a, Brownstein et al. 2003, Ogden et al. 2014). In Maine, Rand et al. (2004a) showed that for blacklegged tick females to lay eggs (in May), and for those eggs to hatch, about ~1,240 (± SD 143) degree-days (DD) >6°C (42.8°F) must accumulate. They mapped isolines of 1,240 DD>6°C attained by the end of the months of August through December and found that the 1,240 DD>6°C threshold was not attained in Maine's northern tier by the end of August (Fig 1.5). Few DD accumulated beyond August (Rand et al. 2004a). Light-mediated diapause (e.g., Ogden 2018) may preclude some larval questing beyond August, thus attainment of sufficient DD by summer's end is important to completion of the lifecycle of *I. scapularis*. Interestingly, Rand et al. (2004a) compared 1,240 DD>6°C isolines for the decades 1971-1980 versus 1991-2000 and found no decadal northward shift in the 1,240 DD>6°C isoline. Attendant to abrupt climate change, that 1,240 DD>6°C isoline (i.e., threshold) is now visibly shifting northward into the northern tier (Fig. 1.9). Years where 1,240 DD>6°C is achieved by the end of August should lead to larger larval cohorts in the same year, and larger nymphal and fall adult cohorts the following year, assuming a mild intervening winter.

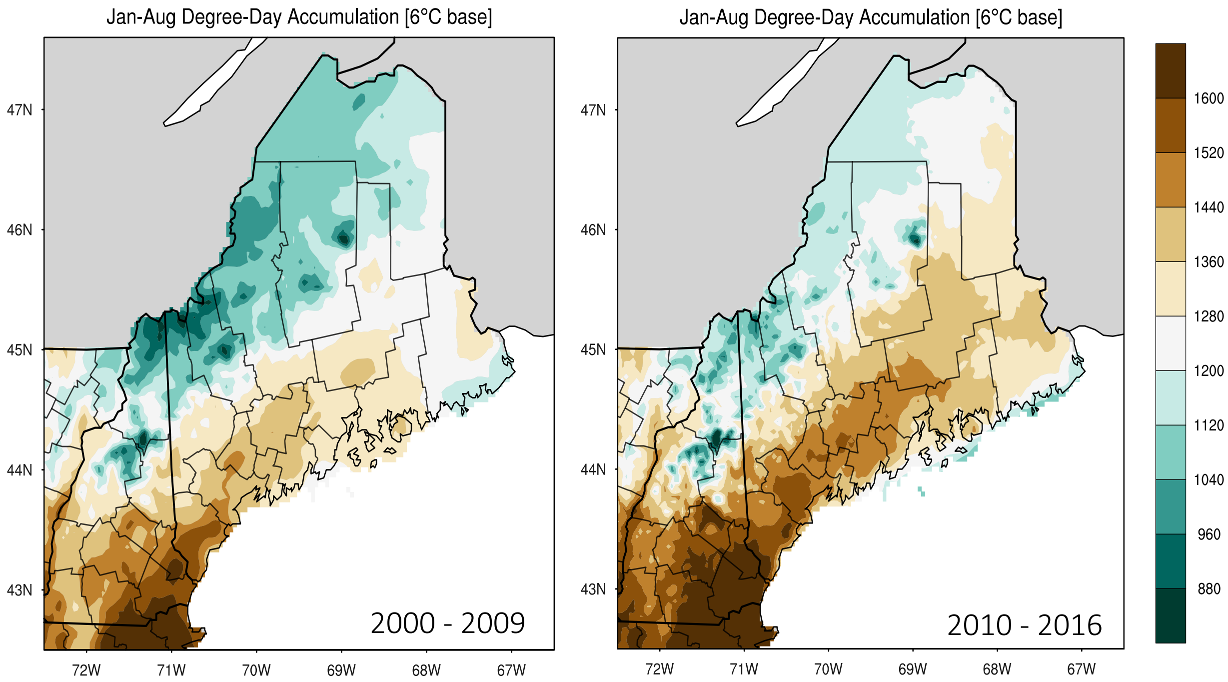

Figure 1.9. Accumulation of degree-days >6°C by the end of August for the last and current decade. Source: PRISM (2004).

In addition to temperature, humidity (and its converse, vapor pressure deficit) constrains activity, development duration, and survival of *Ix odes* ticks (Yuval and Spielman 1990, Needham and Teel 1991, Stafford 1994, Bertrand and Wilson 1996; Vail and Smith 1998, Lindsay et al. 1998, Eisen et al. 2002, Eisen et al. 2003, Perret et al. 2003, Schulze and Jordan 2003, Gray et al. 2009, Estrada-Pena 2002, Diuk-Wasser et al. 2010, Berger et al. 2014a, Berger et al. 2014b, Eisen et al. 2016). Low humidity leads to mortality directly through desiccation or indirectly by preventing questing and reducing the likelihood of finding a blood meal (Eisen et al. 2016). In the laboratory at 27°C, Stafford (1994) found 95% of larvae survived 28d at 100% RH and 43% at 93% RH, whereas for nymphs, survival was 100% at 149d at both 100% and 93% RH, but dropped substantially at ≤75% RH. In the field, Berger et al. (2014b) found nymphal abundance in Rhode Island declined where RH was <82% for at least 8hr. If not too hot, increasing average summer humidity should allow for increasing questing activity of nymphs, with earlier starts and later ends to the questing season leading to longer season duration.

Taken together, the literature suggests that *I. scapularis* survival is more likely where *I. scapularis* are subject to sufficient degree-day accumulation (e.g., ~1,240 degree-days>6°C) to promote egg laying and hatching, with prevailing seasonal temperature averages between ~-10°C and ~30°C and humidity ≥75% to promote increased questing activity and higher probability of survival.

1.2.5 Variations in White-tailed Deer Density

Against the backdrop of changing climate has been variation in Maine's white-tailed deer (*Odocoileus virginianus*) population. The white-tailed deer is the primary host of adult *I. scapularis* within its US range (e.g., Telford 2017) and host larval and nymphal *I. scapularis* as well (Watson and Anderson 1976). Rand et al. (2003) found deer pellet group counts (a surrogate for deer density) were correlated with adult *I. scapularis* abundance in southern Maine, and that few ticks were collected at deer densities lower than ~18/ mi^2 (<7/km^2). To suppress *I. scapularis* ticks and Lyme disease, several investigators have posited that density of white-tailed deer should be lowered to below a threshold in the range of 8-13/mi^2 (Telford 1993, Telford 2002, Stafford et al. 2003, Stafford 2007, Kilpatrick et al. 2014, Telford 2017).

Over the past several decades deer densities in Maine's southern tier have been above 8-13/mi^2 but below this threshold in the northern tier (MEIFW 2007, MEIFW 2017).

1.2.6 Aims and Hypotheses

Given decadal-scale shifts in seasonal temperature and humidity regimes in Maine, we expected that latent developmental responses (Ogden et al. 2014) would manifest as increases in the rate of submissions of *I. scapularis* to the passive surveillance program, as well as earlier weeks of first and peak weeks of submissions, later last weeks, and longer season duration, particularly in the northern tier of the state. We expected changes in submissions rates and phenology to differ between Maine's northern versus southern tier (Fig. 1.3) given differing climate and deer host densities. Our aims were to 1) characterize northern versus southern tier temporal trends in *I. scapularis* submissions rate (an index of abundance) and phenology (first, peak, and last week of submission, and season duration); 2) compare trends in *I. scapularis* submissions rate versus juvenile *I. scapularis* burdens on birds and fall-flagged adult abundance from a field site in southern Maine; and 3) determine whether questing *I. scapularis* submissions rate and phenology were correlated with climatological variables, deer densities, and for nymphs, Lyme incidence. Our hypotheses were

1. Submissions rate, first/peak/last week, and season duration of northern tier *I. scapularis* would trend up over time, whereas southern tier *I. scapularis* might show an early uptrend then level off, which could reflect establishment of stable *I. scapularis* populations in the southern tier;

2. Submissions rate, first/peak/last week, and season duration would be correlated with annual DD>6°C attained by the end of August the previous year (nymphs, fall adults), average

minimum temperature of the current year (spring adults, nymphs, fall adults), summer average humidity of the current year (nymphs, fall adults), and fall average minimum temperature of the current year (fall adults). We hypothesized that these correlations might hold true for the northern tier across the duration of the time series, but possibly only for the early half of the time series for the southern tier, if *I. scapularis* appear to have stabilized in the southern tier.

3. Nymphal and fall adult *I. scapularis* submissions rates would be correlated with annual deer density in the southern but not northern tier due to low deer densities in the latter.

4. Lyme incidence would be correlated with nymphal *I. scapularis* in the northern but not southern tier due to ongoing increases in Lyme incidence in southern tier counties (Fig. 1.2) versus declining *I. scapularis* submissions (Fig. 1.6).

In reality, a proportion of any cohort may not be questing due to weather-dependent quiescence or weather-independent, behavioral or developmental diapause (Eisen et al. 2016, Ogden et al. 2018). Here we assume that the submissions rate indexed annual abundance of questing *I. scapularis*, and captured latent developmental responses of *I. scapularis* to decadal-scale shifts of seasonal temperature and humidity regimes and deer host density.

1.3 Methods

1.3.1 Study Area

Maine, the most northeastern of the United States, encompasses 86,542 km^2 and 4.5° latitude (42.97-47.46°N, 66.95-71.08°W), and 924 has minor civil divisions (towns), 512 of which are populated. With the exception of agricultural land along its eastern border with Canada, the northern half of the state is mix of spruce and fir (Picea and Abies spp.) forests and hardwood stands, principally of maple and oak (Acer and Quercus spp.). A series of higher elevations (600-1,600 m) occupies the northwestern half of the state. The majority of its human population of 1.3 million resides in its southern half, generally within an 80-km-wide coastal plain with elevations <150 m (Rand et al. 2007). *I. scapularis* range from established on the coast to emerging in the northern tier, white-tailed deer densities range from moderate (moderate relative to states such as Connecticut and New York) to low in the northern tier, and local climates range from mild on the coast, to cold in the northern interior and higher elevations (Rand et al. 2007).

We divided the state into northern and southern tiers (Fig. 1.3) using as guides both Lyme incidence (counties below/above state average as described above) and the pattern of degree-day accumulation (Fig. 1.9), and deer densities (low in the northern versus higher in the southern tier wildlife management districts, MEIFW 2017). Counties with Lyme incidence below the statewide average aligned well with counties where average 2000-2009 degree-day accumulation 19≤1,240 degree-days by the end of August (Fig. 1.9). Although Washington County is coastal, the cooler climate is seen as a strip of green along the Downeast coastline.

Birds and vegetation were sampled for ticks from within a 15-ha section of Laudholm Farm (42° 20' 00" N, 70° 32'45" W), a 175-ha wildlife sanctuary within the Wells National Estuarine Research Reserve in Wells, Maine. The study site borders the Atlantic Ocean and habitat comprised a second-growth forest of red maple, (*Acer rubrum*), yellow birch (*Betula lutea*) and white pine, (*Pinus strobus*) with a thick understory of honeysuckle (*Lonicera* *canadensis*) and Japanese barberry (*Berberis thumbergii*), successional upland meadows, and mowed fields (Rand et al. 1998).

1.3.2 Datasets

1.3.2.1 Passive Tick Surveillance

To meet our first aim (characterize northern versus southern tier trends in questing *I. scapularis* abundance and phenology), we used a passive tick surveillance dataset. Passive surveillance data index entomological risk (Johnson et al. 2004, Rand et al. 2007, Ripoche et al. 2018) and reflect the seasonality of *I. scapularis*. From 1989-2013, a free-of-charge, statewide tick identification program was run at the Vector-borne Disease Laboratory at the Maine Medical Center Research Institute (Rand et al. 2007). In 1989, lab staff announced the identification service to the general public, clinicians, and veterinarians by way of lectures, newsletters, and media communications. Staff also targeted sparsely populated areas by contacting entities such as summer camps and hunting camps. Thereafter, ticks were passively submitted. Data collected from persons submitting ticks included date found and town where the tick was thought to have been acquired (not the tick submitter's town of residence). Laboratory staff identified the species, stage, and engorgement level of the tick and returned this information to the tick submitter (Rand et al. 2007).

The program was brand-new in 1989 and recruitment was active. The program end was announced at summer's end in 2013, which likely biased fall adult *I. scapularis* submissions downward in 2013. Considering these potential biases (Clow et al. 2017), we dropped 1989 from the final dataset and did not use 2013 data for the fall adult time series. Ninety-seven percent of *I. scapularis* hosts were humans, dogs, and cats. We excluded the 3% of submissions where ticks were unknown or were found on livestock (cows, sheep, goats, horses) and wildlife species since livestock and wild animals did not necessarily have statewide representation (for a complete list of livestock and wild animal hosts see Rand et al. 2007). The granularity of the raw data was daily at the town level by *I. scapularis* cohort: spring adult, nymph, fall adult.

To characterize *I. scapularis* abundance we summarized the daily date to annual number of submissions of spring adult, nymphal and fall adult *I. scapularis* by tier. We obtained annual census data by town (minor civil division) for the State of Maine from the U.S. Census Bureau (U.S. Census Bureau 2018), then summarized annual population by tier. We calculated annual spring adult, nymphal and fall adult *I. scapularis* submission rate by tier as

tick count/population x 100,000

to arrive at ticks submitted per 100,000, analogous to conversion of disease case counts to disease incidence (cases/100,000). Annual submission rate served as a proxy to size of the questing tick population, 1990-2013 (1990-2012 for fall adults).

To characterize *I. scapularis* phenology we needed to define first, peak, and last week of submission by tier (northern/southern, Fig. 1.3). We summarized the daily data to the level of cohort by week/year by tier. We tried using second-order derivatives to locate first, last, and peak weeks, similar to the method of Moore et al. (2014), but found using the actual first/peak/last weeks a better job of identifying these phenological benchmarks. We defined spring adults as any submitted before or during week 34 and fall adults as those found after week 34. The cut point should have minimal effect on the analysis of phenology since the same cut point was used for all years, because few adults are found in the summer, and because extension of the spring and fall adult seasons would be due to earlier springs and later falls, respectively. Using first and last week we calculated duration of season in number of weeks. This resulted in first/peak/last week and season duration for each year, 1990-2013 (fall adults 1990-2012).

1.3.2.2 Active (Field) Tick Surveillance: Subadult *I. scapularis* on Birds and Questing Fall-flagged Adult *I. scapularis*

Our second aim was to compare trends in *I. scapularis* from the passive surveillance dataset to trends in *I. scapularis* from active (field) surveillance. Each year from 1989, weekly bird-banding has been conducted from 15 May through 1 September (950 ± 10 net-hours per year) at Wells National Estuarine Research Reserve using mist nets opened at sites along forest edge and within the forest. All birds were identified to species and age recorded as hatch year (fledgling), or after-hatch year (>1 year old). Prior to release, each bird was closely examined, particularly around the head and neck, by using a head-mounted magnifying loupe (Rand et al. 1998). All ticks were removed with forceps and transported to laboratory and identified to stage and species. Only larval and nymphal *I. scapularis* were found on birds. Sampling was consistent (weekly) through 2015. We used the same 17 ground-nesting or ground-feeding species listed in Rand et al. (1998) to calculate larval and nymphal burdens (ticks per bird).

Each year from 1989, questing adult ticks have been collected at Wells National Estuarine Research Reserve at least once annually during the height of the fall adult questing season, October through early November. From this we calculated the number of ticks per hour as an index to tick abundance. It was of ancillary interest to see if there were trends in *B. burgdorferi* infection rates in these questing adult ticks, since *B. burgdorferi* may be expected to amplify in the zoonotic cycle as the vector tick becomes established (Ginsberg 1993) and might increase even if tick densities are not increasing. As part of the long-term questing adult tick sampling a subset of ticks was dissected, and the midguts examined by a direct fluorescent antibody test, as per Donahue et al. (1987). From this the *Borrelia* sp. infection prevalence was calculated.

1.3.2.3 Climatology, Deer Density, and Lyme Incidence

To meet our aim, which was to determine whether questing *I. scapularis* submissions rate and phenology were correlated with climatological variables, deer densities, and Lyme incidence (nymphs only), we obtained data on climatology, deer, and Lyme incidence.

We obtained climatology from Oregon State University's Parameter elevation Regression on Independent Slopes Model (PRISM 2004). PRISM is the U.S. Department of Agriculture's climatological dataset and uses weather station point measurements with a weighted regression scheme to account for climate regimes associated with orography, rain shadows, temperature inversions, slope aspect, coastal proximity, and other factors (NCAR 2015). Monthly reanalysis data were available at 2.5 arcmin (4 km) resolution for 1895 through present in NetCDF format. We downloaded monthly gridded NetCDF files for the continuous United States (CONUS) which included minimum, average, and dewpoint temperature at 2m in degrees Celsius (t2min, t2ave, t2dpt), total precipitation in cm (prcp), for 1990 through 2013. Using the National Center for Atmospheric Research Command Language (NCL 2017), and the Maine shapefile, we masked the CONUS data to Maine only, then aggregated the monthly gridded data to the year-month-county level.

With the annual monthly climatology, we calculated annual number of degree-days >6°C attained by the end of August for each county using the formula (t2ave - 6°C) × 30.5. Then, using the meteorological seasons of winter as December-January-February (DJF), summer as June-July-August, and fall as September-October-November, we then calculated annual seasonal averages for fall and winter t2min. Last, we calculated average monthly vapor pressure (VP) and saturated vapor pressure (SVP) in Pascals using t2ave, and from this, annual average monthly relative humidity (RH) by county. The formulas were: $VP = 6.112 \times e^{(17.62 \times t2ave/243.12 + t2ave)} \times 100$, $SVP=6.112 \times e^{(17.62 \times t2dpt /243.12 + t2dpt)}\times100$, and $RH=SVP/VP \times 100$ (WMO 2008, p. I.4–29). We then aggregated to the level of northern/southern tier (Fig. 1.3).

We obtained deer data from the Maine Department of Inland Fisheries and Wildlife (MEIFW). During the hunting season (the regular firearms season is generally in November), MEIFW tracks hunter-killed deer at deer registration stations around the state, capturing information including sex, age, and town of kill. MEIFW uses deer registrations to calculate a buck kill index (BKI), which is the number of hunter-killed deer per 100 square miles. During the years 1987-2005 (n = 18 years), MEIFW used a variation of a sex-age-kill model to estimate deer/mi^2 for each WMD, with inputs including BKI and hunter effort (MEIFW 2007). After 2005, MEIFW was no longer able to capture hunter effort. However, through a system of regression equations relating deer/mi^2 to BKI (MEIFW 2007 Appendix A), MEIFW has produced estimates of deer/mi^2 for years after 2005. We obtained equations from MEIFW to estimate deer/mi^2 for each WMD for the years 1990-2013. In 2006, WMD 29 was reconfigured to no longer include the Downeast coast of Washington County (Fig. 1.3) which has relatively low deer density, but to include the offshore islands, most of which have high deer densities and were part of old WMD 25. To compensate for this, we used the equation for old WMD 25 to estimate deer density in new WMD 29 which probably resulted in conservative annual estimates for new

WMD 29. We downloaded the shapefile of Maine's 30 Wildlife Management Districts (MEGIS 2017), added the annual deer/mi^2 to it, then used the zonal statistics tool in ArcGIS® (ESRI 2018) to aggregate annual deer densities to the level of northern/southern tier.

We obtained town-level Lyme disease incidence (1993-2014) for all Maine towns from the Maine Center for Disease Control through a Memorandum of Understanding between MECDC and the author. In 2008 a new CDC case definition created a "probable" category. For consistency, we used only "confirmed" cases. We aggregated Lyme incidence to the level of tier.

1.3.3 Analysis

To visualize northern versus southern tier temporal trends in all the time series we used the SAS® statistical graphics procedure SGPLOT (SAS 2018) to fit locally weighted scatter plot smoothing (loess) curves to the time series (Cleveland et al. 1988). For each time series we accepted the default smoothing parameters supplied by SAS® SGPLOT®. Implicit in this approach for the *I. scapularis* time series was the a priori assumption that even in the presence of interannual variation, there were trends that reflect the emergence and establishment of the invasive vector tick, *I. scapularis*.

Tick populations may reach a dynamic equilibrium once established (Ginsberg 1993, Ogden et al. 2007) and a way to characterize this was to check for evidence that *I. scapularis* might have initially increased during early years, then leveled off. We inspected the *I. scapularis* loess fits for breakpoints to visually identify the year or range of years where there might be changes in slopes—breakpoints—in the time series. To statistically assess breakpoints, we used the SAS® procedure AUTOREG with the Chow test which compares equality of the subset regression slope coefficients, β1 and β2, on either side of year_i:

$$y_1 = \beta_0 + \beta_1 X_1 \text{ with } n_1 \text{ observations, year} < \text{year}_i$$

$$y_2 = \beta_0 + \beta_2 X_2 \text{ with } n_2 \text{ observations, year} \geq \text{year}_i.$$

Where the Chow test was significant, we followed with piecewise regressions on either side of the breakpoint (e.g., year < 2000, year ≥ 2000) to obtain the separate regression slopes. In the regressions there was no autocorrelation among residuals (Durbin-Watson tests not significant, all $P > 0.05$).

To determine whether questing *I. scapularis* submissions rate and phenology were correlated with climatological variables, deer densities, and Lyme incidence (objective 3), we obtained Spearman correlation coefficients for the strength of association between the explanatory variables as described in the hypotheses. We used the one-year lag of DD>6°C because the current years' nymphs and adults could be influenced by degree-day accumulation that influenced oviposition and eclosion the previous year. We used current, one-year, and two-year lags of deer density because all stages of *I. scapularis* feed on white-tailed deer and the cohort size of questing nymphal and fall adults could be related to deer blood meals they obtained in the current and prior years. According to Cohen (1988), a correlation > 0.5 is large and 0.5-0.3 moderate. Here, we thought that pairwise correlation coefficient ≥ 0.5 at $P \leq 0.05$ would offer sufficient biological insight into what factors could have influenced changes in *I. scapularis* submissions rate and phenology.

1.4 Results

1.4.1 Summary Statistics

During 1990-2013, the passive surveillance program received 19,506 *I. scapularis*, 19,424 of which were identified to stage: 246 larvae, 1,903 nymphs and 15,725 females, and 1,100 males. Among nymphs, 81%, 2%, and 15% were found on humans, dogs, and cats, respectively and among female ticks, 62%, 23%, and 11% were found on humans, dogs, and cats, respectively. From the northern tier, five larvae were submitted before 2000 and 2 after. Eighty-six and 153 larvae were submitted from the southern tier before 2000 and on or after 2000, respectively. In the northern tier, submissions of nymphs were very low with only 0 to 4 per year submitted 1990-1999, and 4 to 22 per year submitted 2000-2012.

I. scapularis submissions rates were lower in the northern than southern tier for all tick stages. For spring adults, northern tier first week of submission was later, last week of submission was earlier, and duration of season was shorter (16.0 versus 25.4 weeks) than in the southern tier; also peak week was 2.4 weeks later (Table 1.1). Because of early low submissions, e.g., from zero to one or two submissions per year, we did not calculate phenological measures for nymphs in the northern tier. For fall adults, northern tier first week of submission was later, last week of submission was earlier, and duration of season was shorter (10.2 versus 13.4 weeks) than in the southern tier, but peak weeks did not differ. The northern tier was cooler than the southern tier by all measures of temperature although relative humidity did not differ by tier (Table 1.1). Deer density was lower in the northern than southern tier as was Lyme incidence (Table 1.1).

Table 1.1. Summary statistics for abundance and phenology of questing *I. scapularis* (nymphs, fall and spring adults) acquired through passive surveillance (a tick identification program), 1990-2013, Maine. Also included are summary statistics for *I. scapularis* subadult burdens on breeding songbirds, questing adult *I. scapularis* per hour from flagging, climatological variables, white-tailed deer density, and Lyme disease incidence (cases per 100,000) in the northern (N) and southern (S) tiers of Maine, 1990-2017. Nymphal passive surveillance data were too sparse in the northern tier to obtain phenological metrics (season first/peak/last week and duration).

Variable Type	Variable	Tier	years	mean	SE	min	max	P^b
I. scapularis spring adults from passive surveillance (1990-2013)								
	count	N	24	43.0	7.90	3.0	132.0	
		S	24	239.9	28.43	62.0	653.0	<0.0001
	submission rate (count per 100,000)[a]	N	24	10.4	1.89	0.7	31.7	
		S	24	27.3	3.15	7.7	75.1	0.0001
	week of first submission	N	24	13.3	1.03	2.0	23.0	
		S	24	5.6	0.85	1.0	15.0	<0.0001
	peak week of season	N	24	19.0	0.48	13.0	25.0	
		S	24	17.6	0.36	14.0	20.0	0.05
	week of last submission	N	24	29.3	0.53	25.0	34.0	
		S	24	31.0	0.54	26.0	34.0	0.03
	duration of season in weeks	N	24	16.0	1.34	2.0	29.0	
		S	24	25.4	0.88	16.0	31.0	<0.0001
I. scapularis nymphs from passive surveillance (1990-2013)								
	count (number submitted)	N	24	5.5	1.14	0.0	22.0	
		S	24	69.8	10.67	16.0	250.0	<0.0001
	submission rate (count per 100,000)[a]	N	24	1.3	0.27	0.0	5.3	
		S	24	7.9	1.20	2.0	28.7	<0.0001
	first week of season	S	24	17.5	0.63	7.0	21.0	
	peak week of season	S	24	25.4	0.52	20.0	33.0	
	last week of season	S	24	40.3	0.77	29.0	46.0	
	season duration (in weeks)	S	24	22.8	1.04	14.0	35.0	
I. scapularis fall adults from passive surveillance (1990-2012)								
	count	N	23	59.7	9.70	5.0	223.0	
		S	23	341.3	30.44	112.0	648.0	<0.0001
	submission rate (count per 100,000)[a]	N	23	14.5	2.33	1.2	53.5	
		S	23	39.2	3.41	13.8	74.5	<0.0001
	week of first submission	N	23	38.4	0.38	35.0	43.0	
		S	23	37.3	0.26	35.0	39.0	0.04
	peak week of season	N	23	42.7	0.31	39.0	45.0	
		S	23	43.0	0.30	41.0	47.0	0.74
	week of last submission	N	23	48.7	0.37	46.0	52.0	
		S	23	50.7	0.30	48.0	53.0	0.002
	duration of season in weeks	N	23	10.2	0.62	3.0	15.0	
		S	23	13.4	0.35	10.0	17.0	0.001
I. scapularis subadults from active surveillance: breeding birds (1990-2015)								
	larval burdens (ticks/bird)	S	28	0.9	0.10	0.0	1.9	
	nymphal burdens (ticks/bird)	S	28	1.7	0.18	0.2	3.9	
I. scapularis subadults from active surveillance: flag/drag sampling (1989-2017)								
	adults per hour	S	26	73.4	6.61	11.1	150.9	
	Borrelia burgdoferi infection %	S	24	56.8	1.65	37.1	72.4	
Climatology (1990-2017), deer (1990-2017), and Lyme incidence (1993-2015)								
	DJF_t2min	N	28	-14.2	0.40	-17.9	-10.1	
		S	28	-10.5	0.36	-13.7	-7.1	<0.0001
	JJA_t2max	N	28	23.4	0.14	22.0	25.0	
		S	28	24.5	0.16	22.6	25.9	<0.0001
	JJA_RH	N	28	65.4	0.43	59.7	68.9	
		S	28	66.7	0.49	61.1	71.1	0.08
	DD>6°C_Aug	N	28	1180.5	14.46	1031.2	1322.5	
		S	28	1359.3	14.78	1205.8	1526.8	<0.0001
	SON_t2min	N	28	1.8	0.17	-0.1	3.5	
		S	28	3.8	0.15	2.4	5.4	<0.0001
	Deer/mi^2 (1990-2017)	N	28	5.6	0.15	3.7	6.9	
		S	28	14.3	0.53	9.5	20.2	<0.0001
	Lyme incidence	N	22	7.3	1.45	0.0	21.9	
		S	22	53.9	11.85	2.4	185.3	0.0002

[a] (Count of ticks submitted/population) x 100,000

[b] Wilcoxon rank-sum tests for differences between nothern and southern tier.

1.4.2 Trends in Questing *I. scapularis* Submissions Rate and Phenology

Consistent with our first hypothesis, northern tier *I. scapularis* submissions rates increased over time, (Figs. 1.8a, 1.9a, and 1.10a), but in contrast, *I. scapularis* submissions rates in the southern tier increased only through the early 2000's (~2001-2003), then leveled off or possibly declined (Figs. 1.8b, 1.9b, and 1.10b).

Partially consistent with our first hypothesis, phenological shifts in *I. scapularis* were seen not as earlier peak weeks (Figs. 1.8c, 1.9c, and 1.10c), but rather as longer seasons (Figs. 1.8d, 1.9d, and 1.10d) by virtue of earlier and later weeks of submission (Figs. 1.8c, 1.9c, and 1.10c). Increasing season length was seen in the northern tier for the duration of the time series but only in the early part of the southern tier series.

1.4.2.1 Spring Adult *I. scapularis*

In the northern tier the annual spring adult submissions rate increased over the years from 1990-2012 as described by the loess curve in (Fig. 1.10a) and a significant positive regression slope coefficient ($\beta_1 = 1.13$, $P < 0.0001$, Table 1.2). Phenological changes over time were seen in the northern tier only, where season duration became longer by virtue of first week of submission earlier, week of last submission later (Figs 1.10c,e; Table 1.2).

In the southern tier spring adults visually appeared to increase up to 2004 (Fig. 1.10b). Chow tests were significant at years 1999 through 2004 (Table 1.2), so we selected a break point of 2004 from the loess curve. Piecewise regression yielded a significant positive slope coefficient where year <2004 (Table 1.2) and no trend thereafter.

1.4.2.2 Summer Nymphal *I. scapularis*

In the northern tier the annual nymph submission rate increased over the years during 1990-2012 (Fig. 1.11a, left panel), and a significant positive regression slope coefficient ($\beta 1 = 0.15$, $P < 0.0001$, Table 1.2). With low volume of nymphal submissions in the northern tier we did not test phenology of nymphs, but the loess curve suggested duration of season increased (Fig. 1.11c).

In the southern tier the nymph submission rate increased up to 2001 then leveled off, as described by the change point of the loess curve at year 2001 (Fig. 1.11b), and Chow test significant at year 2001 ($P = 0.02$, Table 1.2). In the piecewise regressions (Table 1.2) there was a significant positive regression slope coefficient where year < 2001 ($\beta 1 = 1.90$, $P = 0.002$) and no trend thereafter. Phenological changes over time in nymphs were seen in the southern tier, where season duration became longer by virtue of week of last submission later (Figs. 1.11d,f; Table 1.2), but only up to 2001 as suggested by the loess curve. Chow tests were significant at all years tested so we selected 2001 as the change point. Piecewise linear regression confirmed week of last nymphal submission later, and season duration longer, up to 2001 (Table 1.2).

1.4.2.3 Fall Adult *I. scapularis*

In the northern tier the annual fall adult *I. scapularis* submission rate increased over the years in the northern tier during 1990-2012 (Fig. 1.12a). Phenological trends were seen in the northern tier only, with season duration longer by virtue of first week of submissions earlier and last week later (Figs 1.12c,e; Table 1.2). Chow tests indicated a changepoint at 2003; season duration increased where year < 2003 and also ≥ 2003, but at a slower rate (Table 1.2).

In the southern tier fall adults increased up to 2001 as suggested by the loess curve (Fig. 1.12b). All Chow tests were significant within the range tested 1999-2004 (Table 1.2), and piecewise regression significant where year <2001 (β_1 = 4.97, *P* = 0.0005) indicating an increase in submissions, but not ≥ 2001 (β_1 = -2.04, *P* = 0.08) indicating no trend, though at 0.05 ≤ *P* ≤ 0.10 could be interpreted as a marginally significant downward trend.

1.4.3 Feeding Subadult *I. scapularis* Burdens on Resident Breeding Birds and Questing Fall-flagged Adult *I. scapularis* Abundance

At the Wells National Estuarine Research Reserve, juvenile *I. scapularis* parasitizing birds as well as fall-flagged questing adult *I. scapularis* showed initial increases followed by leveling or declines (Figs. 1.13, 1.14). These time series mirrored the passive surveillance data although temporal alignment of the breakpoints was not perfect. Annual nymphal and larval *I. scapularis* burdens on breeding adult and juvenile songbirds increased up to 1999 then declined, as described by the loess curve in Fig. 1.13 and Chow tests significant at year = 1999, and piecewise regressions (Table 1.2). This mirrored the patterns seen in the passive surveillance data. We note the highest year for nymphal burdens on birds was in 2000 (Fig. 1.13a), coinciding with the spikes seen in nymphal and fall adult surveillance data in 2000.

Fall-flagged adult *I. scapularis* collected per hour increased up to about 2004 then declined, as described by the loess curve in Fig. 1.14a, and piecewise regressions (Table 1.2). Chow tests were significant at all years (Table 1.2), so we based the piecewise regressions on a changepoint of 2004 (Table 1.2). We note 2003 was the highest year for adult ticks sampled per hour (Fig. 1.14a) unlike the year 2000 in the passive surveillance and bird burden data. There was no trend in *Borreli*a infection rate in the fall-flagged ticks (Fig. 1.14b).

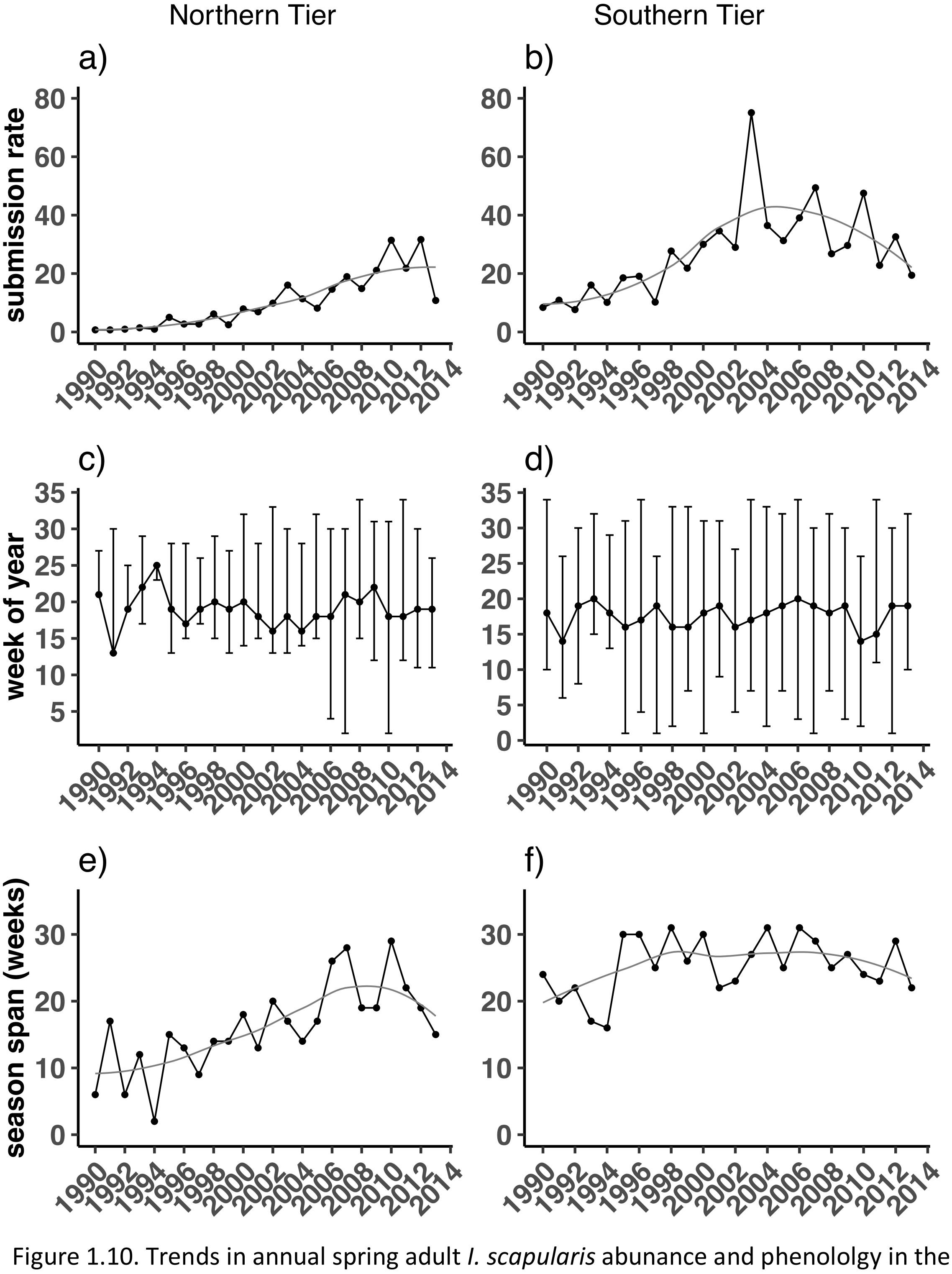

Figure 1.10. Trends in annual spring adult *I. scapularis* abunance and phenololgy in the northern (left column) and southern (right column) tiers of Maine, 1990-2013. Plots (a) and (b) show abundance (rate of tick submissions), (c) and (d) show season start and end weeks (bottom/top of bars) and trends in peak week, and (e) and (f) show trends in season duration. Plots (a), (b), (e), and (f) include smooth curves (locally estimated scatterplot smoothing from the R package.)

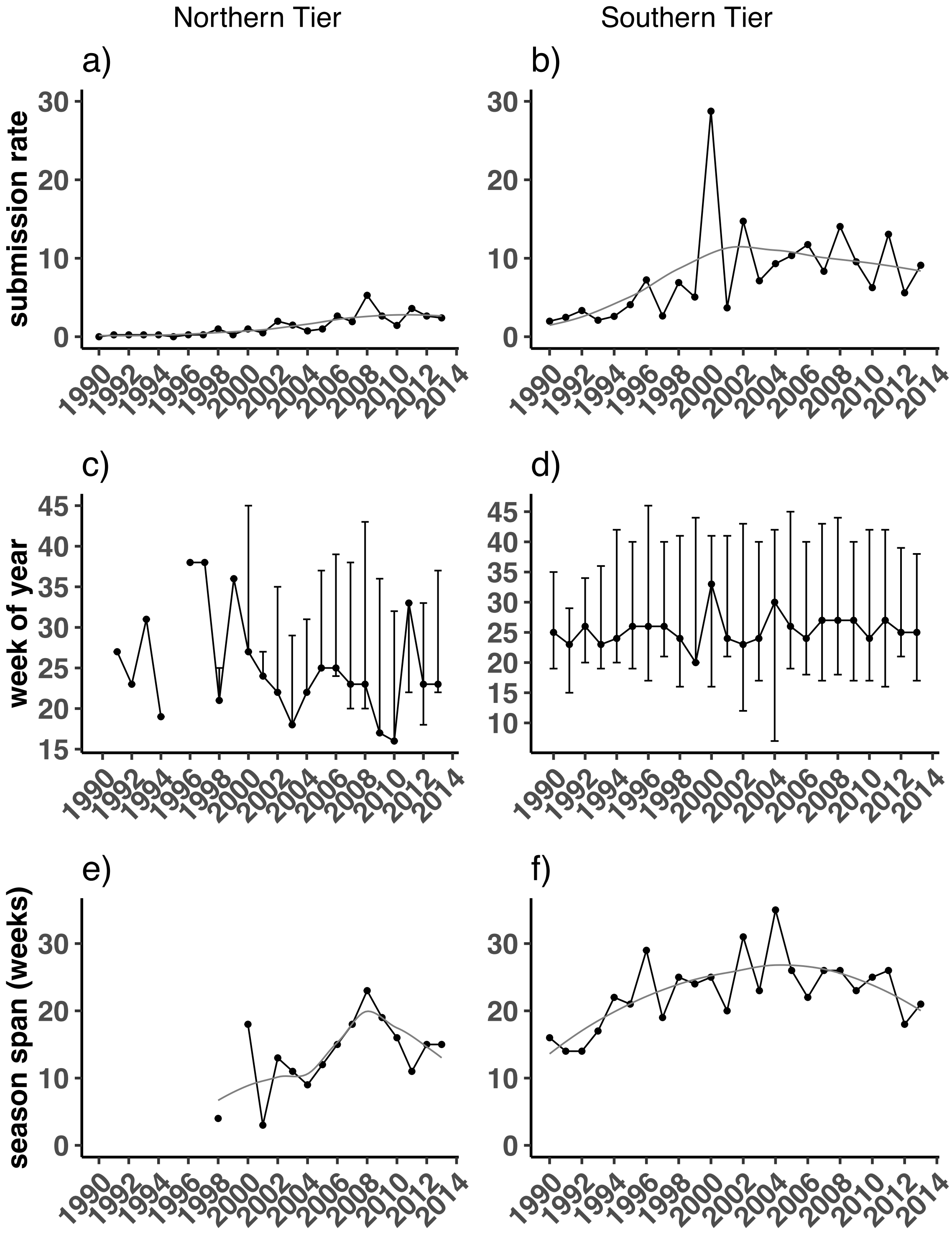

Figure 1.11. Trends in annual nymphal *I. scapularis* abunance and phenololgy in the northern (left column) and southern (right column) tiers of Maine, 1990-2013. Plots (a) and (b) show abundance (rate of tick submissions), (c) and (d) show season start and end weeks (bottom/top of bars) and trends in peak week, and (e) and (f) show trends in season duration. Plots (a), (b), (e), and (f) include smooth curves (locally estimated scatterplot smoothing from the R package.)

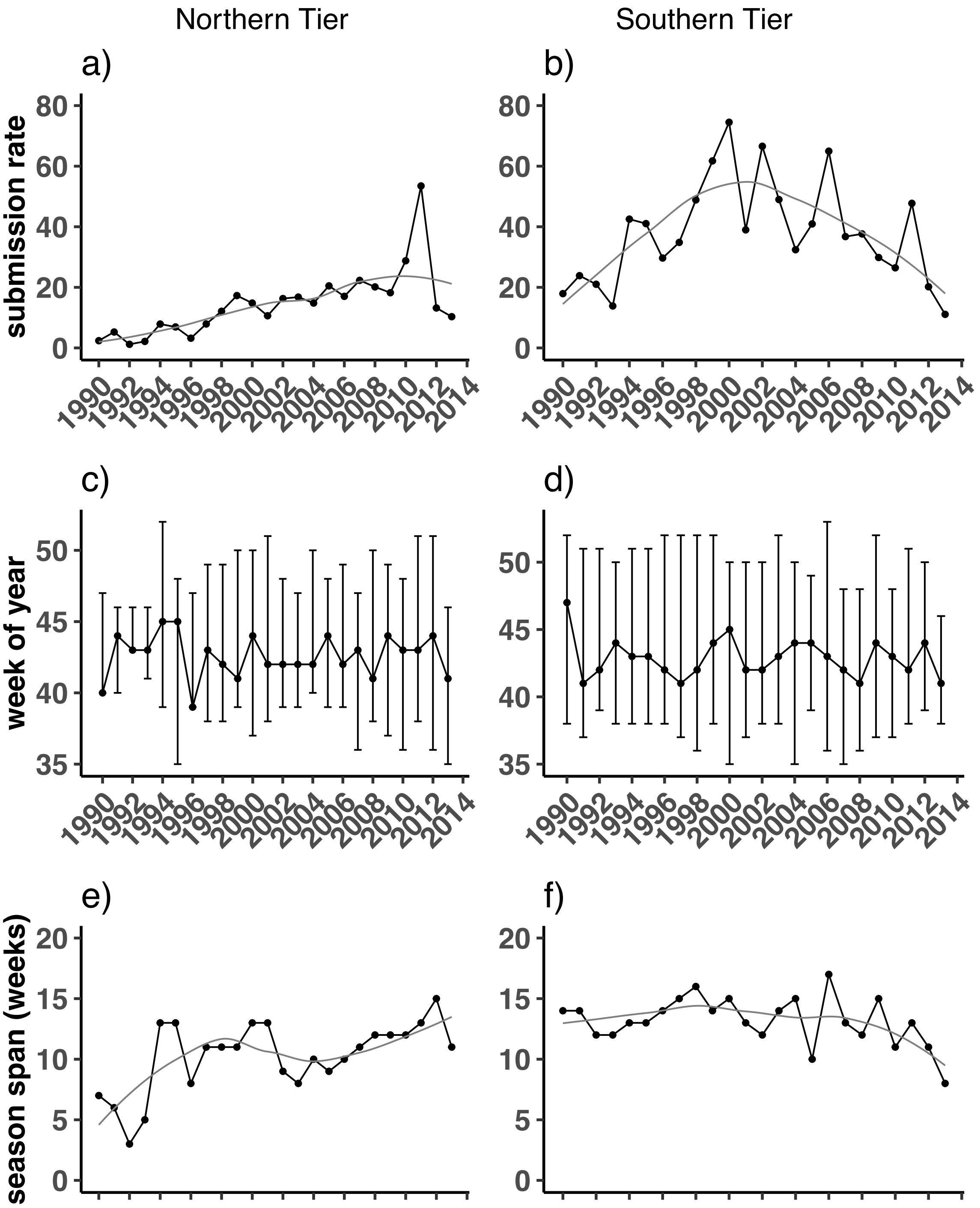

Figure 1.12. Trends in annual fall adult *I. scapularis* abunance and phenololgy in the northern (left column) and southern (right column) tiers of Maine, 1990-2013. Plots (a) and (b) show abundance (rate of tick submissions), (c) and (d) show season start and end weeks (bottom/top of bars) and trends in peak week, and (e) and (f) show trends in season duration. Plots (a), (b), (e), and (f) include smooth curves (locally estimated scatterplot smoothing from the R package.)

Table 1.2. Linear regression equations relating abundance and phenology of *I. scapularis* (nymphs, fall and spring adults) and *B. burgdoferi* infection rate to time in the northern (N) and southern (S) tiers of Maine, 1989-2017. Significant Chow tests at the years 1997 through 2004 indicated change points within the time series at those years. Piecewise regression was conducted for series before and after the selected change point. Nymphal data were too sparse in the nothern tier to test the phenological metrics (season first/peak/last week and duration).

Variable			Linear regression on year					Significant change point (CP) year(s) (Chow tests)								CP	Piecewise regression			
			Parameters				Model										< CP		≥ CP	
Type	Tier	Variable	β1	SE	*t*	*P*	R^2	1997	1998	1999	2000	2001	2002	2003	2004	Selected	β1	*P*	β1	*P*
I. scapularis spring adults from passive surveillance (1990-2013)																				
	N	submission rate	1.13	0.14	7.8	***	0.74													
	N	first week of season	-0.46	0.12	-4.0	**	0.42													
	N	peak week	-0.02	0.07	-0.3		0.00													
	N	last week of season	0.19	0.07	2.8	*	0.26													
	N	season duration	0.65	0.14	4.6	**	0.49													
	S	submission rate	1.20	0.39	3.1	**	0.30			*	*	*	**	**	**	2004	3.26	**		
	S	first week of season	-0.14	0.12	-1.2		0.06													
	S	peak week	0.02	0.05	0.4		0.01													
	S	last week of season	0.03	0.08	0.4		0.01													
	S	season duration	0.17	0.12	1.4		0.08													
I. scapularis nymphs from passive surveillance (1990-2013)																				
	N	submission rate	0.15	0.03	5.9	***	0.61													
	S	submission rate	0.35	0.16	2.2	*	0.18					*				2001	1.46	*		
	S	first week of season	-0.07	0.09	-0.8		0.03													
	S	peak week	0.07	0.08	1.0		0.04													
	S	last week of season	0.23	0.10	2.3	*	0.19	**	**	**	**	**	**	**	**	2001	1.12	**		
	S	season duration	0.31	0.14	2.2	*	0.18	**	*	*	*	*	*	**	**	2001	1.17	**		
I. scapularis fall adults from passive surveillance (1990-2012)																				
	N	submission rate	1.27	0.23	5.5	***	0.59													
	N	first week of season	-0.15	0.05	-3.0	**	0.30													
	N	peak week	0.02	0.05	0.4		0.01													
	N	last week of season	0.12	0.05	2.3	*	0.20							*		2003	0.30	*		
	N	season duration	0.26	0.08	3.4	**	0.36							**	*	2003	0.54	*	0.64	***
	S	adundance	0.49	0.52	1.0		0.04	*	**	**	**	**	**	**	**	2001	4.97	**	-2.04 [a]	
	S	first week of season	-0.04	0.04	-1.0		0.04													
	S	peak week	-0.02	0.05	-0.3		0.01													
	S	last week of season	-0.08	0.04	-2.0		0.16													
	S	season duration	-0.05	0.05	-0.8		0.03													
I. scapularis subadults from active surveillance: breeding birds (1990-2015)																				
	S	larval burdens	-0.04	0.01	-3.0	**	0.28	**	**	**	**	**	**	**	**	1999	0.10		-0.08	**
	S	nymphal burdens	-0.02	0.02	-0.6		0.02	**	**	**	**	**	**	**	**	1999	0.25	**	-0.12	**
I. scapularis subadults from active surveillance: flag/drag sampling (1989-2017)																				
	S	adults per hour	1.30	0.84	1.5		0.09		**	**	**	***	***	***	***	2004	8.17	**	-4.15	*
	S	% *Bb* -positive	0.30	0.23	1.3		0.07													

[a] *P* = 0.08

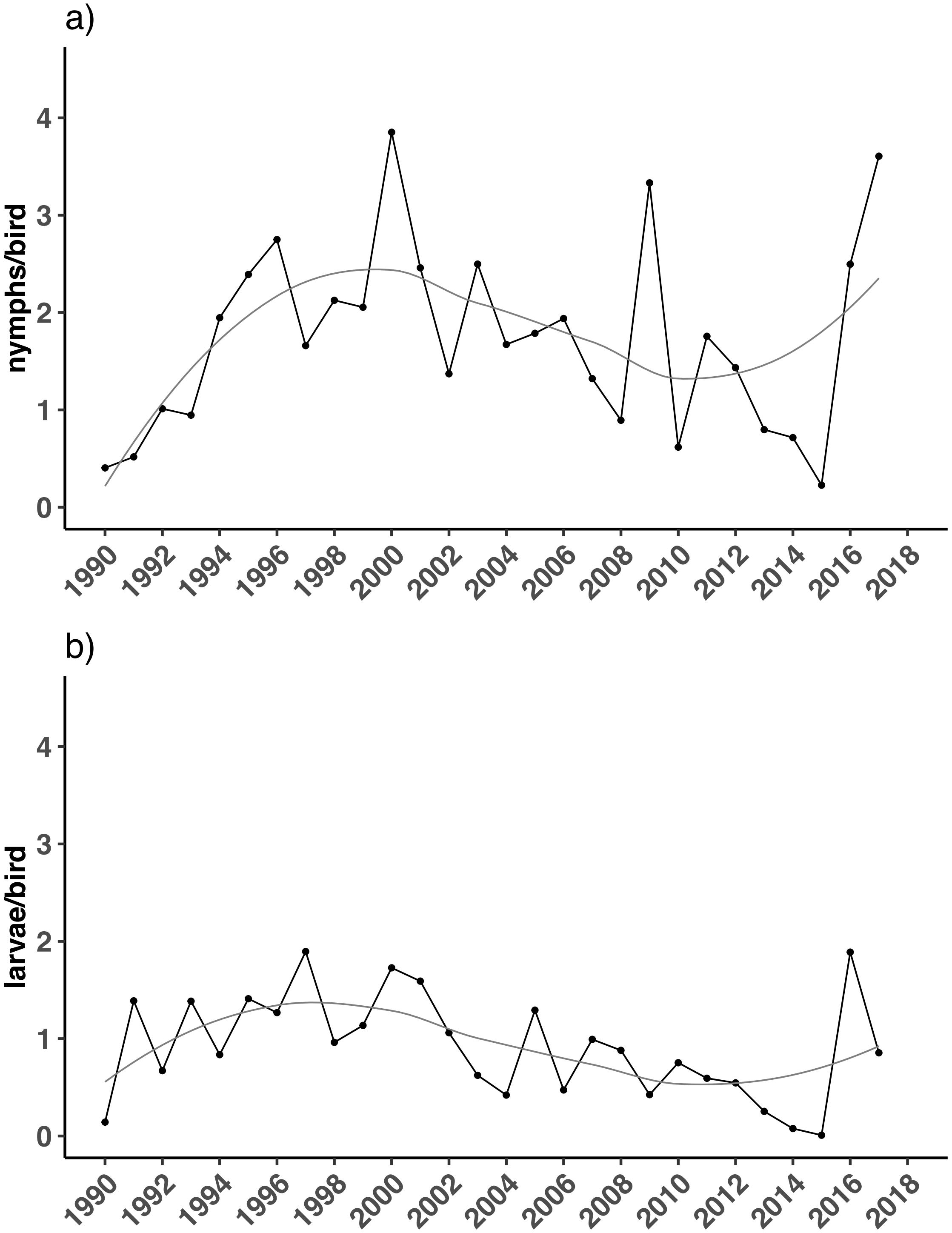

Figure 1.13. Trends in summer nymphal (a) and larval (b) *I. scapularis* burdens (ticks per bird) on breeding adults and juvenile songbirds mist-netted at Wells National Estuarine Research Reserve, Wells, Maine, 1990-2015.

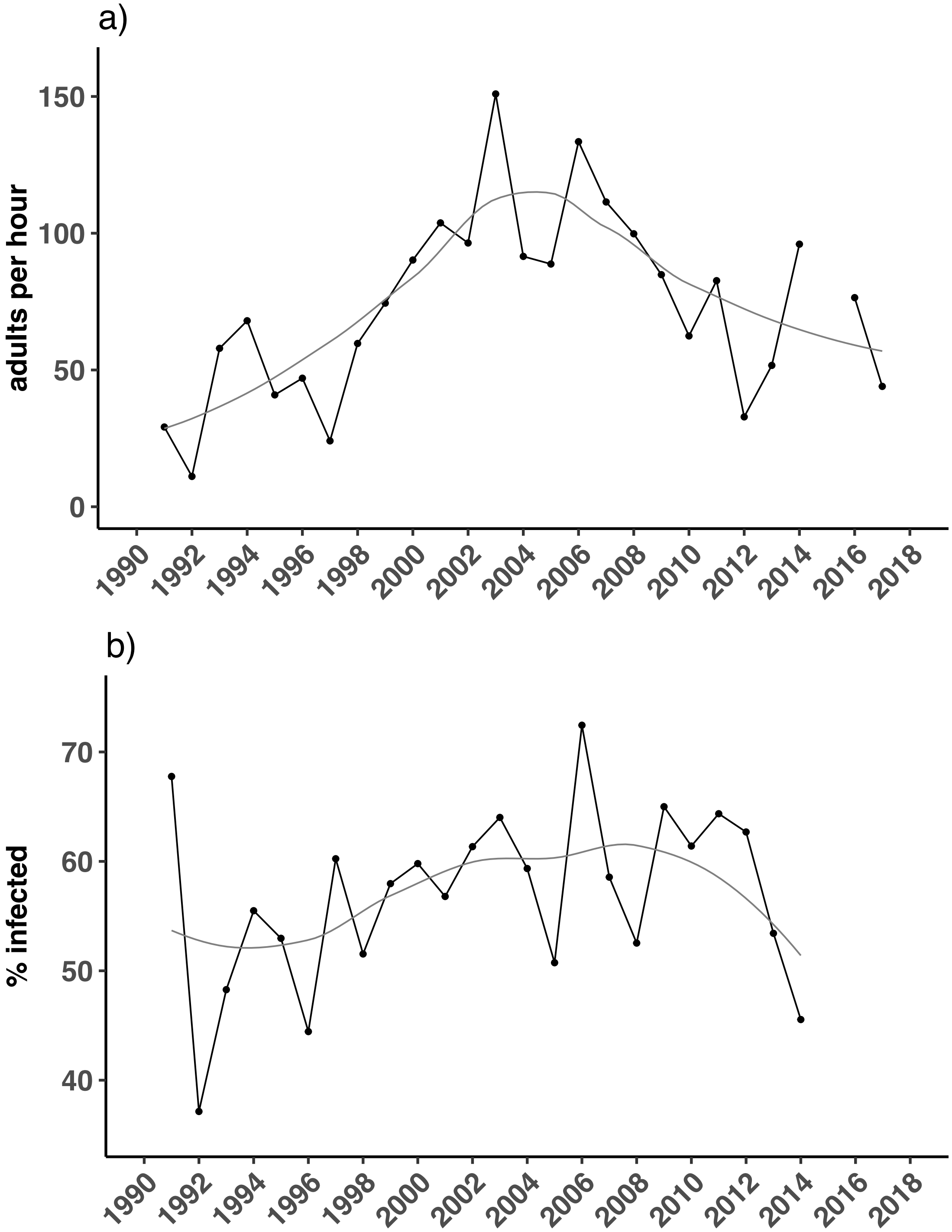

Figure 1.14. Trends in (a) fall adult *I. scapularis* flagged per hour and (b) *B. ferrferi* infection rate in those ticks, Wells National Estuarine Research Reserve, Wells, Maine, 1990-2017.

1.4.4 Potential Correlates of *I. scapularis* Submissions Rate and Phenology

1.4.4.1 Indicators of Changing Climate

Over 1990-2017, there was a significant positive trend in winter average minimum temperature in the northern tier (Fig. 1.15a). Summer average maximum temperature (Fig. 1.16) did not rise, but summer average relative humidity increased in both tiers (Fig. 1.17). Fall average minimum temperature rose in both tiers (Fig. 1.18).

Lack of trend in accumulation of degree-days >6°C by the end of August was attributable to high interannual variation, but in the 28-year series that 1,240 DD>6°C by the end of August was exceeded in only six years in the northern tier versus 26 years in the southern tier (Fig. 1.19).

1.4.4.2 White-tailed Deer

White-tailed deer density averaged 5.5/mi^2 in the northern tier, with a low of 3.7/mi^2 seen in 2009 (Fig. 1.20a, Table 1.1). Deer density in the southern tier averaged 14.3/mi^2, ranging from 9.5/mi^2 in 1990 in 20.2/mi^2 in 2000 (Fig. 1.20b). This was followed by a decline to a local minimum of about 11-12/mi^2 2009-2011 and a rise thereafter.

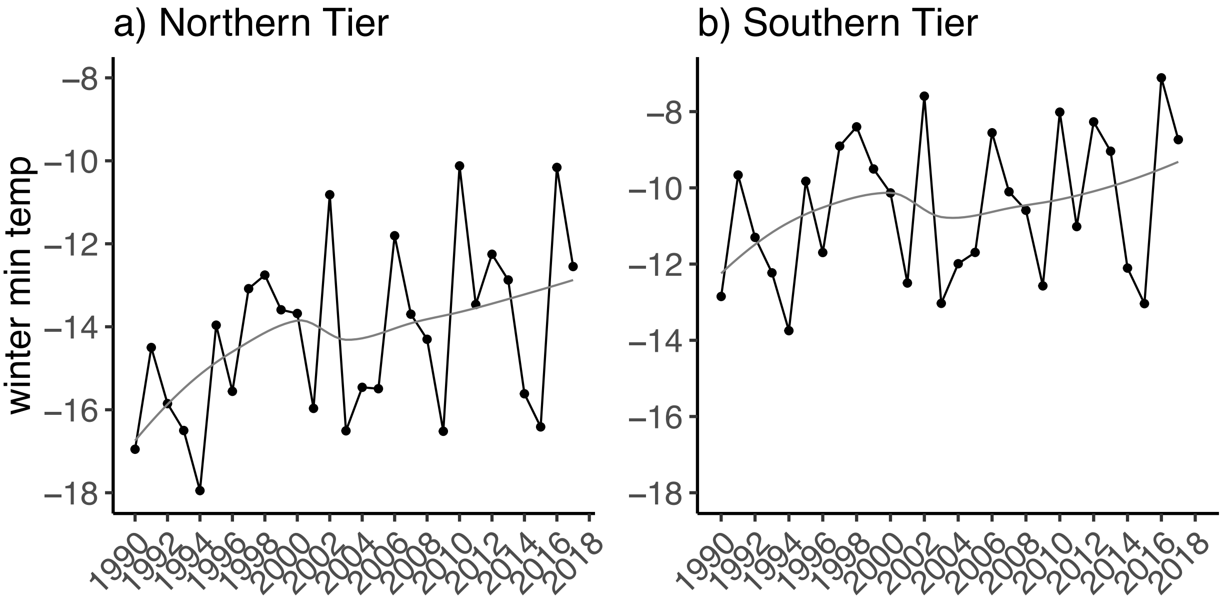

Figure 1.15. Trends in winter average minimum temperatures in the northern (a) and southern (b) tiers of Maine, 1990-2017.

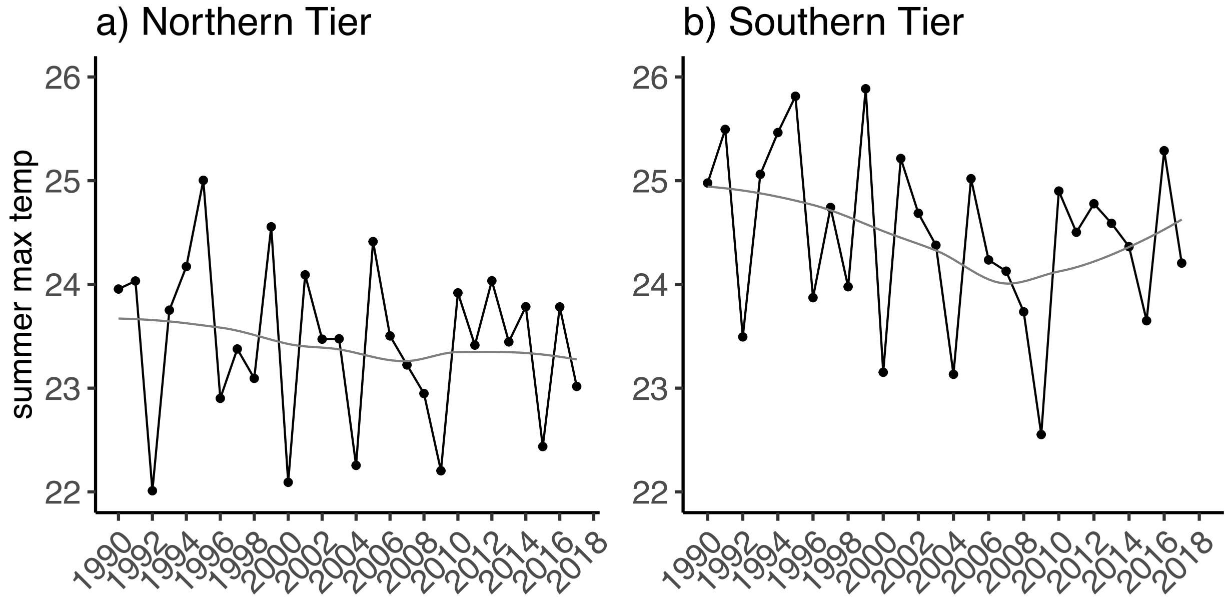

Figure 1.16. Trends in summer average maximum temperatures in the northern (a) and southern (b) tiers of Maine, 1990-2017.

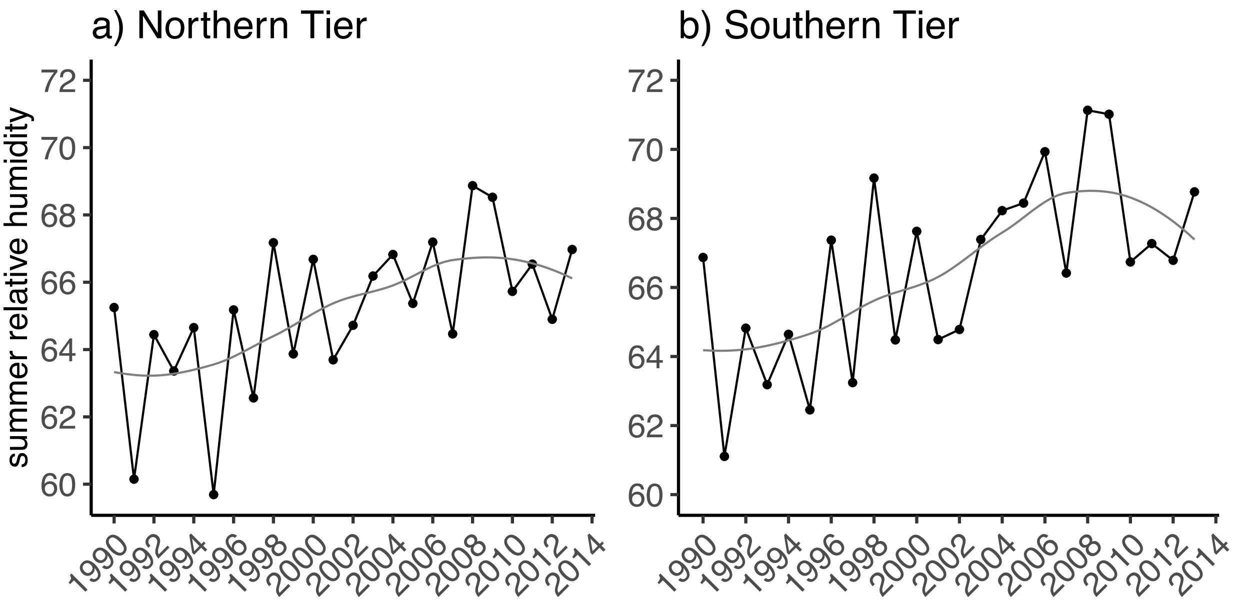

Figure 1.17. Trends in summer average relative humidity in the northern (a) and southern (b) tiers of Maine, 1990-2017.

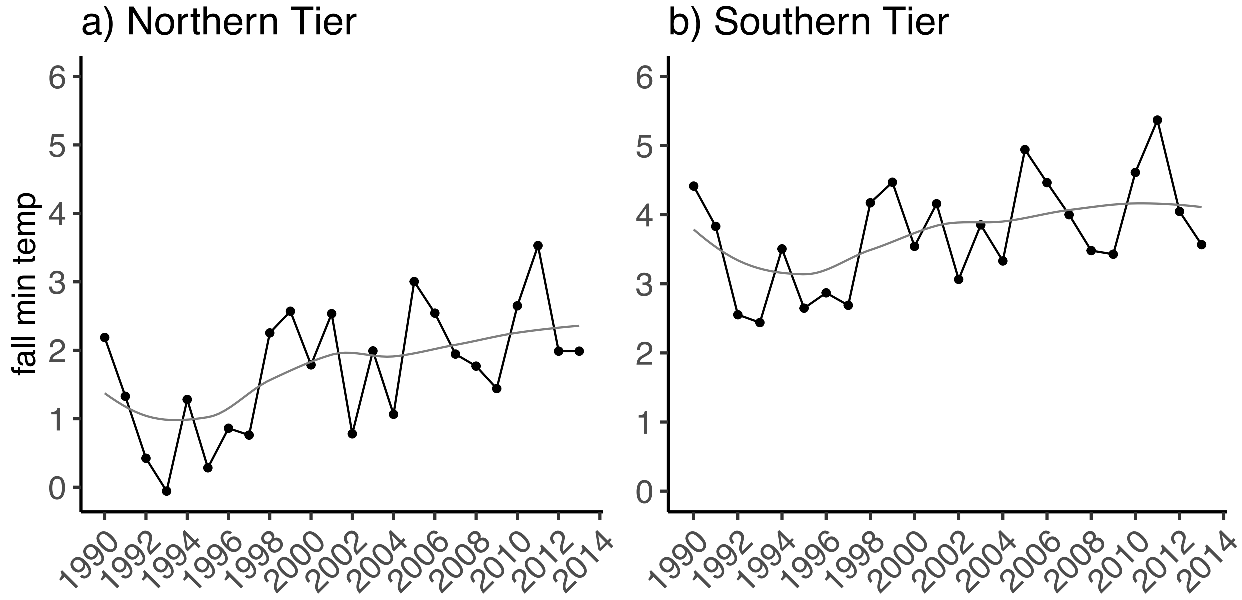

Figure 1.18. Trends in fall average minimum temperatures in the northern (a) and southern (b) tiers of Maine, 1990-2017.

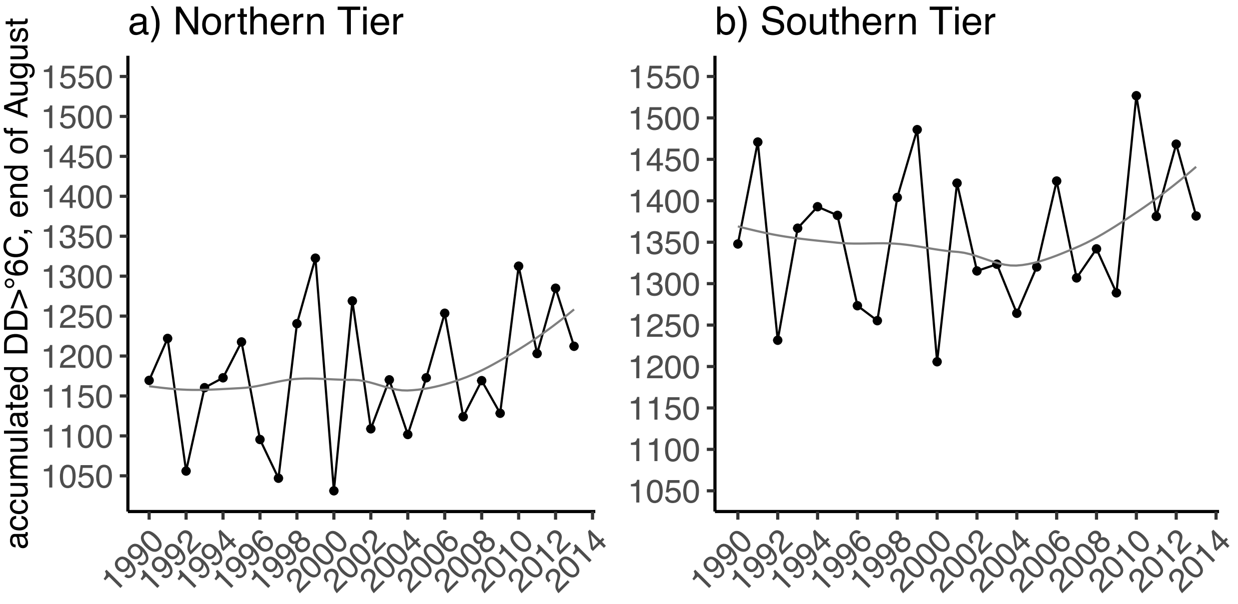

Figure 1.19. Trends in accumulation of degree-days >6°C in the northern (a) and southern (b) tiers of Maine, 1990-2017.

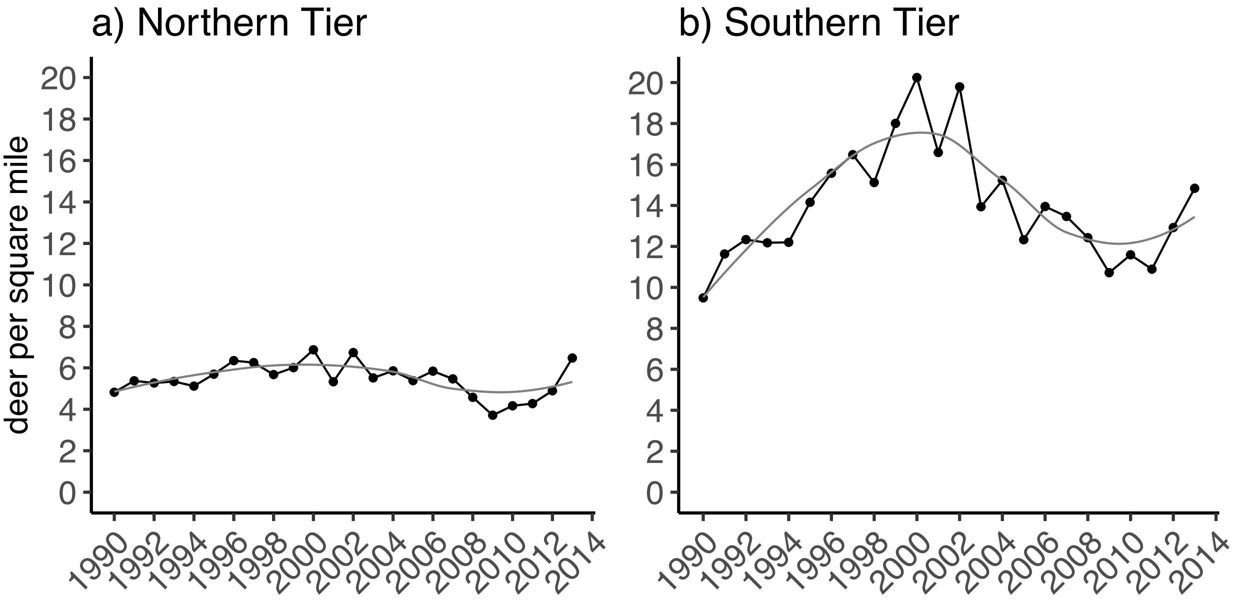

Figure 1.20. Trends in white-tailed deer density (deer/mi2) in the northern (a) and southern (b) tiers of Maine, 1990-2017.

1.4.5 Correlations Among *I. scapularis* from Passive Surveillance and Climatological Indicators of Warming Climate, Deer, and Lyme Incidence

Generally, most correlations between *I. scapularis* and temperature variables occurred in the northern tier during 1990-2013 or during the first decade in the southern tier (Table 1.3). Warmer winters corresponded with earlier appearance (both tiers) and longer season (northern tier) of spring adults. Consistent with our second hypothesis, warmer winters also corresponded with longer season duration of fall adults in the early series of the southern tier. Warmer falls corresponded with higher fall adult submission rates in the northern tier and longer season duration in the early series of the southern tier. Also consistent with our second hypothesis, higher relative humidity corresponded with higher submissions rates of nymphs in both tiers (Table 1.3). However, contrary to expectations, there were no correlations between any *I. scapularis* metrics and degree-day accumulation.

Correlations between *I. scapularis* submission rates and deer density were seen in the southern tier only, consistent with our third hypothesis. In the full southern tier time series (1990-2012), fall adult submission rate was correlated with deer/mi^2 in year$_{t-0}$, year$_{t-1}$, and year$_{t-2}$ (0.48, 0.51, and 0.61, respectively, Table 1.4). In the early southern tier series (1990-1999), there were correlations between all *I. scapularis* stages and deer/mi^2 in the current and lagged years and ranged from 0.65 to 0.85 (Table 1.4). Finally, consistent with our fourth hypothesis, Lyme incidence was correlated with nymph submission rate (0.74) in the northern but not southern tier.

Table 1.3. Spearman rank correlation coefficients (where $P < 0.05$) between *I. scapularis* spring adult, summer nymph, and fall adult submission rate and phenology versus climatological variables, in the northern and southern tiers of Maine, 1990-2013. Ticks were submitted to a passive surveillance program (tick identification service) at the Maine Medical Center. Nymphal data were too sparse in the nothern tier to test phenological metrics (first, peak, and last week of season, and season duration; cells in gray).

			Spring adults	Nymphs			Fall Adults[b]			
	Abundance/ Phenology	Tier	DJF_t2min	DJF_t2min	JJA_RH	DD>6°C_Aug$_{t-1}$	DJF_t2min	SON_t2min	JJA_RH	DD>6°C_Aug$_{t-1}$
Northern and Southern tiers, all years	submission rate	Northern			0.70			0.64		
		Southern			0.69					
	first week of season	Northern	-0.60	▨	▨	▨	▨			
		Southern	-0.53				▨			
	peak week of season	Northern		▨	▨	▨				
		Southern								
	last week of season	Northern	▨	▨	▨	▨				
		Southern	▨							
	season duration	Northern	0.58	▨	▨	▨				
		Southern								
Southern tier, first decade only	submission rate	Southern								
	first week of season		-0.68							
	peak week of season									
	last week of season									
	season duration						0.62	0.60		

[a] DJF_t2min and SON_t2min are average minimum temperature at 2m above ground, JJA_RH is summer relative humidity at 2m, DD>6°C_Augt-1 is cumulative degree-days>6°C by the end of August, one-year lag.

[b] 1990-2012

Table 1.4. Spearman rank correlation coefficients (where $P < 0.05$) between *I. scapularis* spring adult, summer nymph, and fall adult submission rate versus white-tailed deer density in the current and past two years in the northern and southern tiers of Maine, 1990-2013. Submission rate was (number of ticks submitted/population) x 100,000.

		Spring adults		Nymphs		Fall adults[a]		
Geographic Range	Tier	Deer/mi$^{2}_{t-1}$	Deer/mi$^{2}_{t-2}$	Deer/mi$^{2}_{t-1}$	Deer/mi$^{2}_{t-2}$	Deer/mi$^{2}_{t-0}$	Deer/mi$^{2}_{t-1}$	Deer/mi$^{2}_{t-2}$
Northern and Southern tiers, all years	Northern							
	Southern					0.48	0.51	0.61
Southern tier, first decade only	Southern	0.75	0.68	0.66		0.76	0.65	0.85

[a] 1990-2012

1.5 Discussion

With passive surveillance data for 1990-2013, we were available to compare trends in *I. scapularis* abundance and phenology in the warmer southern versus colder northern tier of Maine. Submissions of larval *I. scapularis* from the northern tier indicated the increase in *I. scapularis* in the northern tier was not just a result of long-distance avian dispersal (Smith et al. 1996, Rand et al. 1998, Leighton et al. 2012, Ogden et al. 2006b, Ogden et al. 2008b).

Consistent with our expectations, in the northern tier the *I. scapularis* submission rate and season duration increased, whereas in the southern tier these metrics increased during the first years of the time series but after about ~13 years leveled off. Assuming a true biological signal in the submissions data, ~13 years to establishment is in agreement with the 5-10 years to establishment scenarios Ginsberg (1993) observed empirically and Ogden et al. (2007) observed via simulation. *I. scapularis* submissions rates by the end of the time series in the northern tier were similar to those at the start of the series in the southern tier, suggesting the *I. scapularis* in the north were still emergent versus established in the southern tier. We did not see shifts to earlier peak weeks over time as seen in New York State (Levi et al. 2015); in this study the observed phenological shift was increased season duration.

Consistent with our second set of expectations, *I. scapularis* submission rates and phenological changes were correlated with winter warming in the northern tier across the duration of the time series, but only the early half of the time series for the southern tier (with the exception of the correlation between spring adults and winter for the full southern tier series).Winter average minimum temperatures in the northern tier, and fall average temperatures and summer relative humidity in both tiers increased significantly over the 1990-2017 interval, which from a climate standpoint is a very short time.

It was unexpected that degree-day accumulation was not correlated with *I. scapularis* submission rates and phenological metrics, but there could be several reasons for this. First, we note that in the 28-year degree-day time series 1,240 DD>6°C by the end of August was exceeded in only seven of the more recent years in the northern tier versus 26 years in the southern tier. Second, current-year climatological conditions may obfuscate effects of degree-day accumulation the year before. Larvae were rarely submitted so we could not test for a correlation between larvae and degree-day accumulation. Third, a simple correlation analysis may not work well with threshold relationships.

The relationship between increasing nymphal *I. scapularis* submissions rates and higher summer relative humidity (in both tiers) was consistent with *I. scapularis*' need to avoid desiccation. We note that relative humidity was based on temperature at two meters and not RH at ground level under cover of leaves and duff. Berger et al. (2014b) developed an equation to relate ambient air RH to data loggers in leaf litter as $RH_{litter} = 100/(1 + 7.2145e[-0.0559_{RHair}])$. Applying this equation to our RH summary data (Table 1.1) yielded RH 84.3 (range 79.6 to 86.7) for the northern tier and RH 85.2 (range 80.8 to 88.1) which would not challenge *I. scapularis* nymphs.

Though northern tier climate suitability appears to have improved for *I. scapularis* and will likely continue to do so, current overall ecological suitability for *I. scapularis* in the northern tier may be limited due to low deer densities, which averaged ~5/mi^2 (range 2-9/mi^2). Where a suitable climate envelope exists for *I. scapularis*, tick abundance will depend on adequate host densities and core woodland habitat (Eisen et al. 2016). In the southern part of the Province of Quebec (PQ), Canada, from 1990 to 2008, Ogden et al. (2010) attributed increasing *I. scapularis* populations to warming climate, because they considered habitat, and rodent and deer host densities non-limiting; deer densities were 7.4 to 10.7/km^2 (19 to 28/mi^2). But in Maine's northern tier, low deer densities (2-9/mi^2) may be limiting more rapid establishment of *I. scapularis* even as climate suitability has improved.

Habitat and small mammal host populations are likely non-limiting in Maine's northern tier. Maine has a mix of deciduous, mixed, and coniferous forest cover types. The white-footed mouse, a key host of juvenile *I. scapularis* reservoir of *B. burgdorferi*, has a broad North American distribution (19-49°N 64-112°W, Wang et al. 2009) that includes Maine. The deer mouse (*P. maniculatus*) ranges farther north but overlaps with the white-footed mouse in Maine, and is similar in terms of *I. scapularis* infestation, burdens, and *B. burgdorferi* reservoir competence (Rand et al. 1993, Garman et al. 1994, Oliver et al. 2006, Roy-Dufresne et al. 2013).

Compared to the northern tier, Maine's southern tier climate has been more suitable for *I. scapularis* and there have been more deer. During the emergent phase of *I. scapularis* in southern tier of Maine, average white-tailed deer density in the southern tier increased from 9.5/mi^2 in 1990 to 20.2/mi^2 in 2000, a 113% increase over 11 years. The burgeoning deer population in southern Maine during the early 2000s led the Maine Department of Inland Fisheries and Wildlife (MEIFW) to significantly increase any deer permits to increase hunting pressure on does, and the number of ADPs issued generally declined starting in 2004, as population objectives were met (MEIFW 2017). Deer declined to a density of 11-12/mi^2 in 2009-2011. The rise and fall of deer coincided with the pattern of increase and decrease in *I.*

scapularis in the southern tier and was consistent with our expectation that *I. scapularis* and deer density in the current and past two years would be correlated. However, we emphasize that once *I. scapularis* has become established in an area, we would not expect to observe a decline in tick density unless deer density were lowered and held at or below the posited 8-13/mi^2 threshold (Telford et al. 2017) for several years, so the correlation may be spurious. Apart from deer, density-independent or density-dependent population regulation mechanisms (Fish 1993) could be keeping *I. scapularis* at a state of dynamic equilibrium.

Density-independent weather mechanisms limiting tick development and survival in both winter and summer in Maine could be declining snow cover, increasing frequency of heat waves, and increasing extreme rainfall events. Snow is a ground insulator that improves tick survival (Eisen et al. 2016) and snowfall has been decreasing statewide (Fernandez et al. 2015). Lack of snow followed by an extended cold wave could make the southern tier more hostile than a more snow-covered northern tier. Extended heat waves may drive nymphal *I. scapularis* into the leaf litter even in Maine, as is typical at the southern edge of its range (Stromdahl and Hickling 2012, Arsnoe et al. 2015). Increasing relative humidity in the northeast (Lyon and Barnston 2017) may not compensate for high temperatures during heat waves. Heavy rain may suppress nymphal questing activity (Moore et al. 2014, Berger et al. 2014b), leading to indirect mortality. Density-dependent *I. scapularis* population-limiting mechanisms include grooming behavior by hosts such as white-footed mice (Levin and Fish 1998) and opossums (Keesing et al. 2009), immune resistance acquired by hosts (Wilson et al. 1990, Craig et al. 1996), or predators, parasites, and pathogens of ticks (Fish 1993). Host density-dependence may regulate *I. scapularis* as well (e.g., Fish 1993, Eisen et al. 2016, but see Hazler and Ostfeld 1995).

Quiescence and diapause (Eisen et al. 2016, Ogden et al. 2018) also may play a role in trends and fluctuations observed in *I. scapularis*.

Two independently-obtained datasets from the southern tier—subadult *I. scapularis* burdens on breeding passerine birds, and questing fall adult ticks—demonstrated patterns of increasing *I. scapularis* through the early 2000s, followed by a leveling or decline. Although these data are from just one site, the Wells National Estuarine Research Reserve, they could be another line of evidence that *I. scapularis* may have reached a population asymptote in the southern tier. The Borrelia infection rate in the fall-flagged adults is also consistent with the idea of a dynamic equilibrium in Wells, a long-established site for *I. scapularis*. Ogden et al. (2007) predicted that *I. scapularis* populations should reach a stable cyclical equilibrium within 10 years, assuming typical white-footed mouse densities and high deer densities. High *I. scapularis* host density and ideal tick habitat were characteristic of many parts of the research reserve in Wells.

Amplification of *B. burgdorferi* is expected to follow increases in abundance and range of *I. scapularis* as the pathogen follows the vector (Ginsberg 1993). Partially consistent with our fourth hypothesis, annual Lyme incidence was correlated with nymphal *I. scapularis* submissions rates in the northern tier. However, Lyme incidence was not correlated with nymphal *I. scapularis* in the southern tier because Lyme incidence increased whereas submissions rates leveled off. This putative decoupling of disease incidence and entomological risk could be due in part to increased rate of discovery of tick-borne illness owing to increased clinician and patient awareness and testing effort (Elias et al. 2019). Another possibility is that an increasing proportion of virulent strains of *B. burgdorferi* and/or co-infections in *I. scapularis* could be an emergent feature where *I. scapularis* are established (Brisson et al. 2011, MacQueen et al. 2012).

1.5.1 Limitations of the Study

We have performed simple univariate linear regressions and correlation tests with datasets that are subject to bias. Passive surveillance is not based on random sampling (Clow et al. 2017), and valid criticisms of the Maine tick identification program include submitter fatigue (possibly due to increased familiarity with ticks), and possible lack of familiarity with and in the program where there was lower entomological risk and/or distance from the program. We juxtaposed submissions of nymphal and adult *I. scapularis*, *I. cookei* (woodchuck ticks), which is macroscopically similar to *I. scapularis*, and *Dermacentor variabilis* (dog ticks) found on humans. Non-zero submissions of *I. cookei* and *D. variabilis* indicated some submitters in both tiers were aware of the program from its inception (Fig. 1.21). One might expect increasing public concern or submissions fatigue to respectively increase or decrease submissions of at least *I. scapularis* and *I. cookei* at the same rate, but such was not the case (Fig. 1.21). *I. cookei* nymphs were more commonly submitted in the early years in both tiers, whereas more *I. scapularis* were submitted in later years (Fig. 1.21a,b). These patterns in concurrent submissions of the three most common ticks (93% of submissions) suggested that despite biases there was a relevant biological signal from the Maine submissions data.

Several passive surveillance programs outside of Maine have investigated correspondence between Lyme disease and passive *I. scapularis* submissions in time and space. At both the county and town levels in Rhode Island, USA, Johnson et al. (2004) found Pearson

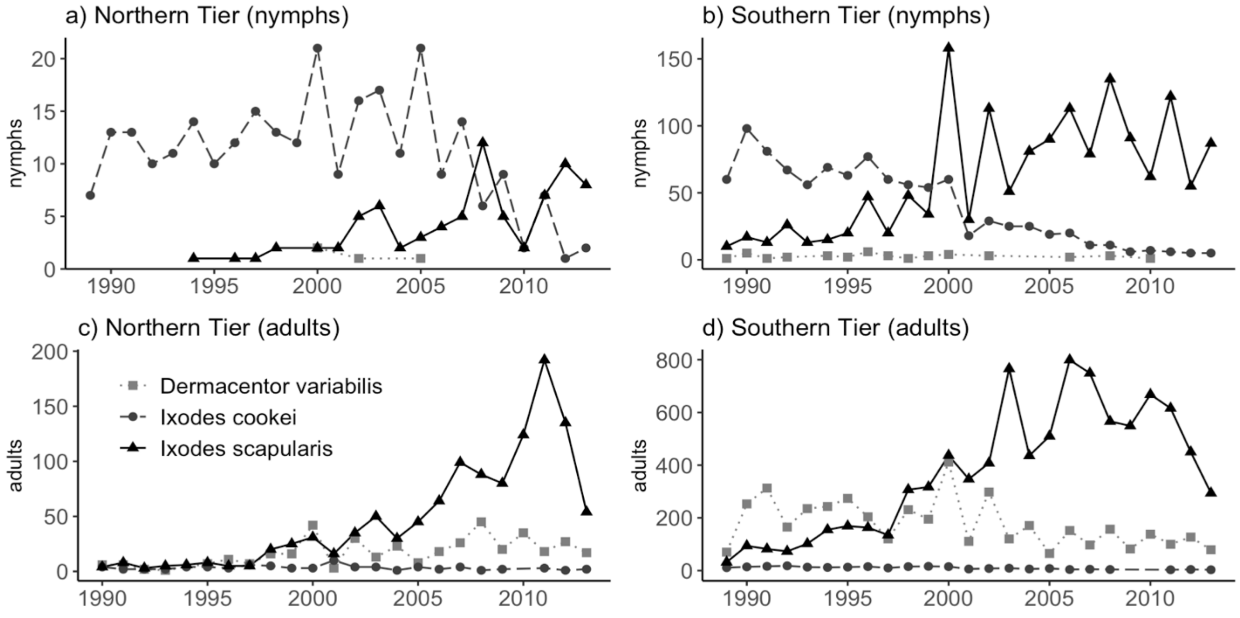

Figure 1.21. Number of submissions of *I. scapularis*, *I. cookei*, and *D. variabilis* nymphs and adults in the northern (a) and southern (b) tiers of Maine and adults in the northern (c) and southern (d) tiers of Maine, 1989-2013.

correlation coefficients (r) ≥0.92 between human Lyme disease cases and the number of submitted *I. scapularis* (stage not specified). At the town level in Quebec, Canada, Ripoche et al. (2018) modeled Lyme incidence as a function of population-adjusted number of passively submitted nymphal *I. scapularis* and a found a correlation coefficient of 0.93 between actual and predicted Lyme incidence. In Connecticut, USA, Shelton (2015) found moderate correlations between Lyme cases and passively submitted *I. scapularis* (stage not specified) at the town level across years, and on an annual basis across towns (both r ~ 0.50), however, Connecticut case reporting methods changed dramatically during the period used for analysis. In Rhode Island, Johnson et al. (2004) found no positive correlation between Lyme cases and passive *I. scapularis* submissions over time but the tick identification program at the time included testing for a fee. Thus, while bias is inherent in any passive surveillance program, these programs have successfully tracked geographic emergence of Lyme disease.

Active (field) surveillance is subject to measurement error (Clow et al. 2018), and certainly the bird burden and flagged adult tick data used here came from one site only and were subject to variation due to weather and sample timing. These data cannot validate the passive surveillance data from the southern tier. But in ecological studies, the choice is usually between short-term sampling at many sites or long-term sampling at one or a few sites. Thus, we offer the field time series as lines of evidence which do not contradict the passive surveillance data. The deer density data were based on regression model predictions, introducing unknown error.

Level of aggregation chosen also can introduce bias (e.g., Openshaw 1984, Dark and Bram 2007). Aggregation of tick, weather, and deer data into northern and southern tiers could have obscured spatial patterns at a finer spatial resolution, and certainly transitional conditions at the northern-southern tier boundary will be obscured by the necessity of conforming to county lines. Temporal aggregation of climatological variables to seasons will obscure temperature extremes, although *I. scapularis* are buffered from temperature and humidity extremes through time spent in the soil/leaf litter layer and exhibit latent developmental responses to seasonal changes (Odgen et al. 2014). Certainly, we know that there are focal areas of deer overabundance (MEIFW 2017) and that tick habitats vary in microclimate, vegetation, and rodent and host communities. Aggregation to the northern/southern tier levels was intended to be as objective as possible based differences in Lyme disease incidence, climate, and deer densities. Critically, characterizing phenological trends of *I. scapularis* required enough data per tier to assess season duration and data were sparse for the northern tier.

A number of tick-associated factors were not included in the correlation analysis. We did not include other landscape-scale conditions associated with *I. scapularis* such as forest fragmentation and suburbanization (Allan et al. 2003, Linske et al. 2018) and invasive plant species invasion (Lubelczyk et al. 2004, Elias et al. 2006, Williams and Ward 2010, Williams et al. 2017), though these conditions co-occur with higher white-tailed deer densities. The relationship between a heat index and *I. scapularis* would probably be more instructive than temperature and humidity separately. Despite these limitations, the results reported here are biologically plausible and will guide future statistical ecological modeling that ascertains the joint contributions of factors driving emergence and regulation of *I. scapularis* in Maine.

1.6 Conclusions

Climate has likely been permissive for *I. scapularis* since before the 1990s in Maine's southern tier, and has been less permissive for *I. scapularis* in the northern tier, but is improving. However, overall ecological suitability for *I. scapularis* in the northern tier may be limited due to low deer densities, which averaged ~5/mi^2 during the study period and to this day. The joint effects of climate, deer, and landscape-scale habitat should be modeled to determine the relative contributions of these factors, and to ascertain to what degree impacts of climate change on *I. scapularis*, and thus disease transmission in the northern tier, could be mitigated through conservative deer density goals for the northern tier. Conversations over the merits of keeping deer herd density low may replace the usual debate over deer reduction.

In the southern tier, *I. scapularis* submissions rates and season duration trended up for ~13 years then leveled to a possible dynamic equilibrium. Teasing out what if any population-limiting mechanisms could be operating on *I. scapularis* and at what geographic scale will be a worthwhile challenge if it leads to ecological insights and tick control strategies.

In Maine's southern tier we may have demonstrated an instance decoupling of reported disease incidence and entomological risk. The challenge will be to tease apart the confounding effects of human diagnostic testing effort versus pathogen amplification and genetic diversification. Otherwise we will frustrate our expectations of lowered tick-borne disease incidence following carefully designed tick control interventions. Maine's laboratory capacity for PCR-based testing has expanded since 2013 and includes the laboratories at the Maine Medical Center Research Institute, The Maine CDC's Maine Health and Environmental Testing Laboratory, and the University of Maine's Cooperative Extension Diagnostic and Research Laboratory. Climate change is exacerbating our problems with blacklegged ticks in Maine. Mapping patterns in strain diversity of the multiple pathogens that *I. scapularis* carry should improve our resilience as our changing environment facilitates invasion of tick and mosquito vectors into Maine.

CHAPTER 2.

BLACKLEGGED TICK RANGE EXPANSION IN RELATION TO WHITE-TAILED DEER AND CLIMATE, IN MAINE, USA

2.1. Abstract

Lyme disease is caused by the bacterial spirochete *Borrelia burgdorferi*, which is transmitted through the bite of an infected blacklegged tick (*Ixodes scapularis*). Geographic range expansions of invasive *I. scapularis* populations over time in the US have been attributed to a mosaic of factors including 20th century reforestation followed by suburbanization, burgeoning populations of the white-tailed deer (*Odocoileus virginianus*) which is the primary reproductive host of *I. scapularis*, non-native plant invasions that provide ideal tick habitat, and, at the northern edge of *I. scapularis*' range, climate change. Maine, a high Lyme incidence state, has been experiencing warmer and shorter winter seasons, and relatively more so in the northern tier. We used a passive tick surveillance dataset to index abundance of *I. scapularis* nymphs within Maine's wildlife management districts, 1990-2013. We used a generalized additive mixed model (GAMM) to model linear and nonlinear relationships between nymphal *I. scapularis* abundance and predictors, while allowing for spatiotemporal dependencies within and among wildlife management districts. *I. scapularis* nymphs increased with increasing deer densities up to ~13 deer/mi^2, but beyond this threshold tick abundance did not vary with deer density. This result corroborated the idea of a saturating relationship between *I. scapularis* and deer density. It was also consistent with empirical studies suggesting deer density must be lowered below ~8-13/mi^2 to lower *I. scapularis* abundance enough to lower Lyme disease. The model also indicated that more ticks were associated with higher relative humidity, warmer

minimum winter temperatures and more degree-day accumulation, and that without deer >4/mi^2 warmer winters would not increase nymphal abundance. The Maine Department of Inland Fisheries and Wildlife northern tier goals range from 10-15/mi^2 and southern tier goals from 15-20/mi^2 for 2030 (MEIFW 2017). We recommended deer densities be kept to ≤10/mi^2 in all of Maine's northern tier to mitigate likely increases in ticks due to future warming. Suburbanization and presence of tick-associated non-native plants did not enter the model because they co-occurred with deer.

2.2 Introduction

The blacklegged or deer tick (*Ixodes scapularis*) is the vector of agents causing Lyme disease, human babesiosis, and human granulocytic anaplasmosis (Spielman et al.1985, Spielman 1988, Bakken et al. 1994). Incidence and geographic ranges of Lyme borreliosis and other tick-borne diseases are rising and spreading in both North America and northern Europe, following northward range expansion of vector ticks, which has been partially attributed to climate warming (Parham et al. 2015). Lyme disease is the most common vector-borne illness in the US (Rosenberg et al. 2018) and is concentrated in the upper Midwest and New England. Formerly, Lyme disease incidence in the southern New England states eclipsed that of the northern New England states, but Maine, New Hampshire, and Vermont have caught up with the rest of the northeast (CDC 2018a).

Lyme cases in Maine have risen dramatically since the first case in 1983, with record case numbers set each year since 2011, and increasing by 82.4% from 2011 to 2017 (from 1,013 to 1,848 cases, MECDC 2018b). Maine had the highest incidence of Lyme disease cases in the

U.S. in 2016 and 2017 (86.4 and 106.6 cases/100,000 people, respectively) and has ranked in the top five states for Lyme incidence since 2008 (42.1 to 84.8; CDC 2018a). Case-counting is inexact (Cartter et al. 2018), but Maine is clearly a high-incidence state. Other tick-borne illnesses on the rise are anaplasmosis, babesiosis, *B. miyamotoi* disease, and Powassan virus neuroinvasive disease (Cavanaugh et al. 2017, MECDC 2018b, Smith et al. 2019a).

Increasing Lyme disease incidence in Maine has been correlated with the range expansion of the blacklegged tick (Fig. 2.1). Reporting on 18 years' worth of data (1989 through 2006), Rand et al. (2007) showed that *I. scapularis* emerged first along the coast then advanced inland, and that submissions of nymphal *I. scapularis* were strongly correlated with reported Lyme disease cases in time and space. Comparison with submissions of macroscopically similar *I. cookei* (woodchuck tick) indicated an increase of *I. scapularis*, not just increased activity on the part of blacklegged ticks or tick submitters (Rand et al 2007).

Geographic range expansion of invasive *I. scapularis* populations over time in the US has been attributed to a mosaic of factors including 20th century reforestation followed by suburbanization, burgeoning populations of the white-tailed deer (*Odocoileus virginianus*), which is the primary reproductive host of *I. scapularis* (e.g., Eisen et al. 2016, Telford et al. 2017), non-native plant invasions that provide ideal tick habitat (Lubelcyk et al. 2004, Elias et al. 2006, Williams and Ward 2010), and, at the northern edge of *I. scapularis*' range, climate change (Leighton et al. 2012, Ogden et al. 2014). We describe known associations between *I. scapularis*, climate, deer, suburbanization, and tick-associated invasive plants in the next sections.

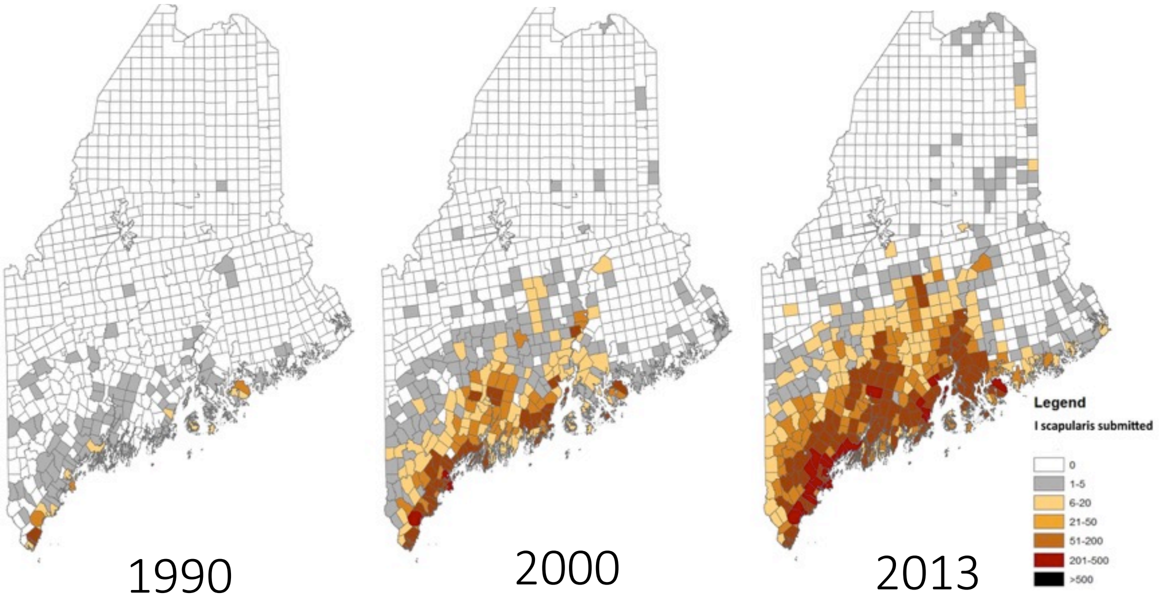

Figure 2.1. Range expansion of the blacklegged tick in Maine, USA, 1990-2013, as measured by *I. scapularis* submitted to Maine Medical Center's tick identification program. Source: Vector-borne Disease Laboratory, Maine Medical Center Research Institute, Scarborough, Maine.

2.2.1 *I. scapularis*, Climate Suitability, and Climate Change in Maine

Climate change in Maine has likely been an ally of *I. scapularis* over the past several decades (Chapter 1). Maine has warmed by about 1.7°C (3°F) between 1895 and 2014, and this warming has been felt most acutely in winter and in the northern part of the state (Chapter 1: Fig. 1.8; Fernandez et al. 2015). Since 1895, annual precipitation in Maine has increased by 15 cm (13%), with most of the additional amount falling in summer and fall (Fernandez et al. 2015). Among several climate scenarios for coastal Maine by 2030 (not all of which assume warming), Birkel and Mayewski (2018) described a moderate warming of 0.5°C, or abrupt warming of 1.7°C by 2030 due to Arctic sea ice collapse leading to further shrinkage of the winter season and more total annual precipitation than the 2010s. A warmer, wetter climate future in Maine would likely further promote *I. scapularis* survival and questing activity and thus we are concerned that risk of tick bite and pathogen transmission will increase.

The climate envelope for *I. scapularis* in Maine will be suitable in locations where *I. scapularis* are subject to sufficient degree-day accumulation (e.g., ~1,240 degree-days>6°C) to promote egg laying and hatching, with prevailing seasonal temperature averages between ~-10°C and ~30°C and humidity ≥75% (Chapter 1). Survival, development, and questing (blood-meal seeking) of Ixodes ticks are constrained by temperature and humidity at all stages of the two-year tick life cycle: egg, larva, nymph, and adult. In brief, temperature affects winter diapause (overwintering), length and timing of inactivity (phenology) and survival of adults and nymphs, summer questing activity (phenology) and survival of nymphs and larvae, and spring/summer phenology of oviposition (laying) and eclosion (hatch) of eggs; humidity modifies the desiccating effects of summer heat on nymphs and larvae (e.g., Lindsay et al. 1995, Rand et al. 2004a, Ogden 2006a, Ogden 2008a, Williams and Ward 2010, Leighton et al. 2012, Ostfeld et al. 2015, Parham et al. 2015, Linske et al. 2019).

In Maine, Rand et al. (2004a) showed that for blacklegged tick females to lay eggs (in May), and for those eggs to hatch, about ~1,240 (± SD 143) degree-days >6°C (42.8°F) must accumulate by the end of August. Light-mediated diapause (e.g., Ogden 2018) may preclude some larval questing beyond August, thus attainment of sufficient degree days by summer's end is important to completion of the lifecycle of *I. scapularis*. During the 1990s and 2000s 1,240 degree-days >6°C (42.8°F) has not been attained in the northern tier but attendant to climate change, the line marking attainment of this threshold has shifted northward (Chapter

1:Fig. 1.9) and this shift may continue. Years where 1,240 DD>6°C is achieved by the end of August should lead to larger larval cohorts in the same year, and larger nymphal and fall adult cohorts the following year, assuming a mild intervening winter. We were interested in whether *I. scapularis* might show nonlinear and/or threshold relationships related to degree-day accumulation, mean winter low temperatures and other seasonal climatologies.

2.2.2 *I. scapularis* and White-tailed Deer

In the US, the white-tailed deer is the primary reproductive host of the adult *I. scapularis* (e.g., Telford 2017) by providing a mating site for adult ticks and blood meals to females and providing ~95% of blood meals to females (Wilson et al. 1990). In the northeastern US, larvae and nymphs also feed on deer (Watson and Anderson 1976, Anderson and Magnarelli 1980, Magnarelli et al. 1995, Garnett et al. 2011, Williams et al. 2018a), as well as on rodents and non-rodent small animals such as lizards (Piesman and Spielman 1979, Spielman et al. 1985, Oliver et al. 1993, Piesman 2002, Oliver et al. 2003, Brisson et al. 2008), and migratory birds (Smith et al. 1996, Rand et al. 1998, Ogden et al. 2008b). Conversely, adult blacklegged ticks feed on medium- to large-sized mammals but almost never on rodents and birds (e.g., Smith et al. 1996, Rand et al. 1998, Scharf 2004, Schulze et al. 2005, Elias et al. 2011). Integrated tick management combines strategies to lower tick abundance by killing ticks outright and to finding ways to interrupt the life cycle of the vector tick. Depriving adult *I. scapularis* of its primary blood meal host—white-tailed deer—is a strategy for long-term tick reduction that can be paired with short-term strategies (Telford 2017).

Several studies have found correspondence between tick abundance and deer abundance (Wilson et al. 1988, Wilson et al. 1990, Deblinger et al. 1993, Rand et al. 2003, Stafford et al. 2003, Kilpatrick et al. 2014), while others have not (Wilson et al. 1984, Jordan and Schulze 2007, Ostfeld et al. 2006). Six studies at seven sites ranging from New Jersey to Maine sought to reduce white-tailed deer densities enough to reduce *I. scapularis* (Kugeler et al. 2016). Deer were reduced to 45-100% from pre-cull densities of 34-251/mi^2 (13-97/km^2) to post-cull densities of 0-65/mi^2 (0-25/km^2) (Kugeler et al. 2016). Fifty to 100% reduction in nymphal *I. scapularis* was achieved at six of the seven sites. The burden of Lyme disease was assessed pre- and post-cull at four of the sites. Where Lyme was possibly reduced, deer were reduced 50-100% from pre-cull densities of 34-118/mi^2 (13-46/km^2) to post-cull densities of 0-13/mi^2 (0-5/mi^2) and where Lyme was not reduced post-cull deer densities remained high at 47/mi^2 (18/km^2).

The three deer reduction experiments connected with possible reductions in Lyme disease were on Great Island, Massachusetts, Monhegan Island, Maine, and Mumford Cove, Connecticut. On Great Island deer were reduced to <6/mi^2 (2.3/km^2) in 1982; nymphal *I. scapularis* declined by >63% and cases declined from ~20 among 162 residents during the five-year pre-cull period to two cases in the decade following (Telford, 1993, 2002). Monhegan islanders voted in 1995 to remove all 113 deer permanently; the number of *I. scapularis* larvae and nymphs on rats declined from 1 to 17 pre-removal to 0 post-removal (Rand et al. 2004a) and among the ~70-resident population, cases declined from 10 in the pre-cull decade to two in the two decades since. In Mumford, Kilpatrick et al. (2014) reported a 76% reduction in tick abundance and 80% reduction in cases of Lyme disease per 100 households in a Connecticut community where deer were reduced by 91%, from 142/mi^2 (54/km^2) to 13/mi^2 (5/km^2). The four studies on Monhegan Island, Maine, Great Island, Massachusetts, Mumford, Connecticut, and Bernard Township, New Jersey provided empirical evidence that if the goal is to lower Lyme incidence, deer density should be lowered to the vicinity of 8-13/mi^2 (3 to 5/km^2) (Telford 1993, Telford 2002, Stafford et al. 2003, Stafford 2007, Kilpatrick et al. 2014).

Taken together, the deer reduction studies suggested the relationship between deer density and tick abundance is nonlinear, with a threshold deer density above which deer reduction does not reduce *I. scapularis* but below which deer reduction does lower tick abundance, with a time lag (Eisen and Dolan 2016). Kilpatrick et al. (2017) described this as a saturating relationship, with tick abundance increasing with increasing deer density up to a moderate but unknown deer density then showing little response as deer abundance increases further. A question we had was whether existing data on Maine *I. scapularis* and white-tailed deer in a model might statistically corroborate the empirically-derived 8-13/mi^2 (3 to 5/km^2) threshold.

2.2.3. *I. scapularis* and Suburbanization

The emergence of the blacklegged tick is tied to 20th and 21st century reforestation and suburbanization of the landscape (Telford 2017). Deciduous and mixed deciduous-coniferous forests are core forest habitat for *I. scapularis* (Eisen et al. 2016), and forest fragmentation as a result of residential development may lead to increased Lyme disease risk (Allan et al. 2003, Brownstein et al. 2005a, Brownstein et al. 2005b). Exposure to blacklegged ticks and risk of transmission seems to occur most typically in the peridomestic environment (Nicholson and Mather 1996, Linard et al. 2007, Zeman and Benes 2014). In Maine, many of the emerging suburbs that are currently experiencing rapid growth were rural areas 40 years ago (Richert 2004). Expansion of service centers and transportation, along with increased development pressure and zoning requirements for large lot sizes have led to the rapid conversion of land from traditional agricultural or timber uses to open, low, and medium-density suburban development (Richert 2004). We thus surmised that proportion of the landscape in deciduous and mixed forest cover in conjunction with proportion in residential development may serve as a good landscape-scale proxy to *I. scapularis* abundance and exposure.

2.2.4 *I. scapularis* and Tick-Associated Non-native Plant Species Invasions

Japanese barberry (*Berberis thunbergii*) is classified as invasive in twenty states and five Canadian provinces, and forms dense thickets that alter soil and site conditions, inhibiting forest regeneration and native herbaceous plant populations (Silander and Klepeis 1999). Japanese barberry is favored when overabundant white-tailed deer browse down native vegetation (Lubelczyk et al. 2004, Elias et al. 2006), and furthermore, it harbors white-footed mice and other small mammals and birds that host *I. scapularis* and serve as reservoirs for *B. burgdorferi* (Williams and Ward 2010). Japanese barberry infestations are favorable habitat for ticks because they provide a buffered microclimate that limits desiccation-induced tick mortality. High vapor pressure deficit (VPD) values are strongly related to tick mortality (Williams and Ward 2010). In Connecticut, control of Japanese barberry reduced the number of ticks infected with *B. burgdorferi* by nearly 60%, by reverting microclimatic conditions to those more typical of native northeastern forests, namely, lower relative humidity/higher vapor pressure deficit, and higher summer temperatures (Williams and Ward 2010). Forests infested with barberry can adversely affect human and pet health because they have greater tick abundance than native vegetation. Ticks also are associated with Japanese honeysuckle (*Lonicera japonica*) and oriental bittersweet (*Celastrus orbiculatus*) (Lubelczyk et al. 2004, Elias et al. 2006). Though these plants have focal distributions, their tendency to invade whole landscapes led us to ask if sightings data might be predictive of *I. scapularis* abundance.

2.2.5 Knowledge Gaps

Numerous data modeling and simulation studies have supported the premise that *Ixodes* ticks and tick-borne disease have advanced northwards in response to warming climate (e.g., Ogden et al. 2008a, Ogden et al. 2008c, Leighton et al. 2012, Ogden et al. 2014) although Randolph (2014) and Ostfeld et al. (2015) cautioned that such models are incomplete without inclusion of non-climatic processes. Likewise, models of *I. scapularis* in relationship to deer and other landscape components be incomplete without consideration of climate. (Kilpatrick et al. 2017) considered the relationship between tick density and low-to-moderate deer density while accounting for effects of cold on tick survival to be a knowledge gap. An advantage of a Maine study is that in the northern tier winters are colder and deer densities lower than in states to the south.

Ideally, data on all climatic and non-climatic processes affecting Ixodes could be assembled into one model, but this is improbable. Still, several landscape-scale studies using combinations of field and remote-sensing data have incorporated climatic and some non-climatic processes in the same models with ticks or tick-borne illness as the response (e.g., Khatchikian et al. 2012) . Robinson et al. (2015) found associations between Lyme incidence in Minnesota and degree-day accumulation and deciduous forest cover. Tagliapietra et al. (2011) found *I. ricinis* abundance was associated with saturation deficit and red deer density. Lyme incidence as an outcome in these types of models can be problematic due to increased disease discovery (Chapter 1; Elias et al. 2019). Fortunately, we had the benefit of a long-term passive surveillance dataset (1989-2013) to model the statistical association between *I. scapularis* and a suite of factors known to be associated with *I. scapularis*.

2.2.6 Aims and Hypotheses

Our aim was to determine whether annual nymphal *I. scapularis* submissions rate could be modeled as linear or nonlinear smooth functions of deer density, seasonal climatology, and several landscape features, at the statewide scale. As described above, relationships between *I. scapularis* and predictors are not likely to be linear and may involve thresholds. Using nymphal *I. scapularis* submissions rate (ticks submitted adjusted for human population size) as an index to tick abundance, our hypotheses were that nymphal *I. scapularis* submissions rate in year_t and WMD_i would be

1. a nonlinear function of deer density at year_{t-2} in WMD_i, exhibiting a positive relationship initially, followed by threshold in the vicinity of 8-13/mi^2, over which there would be no relationship between ticks and deer density. The rationale for year_{t-2} is that the summer nymphal cohort in year_t would be the result of a year_{t-2} adult cohort, most of which fed on deer in fall of year_{t-2}. Larvae (in year_{t-1}) and nymphs (in year_{t-2}) also could have obtained blood meals from deer, but typically would have fed on small mammals as well as birds. The rationale for the specific threshold is based on the 8-13/mi^2 range posited for suppression of ticks and Lyme disease (Telford 1993, Telford 2002, Stafford et al. 2003, Stafford 2007, Kilpatrick et al. 2014);
2. a nonlinear function of degree-day accumulation in year_{t-1} of WMD_i with a threshold in the vicinity of 1,240 degree-days >6°C because larval eclosion depends on accumulation of sufficient degree-days (Rand et al. 2004a, Leighton et al. 2012);

3. a positive nonlinear function associated with mean winter low temperature in year$_t$ and WMD$_i$, with a threshold in the vicinity of -18°C to -10°C (Burks et al. 1996, VanDyk et al. 1996, Brunner et al. 2012) assuming warmer winters improve overwintering survival;
4. a positive nonlinear or linear function of mean summer relative humidity and or mean summer maximum temperature in year$_t$ and WMD$_i$ because greater nymphal activity and survival is associated with higher relative humidity (Williams and Ward 2010), but might be compromised in hot summers;
5. a positive nonlinear or linear function of percentage of land area in, open, low and medium density development, percent of forest with deciduous or mixed cover type, and frequency of Japanese barberry, Japanese honeysuckle, and oriental bittersweet sightings in WMD$_i$.

We considered several other climatological variables closely associated with humidity (precipitation, vapor pressure deficit) and compressed winters (warmer falls, warmer springs). We expected the model would be improved by including time (year), because *I. scapularis* is an invasive species, dispersing into presumably suitable but previously unoccupied habitat (Byers et al. 2015). We also assumed that there would be temporal and spatial autocorrelation within and among WMDs, respectively, and that the models would be improved by incorporating random effects to represent these sources of variation. Adult *I. scapularis* do have a role in Lyme disease transmission in humans, but as human cases of Lyme disease peak in the summer months when nymphs are active (Schwartz et al. 2017), we selected nymphs as the representative stage.

2.3 Methods

2.3.1 Study Area

Maine, the most northeastern of the United States, encompasses 86,542 km2 and 4.5° latitude (42.97-47.46°N, 66.95-71.08°W), and has 924 minor civil divisions (towns), 512 of which are populated. With the exception of agricultural land along its eastern border with Canada, the northern half of the state is primarily commercial forests of spruce and fir (Picea and Abies spp.) being gradually supplanted by hardwood stands, principally of maple and oak (Acer and Quercus spp.). A series of higher elevations (600-1,600 m) occupies the northwestern half of the state. The majority of its human population of 1.3 million resides in its southern half, generally within an 80-km-wide coastal plain with elevations <150 m (Rand et al. 2007). Relative to other high Lyme incidence states in the northeastern US, Maine is unique. This is because tick populations range from established on the coast to emerging in the northern tier, white-tailed deer densities range from moderate (moderate relative to states such as Connecticut and New York) to low in the northern tier, and local climates range from mild on the coast to cold in the northern interior and higher elevations (Rand et al. 2007).

The Maine Department of Inland Fisheries and Wildlife (MEDIFW) manages deer and other game species within 30 Wildlife Management Districts (WMDs) numbered 0 through 29 (Fig. 2.2). WMDs are based on similarities in geographical location, soils, forest cover types, seasonal temperature, rainfall and snowfall, and land use (MEIFW 2007). Currently, WMD-level deer abundances range from 2-5/mi^2 (5-13 deer/km^2) in the north, to 15-25/mi^2 (39-65 deer/km^2) in central and southern areas (MEIFW 2007). WMD 29 is located along the mid- and southern coast and contains all islands with year-round residents not connected to the mainland at low tide or by manmade structures; at times deer densities have exceeded 100/mi^2 on certain islands (MEIFW 2007, Rand et al. 2007). We note that no ticks were acquired in towns corresponding with WMD 0 (Baxter State Park) and WMD 4 and so these two WMDs are not part of the model.

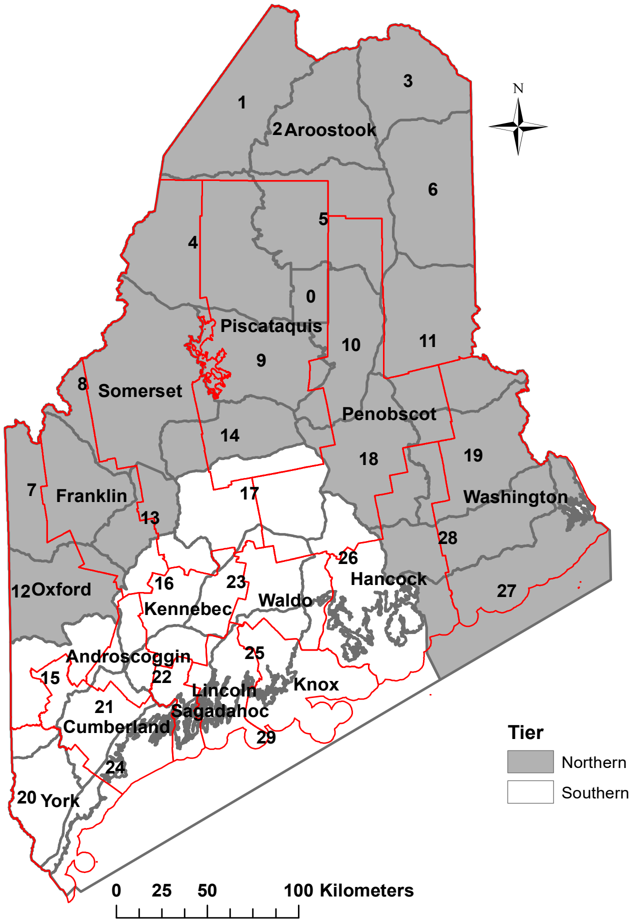

Figure 2.2. Maine's 16 counties (red outlines) superimposed over 30 Wildlife Management Districts (WMDs 0 through 29, gray outlines), with the northern tier WMDs shaded in gray.

2.3.2 Datasets

The data comprised nymphal blacklegged tick submission rates as response variables, and white-tailed deer abundance, climatological variables, and landscape characteristics as candidate explanatory variables (Table 2.1).

2.3.2.1 Shapefiles

We downloaded shapefiles of Maine towns (metwp24.shp) and WMDs (wildlife_mgmt_districts.shp) (Maine GeoLibrary 2017). We used these shapefiles to spatially aggregate and portray data on ticks, white-tailed deer, climatology, and landscape variables to the WMD level.

2.3.2.2 Nymphal *I. scapularis* Submission Rate as an Index of Abundance

The Vector-borne Disease Laboratory at the Maine Medical Center Research Institute ran a free-of-charge, statewide tick identification (i.e., passive surveillance) program in Maine, initiated in 1989, a year after the first *I. scapularis* were reported in the state (Rand et al. 2007). Members of the general public, health care providers, and veterinarians submitted ticks to the program from 1989 through 2013. In 1989, lab staff actively recruited tick submitters by way of lectures, phone calls, newsletters, and media communications. After 1989 there was no active recruitment, and in mid-2013 the lab announced the end of the program. Data collected from persons submitting ticks were: date found and town where the tick was thought to have been acquired, the species of "found-on" host (including age and gender if the host was human), the attachment site if bitten, and any related symptoms. Laboratory staff identified the species, stage, and engorgement level of the tick and returned this information to the tick submitter (Rand et al. 2007). Although passively collected, tick submissions data serve as a good if not excellent index of entomological risk (Rand et al. 2007, Ripoche et al. 2018) and reflect the seasonality of *I. scapularis*. Humans could encounter nymphal and adult ticks carried into the region as larvae and nymphs by migratory birds and these encounters would not reflect an established tick population (Ogden et al. 2006b, Ripoche et al. 2018). But in these areas, tick submissions would be low as would Lyme incidence.

Among 1,903 *I. scapularis* identified by the submissions program, 81%, 2%, and 15% of hosts were found on humans, dogs, and cats, respectively (Chapter 1). We excluded the 3% of submissions where ticks were unknown or found on livestock and wildlife species (Rand et al. 2007) since livestock and wild animals did not necessarily have statewide representation and wildlife do not represent peridomestic risk. We summarized the number of nymphal *I. scapularis* by town and year. To index annual abundance of questing *I. scapularis* nymphs, we obtained annual census data by town (minor civil division) for the State of Maine from the U.S. Census Bureau (U.S. Census Bureau 2018), then divided the number of ticks submitted per town by year by (population x 100,000) to arrive at ticks submitted per 100,000, i.e., the tick submissions rate. This was analogous to conversion of disease case counts to disease rate or incidence (cases/100,000), which allows for comparisons across time and areal units. We did adjust for the “small numbers problem” wherein small changes in case numbers in a geographic unit with a small population can cause wild swings in incidence and cause high disease rates to appear to cluster in areas with small populations (Pringle 1996, Roquette et al. 2018). For this reason, we calculated “tick rates” only where town populations were at least 50, following the lead of the Maine CDC which considers cases in towns with populations under 50 “non-reportable” (MECDC 2018a).

Table 2.1. Variables used in models of nymphal *I. scapularis* submissions rate as a function of predictors in Maine, 1990-2012. As needed, response and explanatory variables were aggregated from their original granularity to the level of wildlife management district and year.

Type	Abbreviation	Definition	Original Granularity	Source
Experimental unit				
	WMD	wildlife management district; 30 total, 28 with a human population	WMD	Maine GeoLibrary[a]
Response: tick abundance index				
	nyrate	nymphal submissions rate: ticks submitted/(human population x 100,000)	town/date tick found	MMCRI VBDL[b]
Predictor				
	year	year	n/a	
	deerlag2	deer/mi2, 2-year lag	WMD by year (1992-2012)	MEIFW[c]
	ddlag1	degree days >6℃ accumulated by the end of August (Jan 1 - Aug 31)	raster, 4km resolution/monthly	PRISM[d]
	DJF_t2min	winter (December-January-February) average minimum temperature	raster, 4km resolution/monthly	PRISM[d]
	MAM_t2min	spring (March-April-May) average minimum temperature	raster, 4km resolution/monthly	PRISM[d]
	JJA_t2max	summer (June-July-August) average maximum temperature	raster, 4km resolution/monthly	PRISM[d]
	SON_t2min	fall (September-October-November) average minimum temperature, 1-year lag	raster, 4km resolution/monthly	PRISM[d]
	JJA_prcp	summer (June-July-August) average total precipitation	raster, 4km resolution/monthly	PRISM[d]
	JJA_RH	summer (June-July-August) average relative humidity	raster, 4km resolution/monthly	PRISM[d]
	JJA_VPD	summer (June-July-August) vapor pressure deficit	raster, 4km resolution/monthly	PRISM[d]
	JJA_PDSI	summer (June-July-August) average Palmer drought severity index	raster, 4km resolution/monthly	PRISM[d]
	pctDEVEL	percent of land cover as open, low, and medium density development	raster, 30km resolution/2011	NLCD[e]
	pctDecMix	percent of land cover as both deciduous and mixed forest	raster, 30km resolution/2011	NLCD[e]
	INVASIVE	Total sightings per hectare of tick-associated invasive plants (JB, AB JH)	point counts/through 2017	MNAP[f]

[a] Maine GeoLibrary, https://www.maine.gov/geolib

[b] Maine Medical Center Research Institute, Vector-borne Disease Laboratory, http://mmcri.org/ns/

[c] Maine Department of Inland Fisheries and Wildlife, https://www.maine.gov/ifw/

[d] Oregon State University's Parameter elevation Regression on Independent Slopes Model (PRISM 2004), http://prism.oregonstate.edu/

[e] National Land Cover Database (NLCD), MultiResolution Land Characteristics Consortium (MRLC), http://www.mrlc.gov)

[f] Maine Natural Areas Program, (JB=Japanese barberry, AB=Asiatic bittersweet, JH=Japanese honeysuckle)

Using ArcGIS® (ESRI 2018), we joined the year-by-town dataset (now with tick submission rate), with the Maine town-level shapefile. We then used the zonal statistics tool in conjunction with the WMD shapefile to summarize tick submission rate to the year-by-WMD level (Table 2.1). The choice of spatial data aggregation level was nontrivial as different aggregation levels can lead to different results; this is the Modifiable Areal Unit Problem or MAUP (e.g., Openshaw 1984, Dark and Bram 2007, Roquette et al. 2018). One reason to aggregate to the WMD level was that we could have more confidence in the tick submission rate at the WMD level than at the town level. A second reason is that the WMD is the basic management unit for big game species including white-tailed deer.

2.3.2.3 Deer Density

During the hunting season (the regular firearms season is generally in November), the Maine Department of Inland Fisheries and Wildlife (MEIFW) Maine tracks hunter-killed deer at deer registration stations around the state, capturing information including sex, age, and town of kill. MEIFW uses deer registrations to calculate a buck kill index (BKI), which is the number of hunter-killed deer per 100 square miles.

Through 2005, MEIFW used a variation of a “sex-age-kill” model, called “HARPOP”, to arrive at estimates of deer/mi^2 for each WMD. HARPOP required a number of inputs including BKI and an index to hunting pressure, called hunter-days of effort/mi^2. HARPOP density estimates corresponded well with those based on pellet group surveys conducted in the 1980’s as ground-truthing (MEIFW 2007). Discontinuation of hunter surveys meant loss of hunter effort data and use of HARPOP ended after 2005. However, to express deer density estimates in public forums on deer management goals, MEIFW regressed HARPOP deer/mi^2 on BKI for each

WMD using the years 1987-2005 (*n* = 18 years). The best-fitting of several candidate regression models (linear, exponential, or power) was selected for each WMD and used to predict deer/mi^2 for years after 2005 (mean R^2 = 0.81, range 0.52 to 0.96, Appendix A). From MEIFW we obtained annual BKI and the equations for each WMD, then estimated annual deer/mi^2 for each WMD, 1990-2013 (Table 2.1). At the end of 2005, a handful of WMDs' boundaries were shifted with the notable change being WMD 29. The former WMD 29 included areas with both higher (WMD 25) and lower (Downeast) deer densities but the new WMD 29 included the offshore islands with historically much higher deer densities: Monhegan Island Plantation, ~114/mi^2 in 1996 (Rand et al. 2004b), Islesboro, ~48 to 62/mi^2 in 2011 and 2012 (Town of Islesboro Deer Reduction Committee 2018). We used the equation for WMD 25 for the new WMD 29. This resulted in conservative estimates of deer density in the new WMD 29, which we thought preferable to losing an experimental unit.

2.3.2.4 Climatology

Oregon State University's Parameter elevation Regression on Independent Slopes Model (PRISM 2004) is the U.S. Department of Agriculture's climatological dataset. PRISM uses weather station point measurements with a weighted regression scheme to account for climate regimes associated with orography, rain shadows, temperature inversions, slope aspect, coastal proximity, and other factors (NCAR 2015). Monthly and daily reanalysis data are available at 2.5 arcmin (4 km) resolution for 1895 through present in NetCDF format. We downloaded monthly gridded NetCDF files for the continuous United States (CONUS) which included minimum, maximum, average, and dewpoint temperature at 2m in degrees Celsius (t2min, t2max, t2ave, t2dpt), and total precipitation in cm (prcp). Using the National Center for Atmospheric Research

Command Language (NCL 2017), and the WMD shapefile, we masked the CONUS data to Maine only, then aggregated the monthly gridded data to the WMD level for 1989-2013.

We calculated the number of degree-days >6°C attained by the end of August for each year-WMD using the formula $(\text{t2ave} - 6°\text{C}) \times 30.5$ with the monthly PRISM data (Table 2.1). Using t2ave, we calculated average monthly vapor pressure (VP) and saturated vapor pressure (SVP) in Pascals, and from this, average monthly relative humidity (RH) and vapor pressure deficit (VPD), by WMD. The formulas were: $\text{VP} = 6.112 \times \exp[17.62 \times \text{t2dpt}/(243.12 + \text{t2dpt})]$, $\text{SVP} = 6.112 \times \exp[17.62 \times \text{t2ave}/(243.12 + \text{t2ave})]$, and $\text{RH} = \text{SVP}/\text{VP} \times 100$, and $\text{VPD} = 1\ \text{SVP} - \text{VP}$ (WMO 2008, p. I.4–29). For each year and WMD, we summarized monthly climatology to obtain average seasonal climatology pertaining to minimum and maximum temperature and degree-day accumulation by the end of August, and precipitation, relative humidity, and vapor pressure deficit (Table 2.1). Climatological time trends were difficult to interpret in map multiples so we presented them as time series.

2.3.2.5 Suburban and Forest Land Cover

National Land Cover Database (NLCD) contains classes of land cover associated with development, which we aggregated to represent suburban land cover. The NLCD is the primary source of land cover data in the United States (Wickham et al. 2010, MRLC 2018) and is a thematic land cover map for the United States based on Landsat images for the years (2001, 2006, 2011), with 20 classes of land cover with a spatial resolution of 30m (the 2011 NLCD includes changes in land cover classes from 2001 and 2006). We used the Evaluation, Visualization, and Analysis (EVA) Tool on the MRLC website (MRLC 2018) to select and download the 2011 land cover raster for Maine.

Using the zonal statistics tool in ArcGIS and the WMD shapefile to define zones, we summarized percent coverage by cover type for each WMD. We aggregated across the classes “Developed, Open Space”, “Developed, Low Intensity”, and “Developed, Medium Intensity”, to create a single new class of open, low, and medium density suburban development. We repeated this for percent forest cover type (deciduous, mixed, evergreen) and added the deciduous and mixed types to create percent deciduous/mixed forest cover (Table 2.1).

2.3.2.6 Tick-associated Invasive Plant Presence

The Maine Natural Areas Program (MNAP), Maine Department of Agriculture, Conservation and Forestry, coordinates a mapping system called iMapInvasives (www.imapinvasives.org). iMapInvasives is an online, GIS-based, mapping and data management tool for invasive species monitoring and management. Data are received from partners through quality-controlled, online submissions and iMapInvasives provides confirmed data points with high confidence in species identification and positional accuracy (Nancy Olmstead, personal communication 2017). Through a Data Use Agreement with the Maine Natural Areas Program, Maine Department of Agriculture, Conservation and Forestry, we downloaded iMapInvasives shapefiles (NAD83 Datum: NAD83 UTM Zone 19N) with spatial point locations of Japanese barberry, Japanese honeysuckle, and oriental bittersweet.

Using ArcGIS, we joined shapefile attribute tables for each of the three species (Japanese barberry, Japanese honeysuckle, and oriental bittersweet), with the town shapefile, and scored the occurrence of any of one of these three species as “tick-associated invasive plant species present”. Using ArcGIS and the WMD shapefile to define zones, we summarized presence counts for each WMD and divided by total hectares of the WMD (Table 2.1).

2.3.3 Statistical Methods

2.3.3.1 Summary Statistics and Visualizations

To characterize and visualize the variables used in the Maine model, we tabulated summary statistics for the northern and southern tiers of the state (Fig. 2.2) and produced maps (*I. scapula*ris, deer, landscape) and time series (climatology).

2.3.3.2 Nymphal *I. scapularis* Model

Generalized additive models (GAMs) extend generalized linear models (GLMs) by using smooth functions to define nonlinear relationships between the response and explanatory variables, and by combining predictor variables additively (Wood 2017). A generalized additive mixed model (GAMM) has the form

$$g(\mu_i) = X_i\theta + f_1(x_{1i}) + f_2(x_{2i}) + f_p(x_{pi}) + \ldots Z_i b + \varepsilon_i$$

where g is a link function that links the expected value to the predictor variables, $\mu_i \equiv E(Y_i)$, the expected value of Y_i, and $Y_i \sim$ is a response from the exponential family distribution, $i=1,\ldots,n$ are n observations; for the parametric part, if any, X_i is a row of the parametric effects model matrix and θ is the corresponding parameter vector (usually with an intercept, β_0); for the smooth components of the model, f_j are smooth functions of the covariates, $x_1,\ldots,x_p$ (Wood 2001, Wood 2017). For the random part of the model, Z_i is a row of a random effects model matrix; $b \sim N(0, \Psi)$ is a vector of random effects coefficients with unknown positive definite covariance matrix Ψ (Wood 2006) and $\varepsilon \sim N(0, \Lambda)$ is a residual error vector, with i^{th} element ε_i and covariance matrix Λ, which is usually assumed to have some simple pattern (Wood 2006). A generalized additive model (GAM) is a special case of GAMM (Wood 2006) without the random part, $Z_i b$, with ε_i i.i.d. $N(0, \sigma^2)$ random variables. Further details on GAMs can be found in Appendix B.

We implemented s generalized additive mixed models (GAMM) using the mgcv gam package R Core Team (2018). We used the square root transform on nymphal submission rate to reduce leverage of a large outlier (very high tick submission rate in WMD 29) and stabilize the mean-variance relationship (Wood 2017). Using the 2-year lag of deer density meant that the years 1990 and 1991 were not part of the model, and we eliminated 2013 as submissions could have been biased by announcement of the end of the tick identification program that year. Thus $n = 614$ (28 WMDs x 22 years, 1992-2013).

The Tweedie distribution (Candy 2004; Dunn and Smyth 2008) is a family of distributions that incorporates the normal, Poisson, and gamma distributions. The mean(μ)-variance (V) relationship is given by $V(\mu) = \mu^p$ for some p, the index parameter, where $p = 0$, $p = 1$, and $p = 2$ are normal, Poisson, and gamma distributions, respectively (Arcuti et al. 2013). A Tweedie model can be thought of as having mixed distributions with a positive mass at zero and non-negative real numbers, i.e., zero-inflated data with $1 < p < 2$. Our response variable, nymph abundance (submission rate), included many zeros. Using the R function tweedie.profile (Dunn 2013) we determined $1 < p < 2$ for the response distributions. The Tweedie model uses the log link by default, which ensures predicted values are positive (Wood 2017). When using the Tweedie distribution, the method for smooth parameter estimation in mgcv gam defaults to restricted maximum likelihood (REML) rather than generalized cross validation criteria (CGV).

The starting main effects nymphal model was:

$$Y_j = f_1(\text{year}_{tj}) + f_2(\text{deer\_lag2}_{tj}) + f_3(\text{DD\_lag1}_{tj}) + f_4(\text{SON\_t2\_min\_lag1}_{tj}) + f_5(\text{DJF\_t2\_min}_{tj}) + f_6(\text{MAM\_t2\_min}_{tj}) + f_7(\text{JJA\_RH}_{tj}) + f_8(\text{JJA\_VPD}_{tj}) + f_9(\text{JJA\_prcp}_{tj}) + f_{10}(\text{pctDEVEL}_{tj}) + f_{11}(\text{pctDECID\_MIXED}_{tj}) + f_{12}(\text{INVASIVE}_{tj}) + \varepsilon_{tj}$$

with *t* indexing years and *j* indexing WMDs.

Concurvity is the GAM analogue of collinearity in a GLM setting and occurs when a smooth term in a model could be approximated by one or more other smooth terms in the model (including smoothers in the random part of the model). Concurvity smooth main effects and a random spatial effect is likely to occur when all effects are at the same scale (Hodges and Reich 2010, Paciorek 2010, Hughes and Haran 2013, Hughes 2014, Hanks et al. 2015).

In an iterative process, we checked for concurvity among candidate explanatory variables, then tested each variable for significance as a main effect, either smooth or linear. If a main effect was concurve with one or more others, we substituted until we found the best predictor. Significance of smooth terms is based on Wald tests of smoothing parameter, βk = 0. i.e., not different from a simple linear relationship. Wald test P-values for smooth terms provide only rough guidance (Wood 2017) and should be used in combination with other fit guidance, e.g., smooth plots and residuals analysis. If a variable was not significant as a smooth main effect, we tested it for significance as a linear main effect. The chosen linear and smooth main effects were predictor variables that were not concurve with any other predictor and provided the best fit. We did not find guidance that described a concurvity score that should trigger concern, and concurvity can be tolerated in some models (Wood 2008). However, in our models it was clear that concurvity scores of ~≥0.30 in the spatial dimension destabilized the smooth terms as seen through changes in the smoothing parameters, wider confidence intervals and counter-intuitive smooths (e.g., ticks negatively related to temperature) (Mur 2008). We note that concurvity scores among the explanatory variables were the same regardless of correlation structure. We tested model fit given four candidate correlation structures (R code is in Appendix B):

1. Temporal "factor smooth" random effect. This random effect was a year × spatial unit interaction (i.e., a tensor product) that imposed a temporal correlation structure arising from repeated measurements on the spatial units (WMDs) but did not impose a spatial correlation structure. To specify this, the term $f_2(\text{year}_{tj}, \text{WMD}_{tj})$ was added to the main effects equations above. In the GAMM context the smooths of WMD over time are allowed to have smooths that vary from the overall main (global) effect of year.

2. Spatial Markov random field random effect. This random effect imposed a global Markov random field (mrf) smooth allowing a single spatial correlation structure among the neighboring areal units across years. The term $f_1(\text{WMD}_j)$ using a queen neighbor structure for the WMDs (Wood 2017) was added to the main effects equations above.

3. Additive temporal-spatial random effect. This random effect imposed, additively, the correlation structures of both the temporal factor smooth and global spatial Markov random field smooth. The term $f_2(\text{WMD}_{tj}, \text{year}_{tj}) + f_3(\text{WMD}_j)$ was added to the main effects equations above.

4. Interacting temporal-spatial random effect. This model differed from Model 3 in that the correlation structure allowed the mrf spatial smoothing among the neighboring areal units (WMDs) for each year of the form. The term $f(\text{WMD}_{tj}, \text{year}_{tj})$ was added to the main effects

equations above and $f_1(\text{year}_{tj})$ was omitted. This was because in the R mccv package, the "te" function that specifies this random effect includes the main effects, so a main time effect would not be separately specified, as would be main effects in an ANOVA (Wood 2017).

We checked for concurvity among the candidate explanatory variables and four candidate random effects. Our primary interest was ecological mechanisms explaining the observed increases in *I. scapularis* over time and space versus pure prediction. Thus, we selected ecological predictors over purely temporal and/or spatial covariance structures that predicted as well or even better than the biological factors.

We assessed the appropriateness of model terms based on measures of fit: residuals plots striving for $\varepsilon_{tj} \sim N(0, \sigma^2)$, i.e., normal residuals without remaining correlations or patterns, Aikake information criterion (AIC), dispersion, deviance explained, adjusted R^2, and the autocorrelation statistic (acf). The adjusted R^2 is approximately square of the correlation between the observed and fitted values, with an adjustment for degrees of freedom. Through this iterative process, we arrived at a final, parsimonious model, selected on the basis of model fit and explanatory value. For reference, we also ran an intercept-only model.

We wanted to assess the proportion of deviance explained by each explanatory variable in the final multivariate model. For each variable, we ran a reduced model missing the variable of interest (enforcing the same smoothing parameters as the full model), then subtracted the percent deviance explained by the reduced model from the percent deviance explained by the final model. Unfortunately, in a multivariate model where covariates are not strictly orthogonal, proportion of deviance explained by individual covariates does not add up to proportion of deviance explained by the full model. Therefore, we divided the proportion of deviance explained by each variable by the sum of percent deviance explained from the reduced models. This approximated the relative contribution of each variable to the proportion of explained deviance. We multiplied this by percent deviance explained in the full final model to approximate proportion of total deviance explained.

2.3.3.3 Validation and Prediction

We set the nymph submission rate to missing for 2012, and used the gam.predict function in conjunction with the final model to output predicted nymph submission rate. We examined the spearman correlation coefficient, Rho (ρ_S) between actual and predicted values for the nymph submission rate and considered correlations strong where $\rho_S \geq 0.7$ (Cohen 1988).

We wanted to predict the joint effect of anticipated climate warming and deer herd management on nymph submission rate. We selected an intermediate climate warming scenario of 1.0°C based on the two warming scenarios (moderate 0.5°C, abrupt 1.7°C) of Birkel and Mayewski (2018). To do this, we established a contemporary baseline ("current" situation), and a scenario with warmer climate, and a scenario with warmer climate and more deer. We established a five-year baseline for all variables (Table 2.1) by averaging across 2008-2012, calling this our "current" situation for the 28 WMDs. We selected a five-year average to represent the current situation because a five-year average for climatology smooths over extremes and is preferable to a shorter span for a baseline (Birkel S., University of Maine Climate Change Institute personal communication 2015). Assuming continued faster winter warming in the northern tier relative to the southern tier (Fig. 2.2), we then added 1.0°C to the "current" seasonal climatology for winter minimum temperature to each WMD for the northern tier and 0.5°C to the southern tier. We also added 100 to the number of degree-days accumulated by the end of August to all northern tier WMDs and 50 to southern tier WMDs. We then tested the effect of warming, plus increases in northern tier deer density to hypotheticals of 10/mi^2 and 15/mi^2. We left deer densities in the southern tier at the contemporary values and set year to arbitrarily to 2018 since we were not predicting a specific year at which the warming would occur. This was to mimic MEIFWs deer density targets in both tiers. We kept values of other predictors in the model constant.

2.4 Results

2.4.1 Summary Statistics and Visualizations

The south-to-north spatial gradient was strong for nearly all variables, with higher nymph submission rates, white-tailed deer densities, warmer climate, along with the time-invariant landscape variables residential development and tick-associated invasive plant sightings characteristic of the southern tier of the state (Table 2.2, Figs. 2.3, 2.4, 2.5). Percent land cover in deciduous and mixed forest cover type varied, but not along a latitudinal gradient (Fig. 2.5b). Consistently higher deer densities can be seen the central WMDs and especially WMD 29, which encompassed the unbridged, off-shore islands, but in the temporal dimension the years 1996 to 2002 marked the period of highest deer densities in the southern tier (Fig. 2.4). Temporal uptrends can be seen for winter, spring, and fall, and degree-day accumulation, particularly in the northern tier (Fig. 2.6a,b,d,e), which appeared to be “squeezing” up towards values in the southern tier. This is consistent with the relatively faster warming in the northern tier depicted in Fig. 1.8 (Chapter 1). The slight downtrend in mean maximum summer temperature was apparent (Fig. 2.6c), which could reflect increased precipitation. Among the moisture variables, uptrends in summer precipitation and relative humidity, could be seen (Fig. 2.6f,g). As the converse of relative humidity, a slight downtrend in vapor pressure deficit could be seen in Fig. 2.6h.

Table 2.2. Summary statistics for variables used in a model of nymphal *I. scapularis* submission rate. There were 28 Wildlife Management Districts (WMDs) used for the summaries (17 in the northern tier, 11 in the southern tier, across 23 years (1990-2013), thus *n* = 644). Significant differences for northern vs.southern tier means are denoted as *** (*P* < 0.001), ** (*P* < 0.01), * (*P* < 0.05), Wilcoxon rank-sum tests.

			Statistic				
Common name	Abbreviation	Tier	mean	SE	min	max	*P*
nymphs	nyrate	Northern	0.8	1.10	0	71.9	
		Southern	14.1	13.25	0	606.8	***
√nymphs	sqrt(nyrate)	Northern	0.2	0.21	0	8.5	
		Southern	2.7	0.79	0	24.6	***
deer/mi^2	deermi2	Northern	4.1	0.74	0	18.2	
		Southern	17.3	1.64	5.4	35.9	***
degree-days/end August	ddgt6endaug	Northern	1185.3	27.44	884.5	1488.4	
		Southern	1382.6	34.15	1085.8	1689.7	***
average winter min temp	DJF_t2min	Northern	-14.1	0.66	-20.2	-6.5	
		Southern	-10.2	0.71	-16.7	-4.7	***
average spring min temp	MAM_t2min	Northern	-2.3	0.42	-6.6	2.7	
		Southern	0.3	0.42	-3.3	4.0	***
average summer max temp	JJA_t2max	Northern	23.5	0.28	20.6	26.2	
		Southern	24.6	0.41	19.8	27.6	***
average fall min temp	SON_t2min	Northern	1.8	0.32	-1.2	5.7	
		Southern	3.9	0.36	1	7.4	***
average summer total precip	JJA_prcp	Northern	10.6	0.71	5.1	20.6	
		Southern	9.7	0.93	4.1	18.6	**
average summer relative humidity	JJA_RH	Northern	65.5	0.68	57.4	75.1	
		Southern	66.5	1.02	59.9	77.2	***
average summer vapor pressure deficit	JJA_VPD	Northern	449.3	8.14	353.8	530.6	
		Southern	485.9	13.34	336.0	575.5	***
% residential development	pctDEVEL	Northern	1.7	0.28	0.1	3.6	
		Southern	8.9	1.91	0.3	26.9	***
% decid or mixed forest	pctDecMix	Northern	45.9	2.67	12.0	64.0	
		Southern	40.1	4.29	0.5	54.3	
invasive plant sightings/ha	INVASIVE	Northern	14.9	10.87	0	180.5	
		Southern	301.9	68.70	0	758.1	***

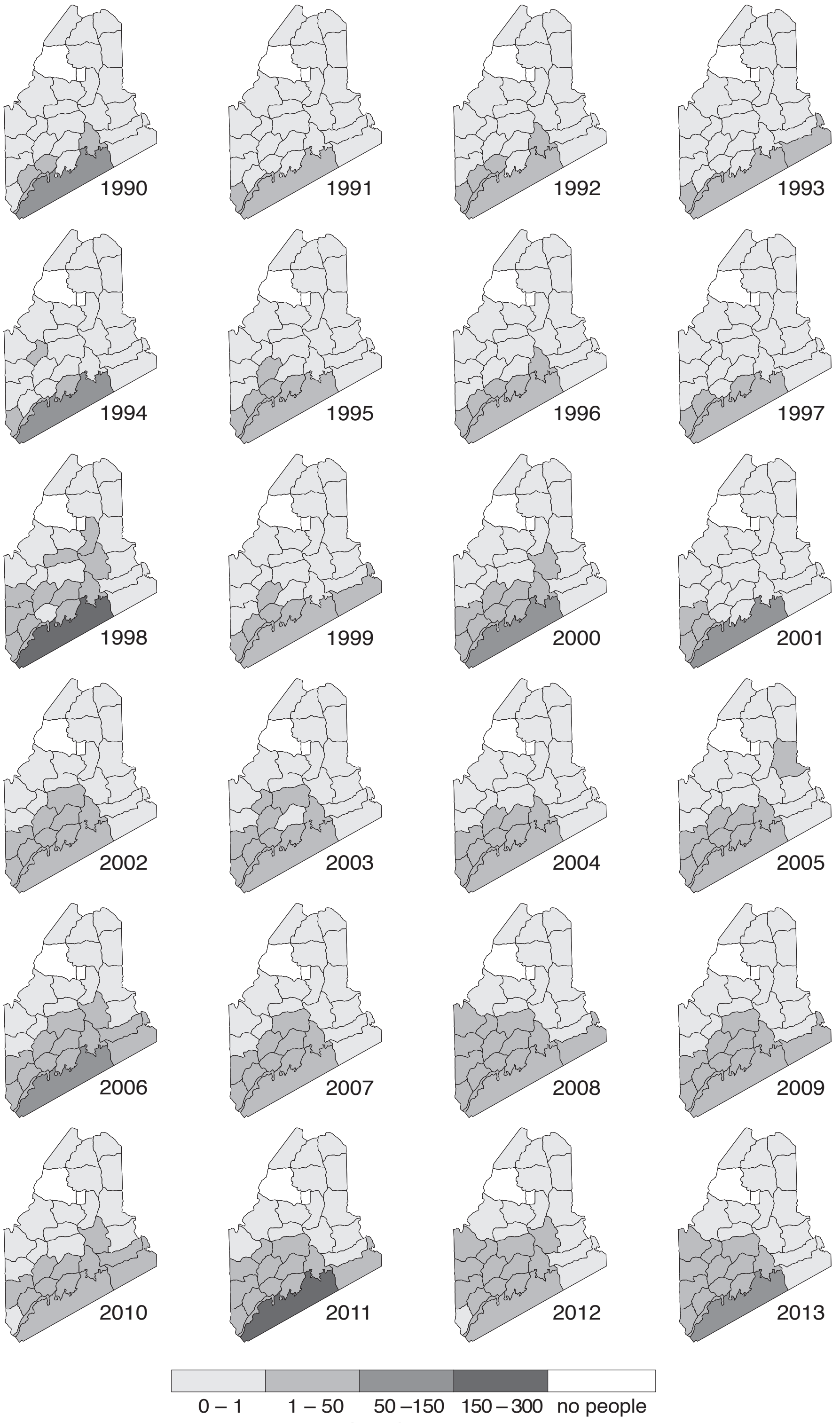

Figure 2.3. Nymphal submission rate for 28 wildlife management districts (WMDs) in Maine, 1990-2013. Two WMDs had no human population.

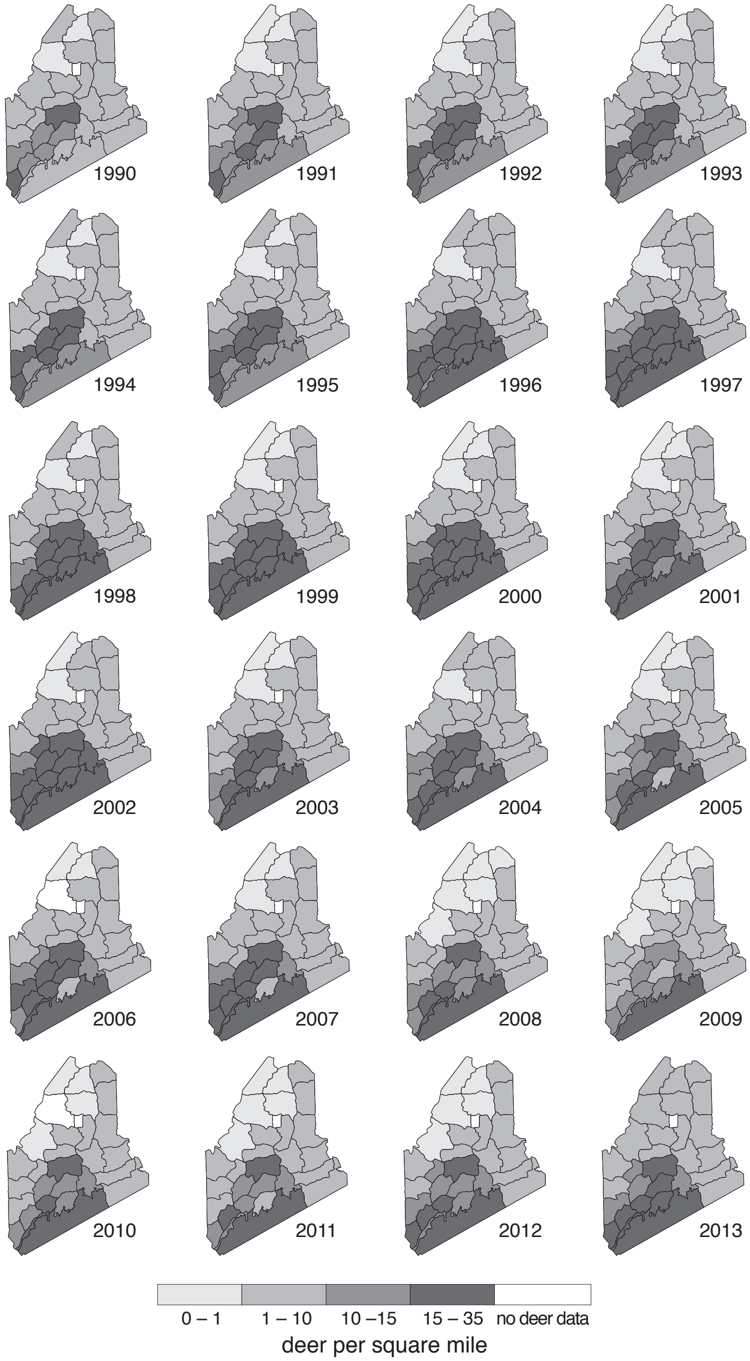

Figure 2.4. Estimated white-tailed deer per square mile in 29 (in some years 28) wildlife management districts (WMDs) in Maine, 1990-2013. WMDs in gray indicate no data.

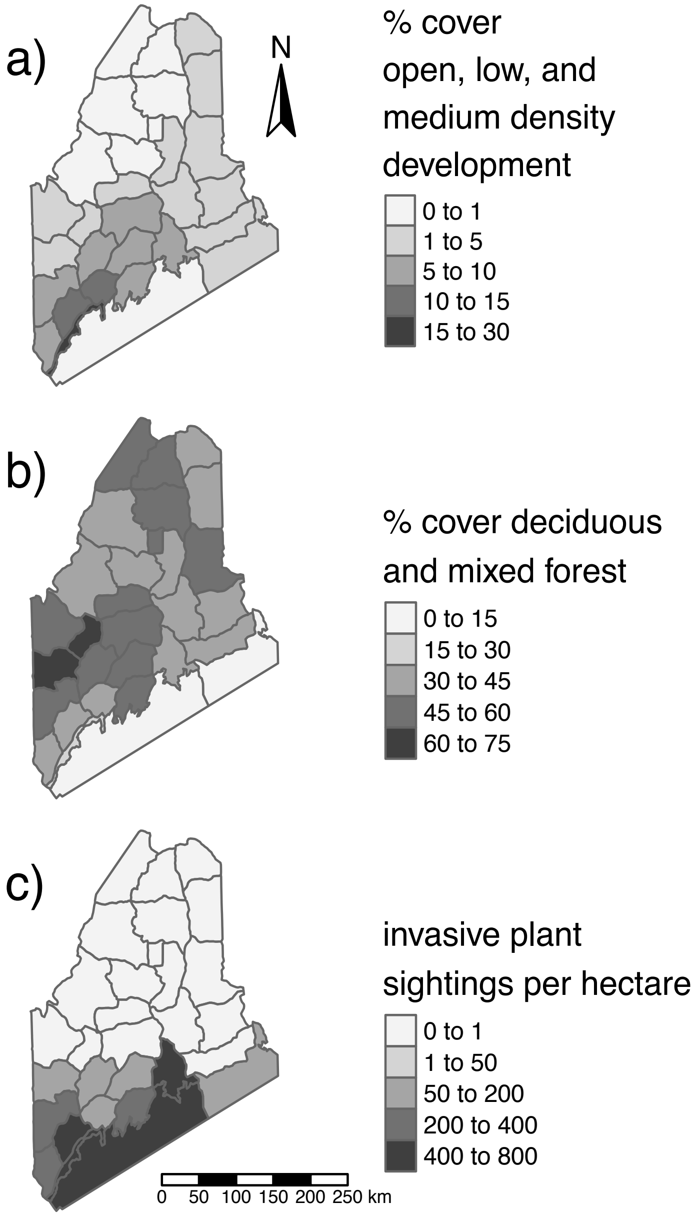

Figure 2.5. Landscape characteristics in 30 wildlife management districts in Maine. Characteristics were taken from the National Landcover Database, 2011 (a, b), and from Maine's *i*MapInvasive program, 2018 (c).

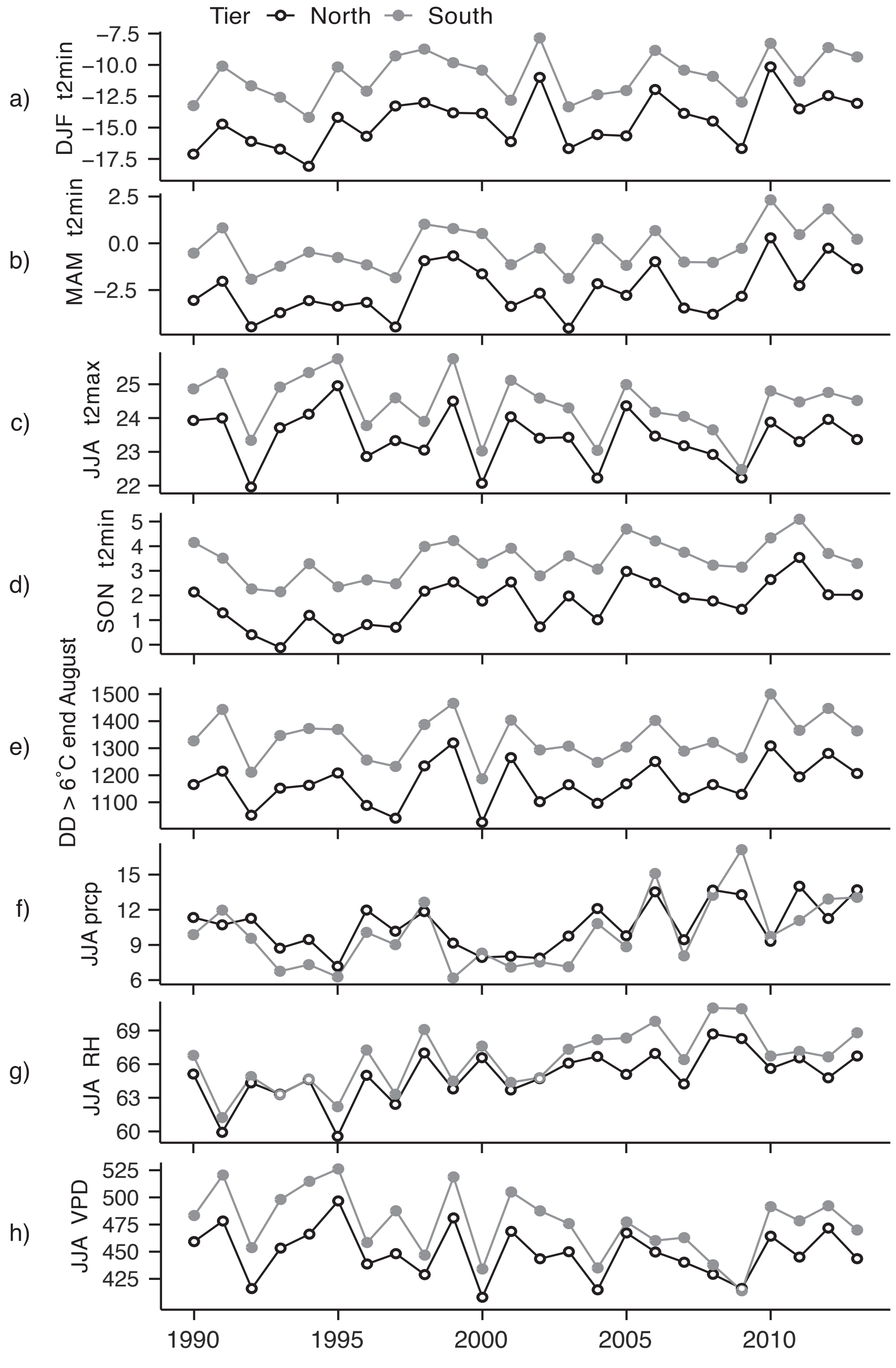

Figure 2.6. Annual average seasonal climatologies in Maine's northern and southern tiers, 1990-2013. Plots are (a) winter minimum temperature, (b) spring minimum temperature, (c) summer maximum temperature, (d) fall minimum temperature, (e) degree-day accumulation by the end of August, (f) summer precipitation, (g) summer relative humidity, and (h) summer vapor pressure deficit.

2.4.2 Nymphal *I. scapularis* Model

Nymphal *I. scapularis* submission rate was best predicted by summer relative humidity and nonlinear smooths of deer density at a 2-year lag, degree-day accumulation >6°C by the end of August at a one 1-year lag, and average winter minimum temperature (Table 2.3). In addition, the model contained a temporal correlation structure arising from repeated measurements (Table 2.3). In a manner analogous to generalized linear modeling, where main effects are conditional on the higher-order interaction, we left the lower order effect (year) in the model as a smooth main effect. Deviance explained = 74% and R^2 = 0.72 (Table 2.3). Variables not included were concurve with and less predictive than variables remaining in the model including the three candidate random spatial autocorrelation structures (Table 2.4). *I. scapularis* were associated percent residential development and invasive plant sightings per hectare, but were concurve with deer and thus not included.

The selected model maximized ecological explanatory value. Although it performed third best in terms of AIC and second best in terms of deviance explained (Table 2.3), it did not suffer concurvity issues as did the models with spatial random effect structures (Table 2.4). Approximate proportion of total deviance explained by each variable was deer 30%, degree-day accumulation 2%, average winter minimum temperature 9%, summer relative humidity contributing 14% (thus 25% explained by climatology), and time–accounting for varying time trends in wildlife management districts–19%.

Table 2.3. Generalized additive mixed models (GAMs) of nymphal *I. scapularis* submission rate as a function of explanatory variables and random time and/or spatial effects, Maine, 1992-2013. Using the two-year lag of deer density removed 1990 and 1991 from the model (experimental unit n = 616 given 28 Maine wildlife management districts and 22 years). Significance of terms is denoted by ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

			Random effect (variance component) type			
Model component	intercept only	no random effects	Temporal only[a]	Spatial only[b]	Additive temporal, spatial[c]	Interacting temporal, spatial[d]
Parametric terms: coefficient (SE)						
Intercept	0.23 (0.07)	-10.42 (1.22)***	-11.64 (1.18)***	-7.14 (1.50)***	-8.30 (1.36)***	-9.46 (1.28)***
JJA_RH		0.14 (0.02)***	0.16 (0.02)***	0.09 (0.02)***	0.11 (0.02)***	0.12 (0.02)***
Smooth terms: estimated df (reference df)[e]						
s(deerlag2)		3.79***	3.76***	1.00	3.65***	3.71***
s(ddlag1)		1.00*	1.28**	1.00**	1.00***	1.14*
s(DJF_t2min)		2.34***	1.77***	1.98*	1.43**	1.00***
s(year)		1.00	1.00	2.33*	1.45*	
ti(year,id)			32.43***		30.17***	
s(id)				20.97***	13.94***	
te(year,id)						10.73***
Fit Measures						
AIC	1944.0	1458.86	1433.32	1434.24	1409.16	1420.07
Deviance	1869.0	581.62	442.06	482.35	379.26	491.23
Deviance explained	0	0.67	0.75	0.72	0.78	0.72
Dispersion	3.1	1.38	1.18	1.22	1.05	1.22
R^2	0	0.59	0.69	0.67	0.78	0.67
acf	0.75	0.28	0.12	0.21	0.03	0.17
Num. obs.	616	616	616	616	616	616
Num. smooth terms	0	4	5	5	6	4

[a] temporal autocorrelation arising from repeated measures on areal units ("factor" smooth); no spatial structure

[b] global (time-invariant) Markov random field "mrf" smooth for spatial autocorrelation among spatial units

[c] temporal autocorrelation arising from repeated measures on areal units plus a global mrf smooth

[d] temporal autocorrelation arising from repeated measures on areal units with spatial autocorrelation (mrf) allowed to vary by year a global "mrf" smooth (same for all WMDs across years)

[e] Estimated df (EDF) are the estimated number of parameters representing the smooth; approximate significance tests for the smooths are Wald tests of EDF = 0 (i.e., the smooth is null/a flat line)

Table 2.4. Matrix of concurvity scores from generalized additive mixed models (GAMMs) of nymphal *I. scapularis* submissions rate as smooth functions of explanatory variables and random time and/or spatial effects, Maine, 1992-2013. Experimental unit n = 616 given 28 wildlife management districts and 22 years. Concurvity scores among explanatory variables were the same regardless of random effect structure.

Type of smooth effect	Model component	Model term	s(year)	s(deerlag2)	s(ddlag1)	s(JJA_t2max)	s(MAM_t2min)	s(DJF_t2min)	s(JJA_prcp)	s(JJA_RH)	s(JJA_VPD)	s(pctDEVEL)	s(pctDecMix)	s(INVASIVES)
Main effect	Explanatory variable	para												
		s(year)	1.00											
		s(deerlag2)	0.03	1.00										
		s(ddlag1)	0.02	0.22	1.00									
		s(JJA_t2max)	0.04	0.13	0.21	1.00								
		s(MAM_t2min)	0.10	0.22	0.29	0.10	1.00							
		s(DJF_t2min)	0.05	0.20	0.26	0.10	**0.58**	1.00						
		s(JJA_prcp)	0.18	0.05	0.05	0.16	0.08	0.09	1.00					
		s(JJA_RH)	0.21	0.04	0.03	0.26	0.13	0.11	0.21	1.00				
		s(JJA_VPD)	0.05	0.14	0.20	**0.87**	0.15	0.11	0.18	**0.39**	1.00			
		s(pctDEVEL)	0.00	**0.48**	0.41	0.26	0.29	0.26	0.04	0.03	0.25	1.00		
		s(pctDecMix)	0.00	0.19	0.12	0.21	0.18	0.24	0.05	0.24	0.20	**0.86**	1.00	
		s(INVASIVES)	0.00	**0.46**	**0.36**	**0.33**	**0.37**	**0.42**	0.05	0.25	**0.33**	**0.96**	**0.83**	1.00
Random effect aka correlation structure	Temporal only[a]													
		ti(year,id)	**0.96**	0.21	0.05	0.07	0.17	0.11	0.28	0.28	0.12	0.00	0.00	0.00
	Spatial only[b]													
		s(id)	0.00	**0.71**	**0.56**	**0.50**	**0.50**	**0.54**	0.12	0.29	**0.44**	**1.00**	**1.00**	**1.00**
	Additive temporal, spatial[c]													
		ti(year,id)	**0.94**	0.21	0.05	0.06	0.17	0.11	0.27	0.28	0.12	0.00	0.00	0.00
		s(id)	0.00	**0.71**	**0.56**	**0.50**	**0.50**	**0.54**	0.12	**0.29**	**0.44**	**1.00**	**1.00**	**1.00**
	Interacting temporal, spatial[d]													
		te(year,id)		**0.50**	**0.36**	0.19	**0.60**	**0.57**	**0.37**	**0.34**	0.24	**0.38**	**0.35**	**0.43**

[a] temporal autocorrelation arising from repeated measures on areal units ("factor" smooth); no spatial structure

[b] global (time-invariant) Markov random field "mrf" smooth for spatial autocorrelation among spatial units

[c] temporal autocorrelation arising from repeated measures on areal units plus a global mrf smooth

[d] temporal autocorrelation arising from repeated measures on areal units with spatial autocorrelation (mrf) allowed to vary by year

Patterns in the residuals indicated reasonable fit (Wood 2017). The Q-Q (quantile-quantile) plot (Fig. 2.7a) shows deviance residuals lying close to the straight line which represents deviance residuals of the theoretical distribution; this indicated the Tweedie distribution was a reasonable choice of response distribution. A handful of outliers (Fig. 2.7a, top right corner) coincided with various WMAs with higher-than-expected predictions of nymph submission rate but there was no basis to exclude them. In the residuals versus linear predictor plot (Fig. 2.7b) the smooth line of residuals in the lower left of the plot was caused by response values of zero and expected when response values contain a mixture of zeros and positive values (Wood 2017). The pattern above the smooth line suggested, apart from outliers at the top of the plot, that variance was approximately constant as the mean increased (Fig. 2.7b). The histogram of residuals (Fig. 2.7c) approached normality though a long right tail represented the outliers. The plot of response against fitted values (Fig. 2.7d) showed a positive linear relationship albeit with scatter and outliers (upper right). Compared to the intercept-only and main effects models, the low acf score and patterns in the residuals were a substantial improvement (Table 2.3, Fig. 2.8a-c). Spatial data may be over dispersed ($\boldsymbol{\sigma}^2/\boldsymbol{\mu} \gg 5$) but dispersion in the chosen model was well under 5 and in the neighborhood of 1 ($\boldsymbol{\sigma}^2/\boldsymbol{\mu}$ =1.18, Table 2.3) as recommended by Zar (2010). In the model validation, correlation between the actual and predicted values for nymph submission rate in arbitrarily selected 2012 was strong (Spearman $\rho = 0.72$).

Consistent with our first hypothesis, there was a positive relationship between *I. scapularis* nymphs and deer up to a threshold deer density, which we visually assessed as 13 deer/mi^2 (Fig. 2.9a). Using second derivatives along the smooth we confirmed with 95%

confidence (Simpson 2014) that the rate of change in nymph submission rate was non-zero where ≤13 deer/mi^2 and zero where >13 deer/mi^2. Response variables in GAMs are zero-mean centered on the y-axis and a smooth plot is read as the relationship between the response and the covariate of interest while keeping other covariates at constant at their means. In Fig. 2.9a horizontal line drawn from 0 on the yaxis intersected the curve at the point corresponding with ~6 deer/mi^2 on the x-axis, indicating nymph submission rate was below average where deer density was <~6/mi^2.

Our second and third hypotheses were that nymphal *I. scapularis* would be a nonlinear function of degree-day accumulation with a threshold in the vicinity of 1,240 degree-days >6°C, and a threshold in the vicinity of -18°C to -11°C. The nonlinear increasing functions showed no thresholds per se, but nymphal submission rate was above average where at least ~1,320 degree-days >6°C had accumulated by the end of the previous August (Fig. 2.9b), and where average winter low temperatures were above about -13°C (Fig. 2.9c).

Consistent with our fourth hypothesis, there was a positive (linear) relationship between nymphs and mean summer relative humidity (Table 2.3). The model predicted a one unit increase in average summer relative humidity would result in a 2% increase in nymph submission rate (obtained by back-transforming the coefficient; $0.16^2 = 0.02$).

Also consistent with our expectations was a global trend of increasing nymphal *I. scapularis* over the years (Fig. 2.9d). The global time trend was essentially linear and slightly increasing, though the smooths of nymphal *I. scapularis* year for individual wildlife management districts differed substantially. Generally the smooths of nymphs over time increased in the northern tier wildlife management districts and decreased in the southern tier wildlife management districts. Therefore, while the random smooths of year helped explained temporal variation in nymphal submissions rate, the statistical relationships between nymphal *I. scapularis* and the deer and climatology predictors ran strongly in the spatial dimension.

Three-dimensional plots (Fig. 2.10a,b) of the final nymphal tick GAM illustrate the additive effects of two covariates on the response (Wood 2017). We constrained prediction surfaces not to extend beyond 10% of the data to avoid prediction where data were sparse or in covariate spaces that were unrealistic (e.g., we did not have high deer densities in the cold, northern WMDs), resulting in the plots' jagged appearance. Higher nymph submission rate was associated with warmer winters and degree-day accumulation (positive rather than flat trend line seen) but only where ~≥4 deer/mi^2. The threshold at ~1,320 DD in the univariate smooth plot (Fig. 2.9c) is seen also in the 3D plot but only where ~≥5 deer/mi^2 (Fig. 2.10b).

Fig. 2.11a is a map of the five-year average, current (as close to current as allowed by the data, 2008-2012) distribution of nymph submission rate. Fig. 2.11b shows the predicted effect of climate warming only. Fig. 2.11c shows the predicted effect of warming and deer management to 10/mi^2 in the northern tier.

In the warming scenario, predicted nymph submission rate increased 1.4-fold (2.0 to 2.7) in the northern tier and 1.3-fold (15.0 to 19.9) in the southern tier. On top of the warming scenario, increasing northern tier deer density from the current five-year average of 3.6 to 10 deer/mi^2 increased nymph submission rate five-fold (2.0 to 10.0) and increasing deer to and 15 deer/mi^2 increased submission rate eleven-fold (2.0 to 22.0). Meanwhile southern tier tick submissions rate stabilized at 20. Thus, under the scenario of warming and deer managed to 15 deer/mi^2 in the northern tier, nymphal abundance in the northern tier caught up with that of the southern tier. This was consistent with the leveling-off pattern seen in southern tier *I. scapularis* in Chapter 1 (Figs.1.11b, 1.13a). However, confidence in these predictions was better for the 10/mi^2 scenario than the 15/mi^2 scenario on the basis of a narrower bivariate confidence intervals where deer density <13/mi^2 (Fig. 2.12).

In summary, *I. scapularis* nymph submission rate was statistically associated in the temporal dimension with year, and in the spatial dimension linearly with increasing summer humidity, and nonlinearly with deer densities up to ~13 deer/mi^2, increasing degree-day accumulation, and warmer winters.

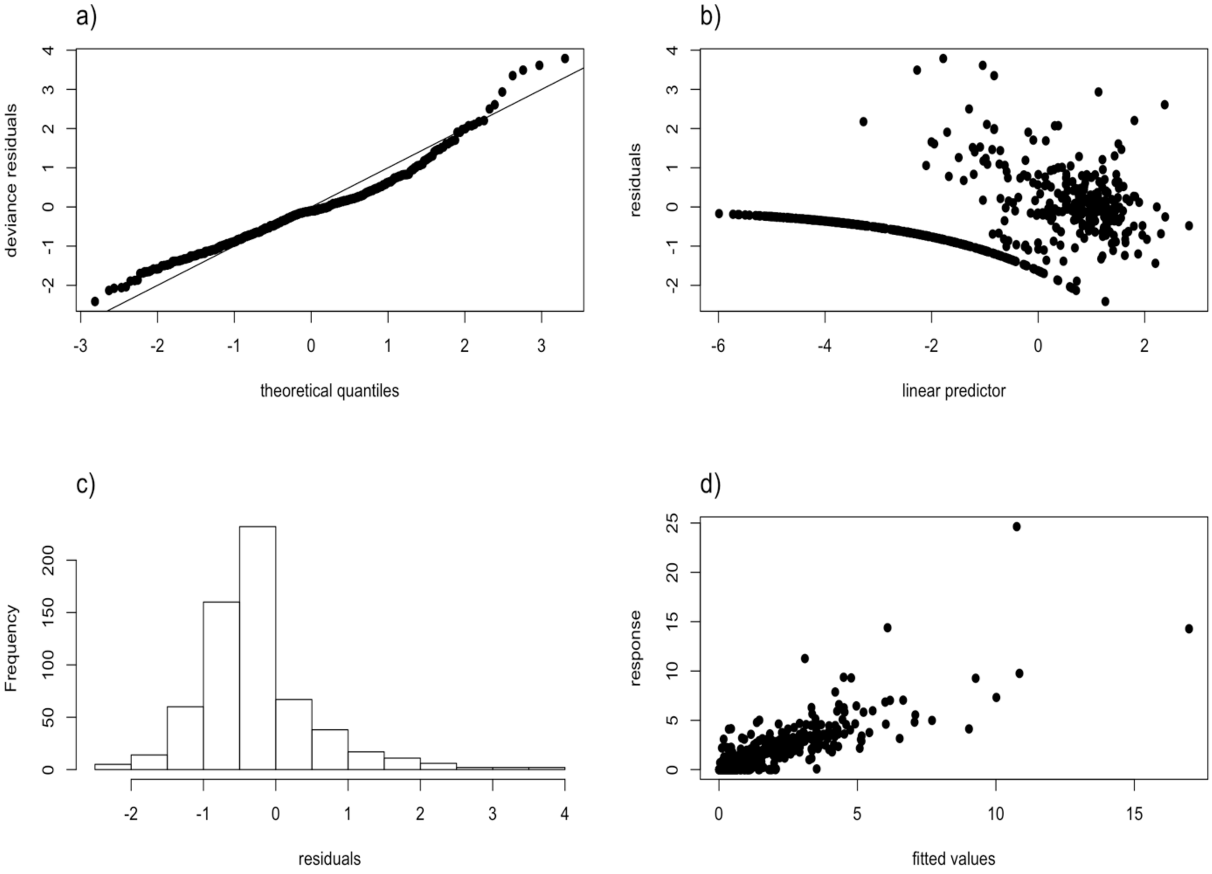

Figure 2.7. Fit diagnostics for the model of nymphal *I. scapularis* submission rate. Plots are (a) a Q-Q (quantile-quantile), (b) residuals vs. linear predictor (c) histogram of residuals and (d) response against fitted values.

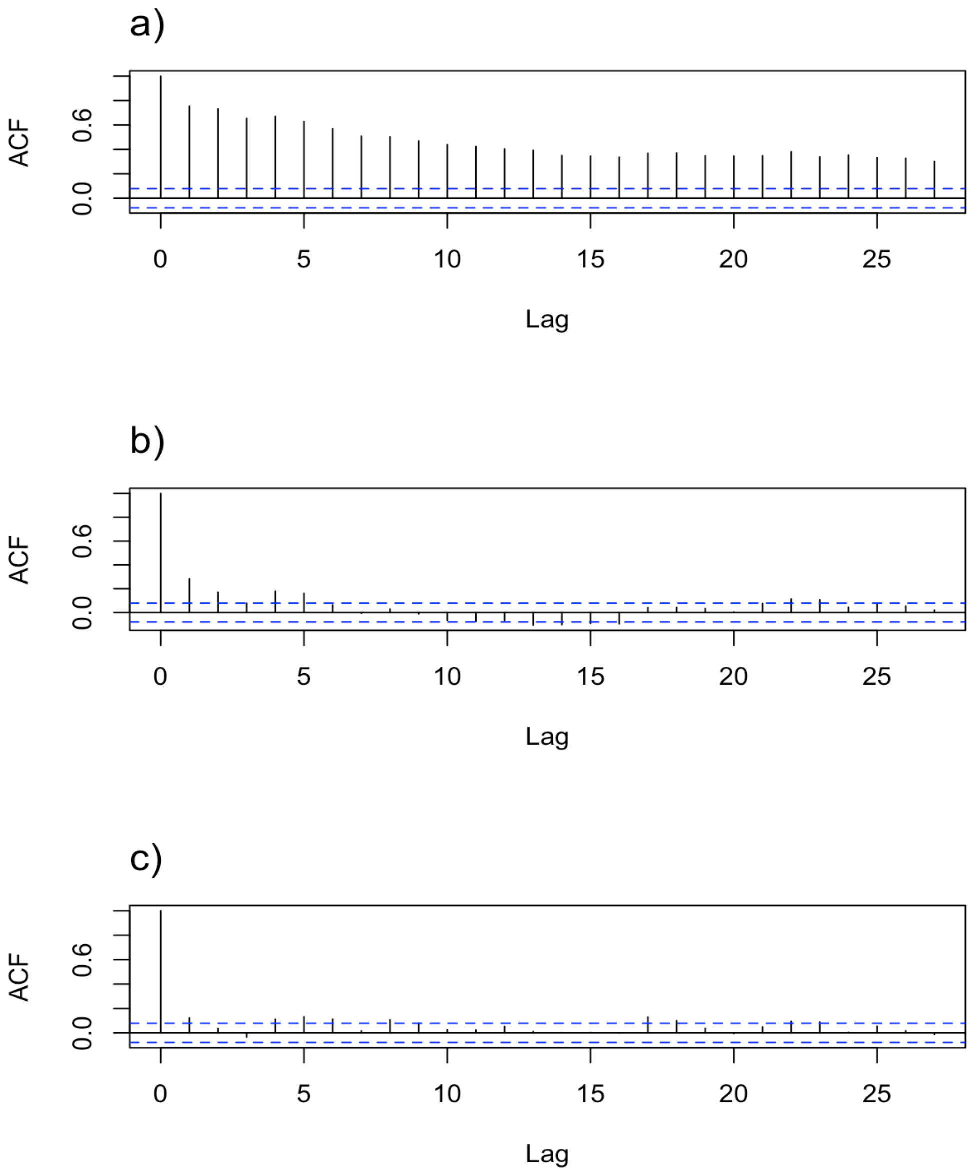

Figure 2.8. Autocorrelation function plots for GAM models of nymphal *I. scapularis* submission rate. Plot (a) is an intercept-only model, plot (b) a model with main effects only (no random effects), and plot (c) the final model with main effects and a temporal random effect.

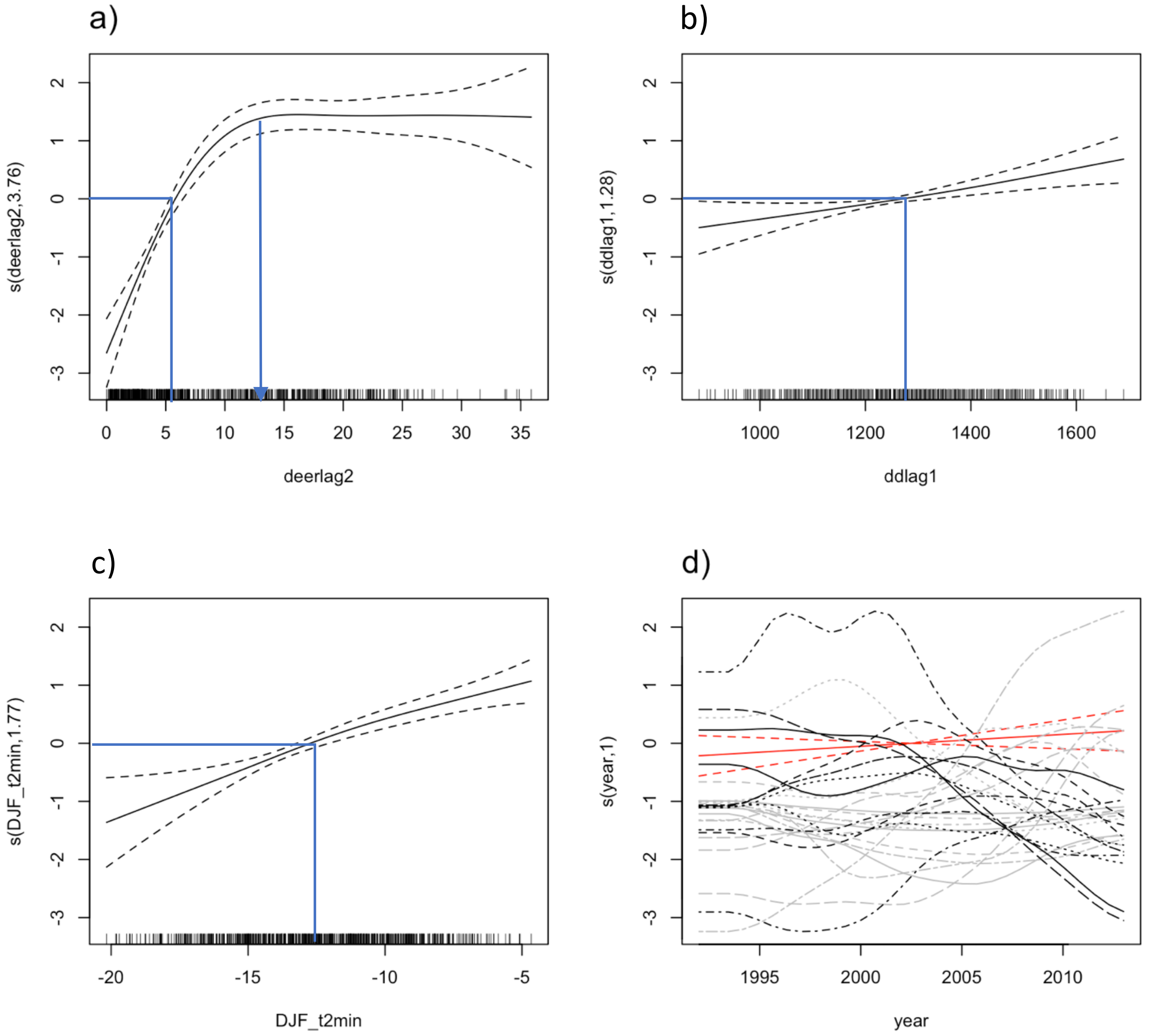

Figure 2.9. Two-dimensional smooth plots allowing univariate visualization of effects of deer and climate on nymphal *I. scapularis* submission rate. In plot (a) nymphs were above average where deer >7/mi and exhibited a response to deer between 0 and ~13 deer/mi, but not above the threshold of ~13 deer/mi; in (b) nymphs were above average where annual degree-day accumulation >6°C by the end of August was over ~1,300; in (c) nymphs were above average where mean winter minimum temperature >~-13°C; and in (d) there was a global upward trend (red lines) but nymphal abundance varied by wildlife management district (southern tier with black lines, northern tier in gray lines).

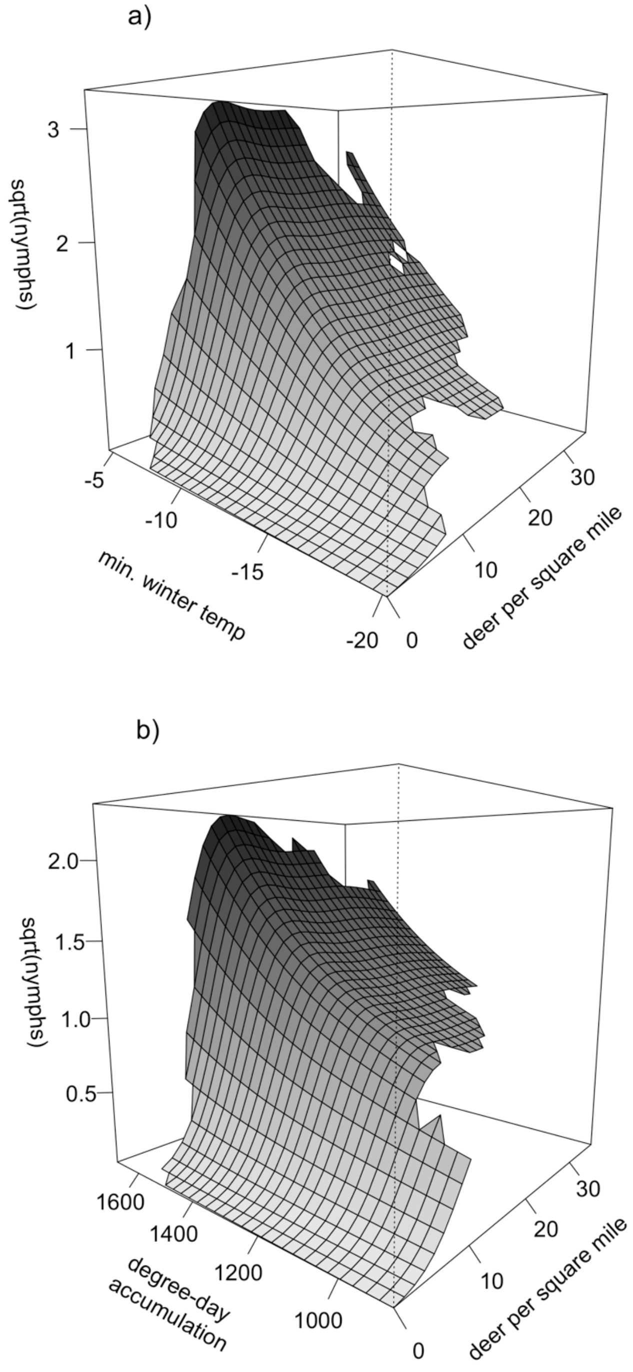

Figure 2.10. Three-dimensional contour plots allowing visualization of pairwise additive effects of explanatory variables on nymphal *I. scapularis* submission rate. Plot (a) shows the joint effect of average minimum winter temperature and deer density, and plot (b) shows the joint effect of degree-day accumulation and deer density.

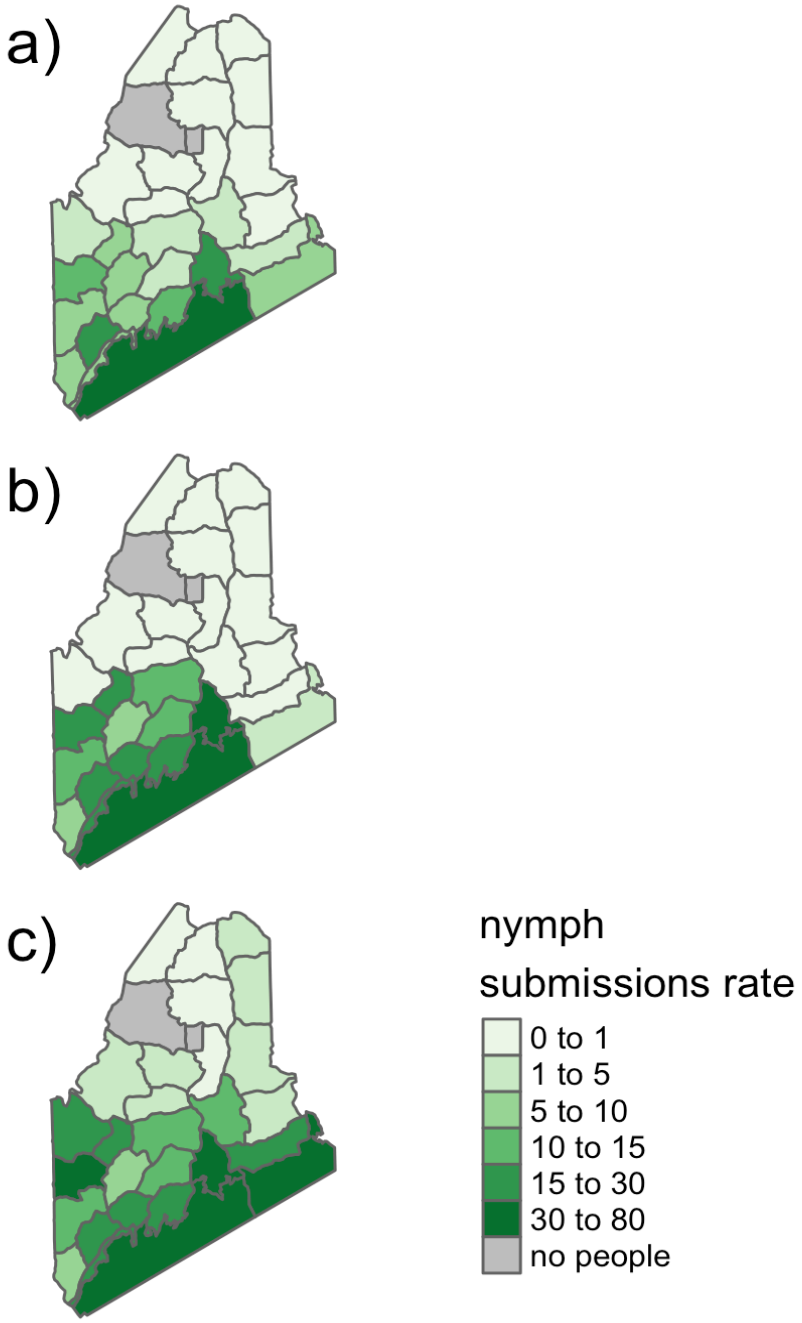

Figure 2.11. Current and predicted nymphal *I. scapularis* submission rate by wildlife management district, Maine. Map (a) is the current five-year average (2008-2012), (b) represents average minimum winter temperatures warmer by 1°C, and map (c) assumed winters warmer by 1°C and white-tailed deer are managed from current <5/mi to 10/mi in the northern tier districts. Two WMDs in northern Maine are blank because there is no human population to submit ticks.

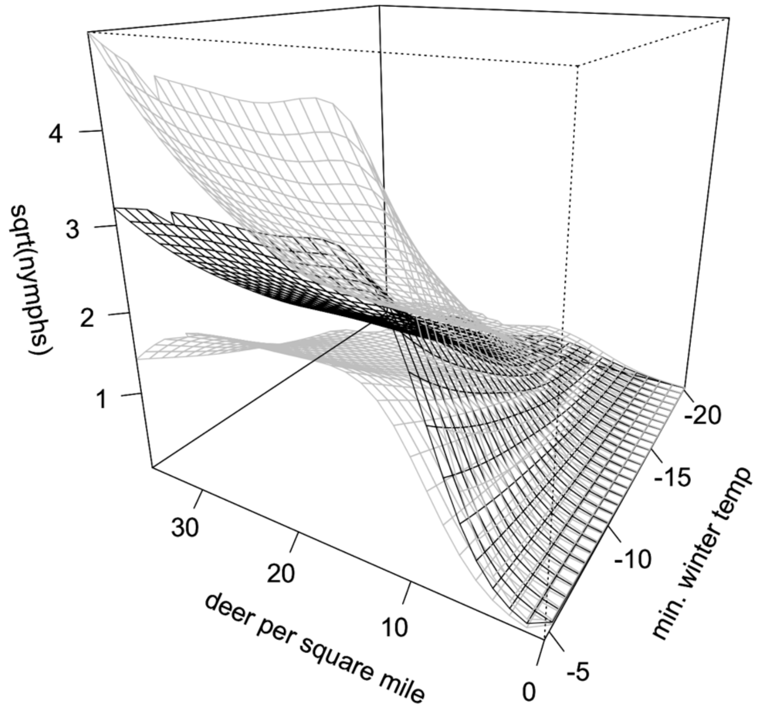

Figure 2.12. Three-dimensional contour plot showing the joint effect of average minimum winter temperature and deer density on nymph submission rate. The upper and lower 80% confidence limits widen at deer densities >13/mi.

2.5 Discussion

We used a passive tick surveillance dataset to index abundance of *I. scapularis* nymphs within Maine's wildlife management districts, 1990-2013, and a generalized additive mixed model to characterize statistical relationships between nymphal *I. scapularis* submissions rate and white-tailed deer, climatological, and landscape predictors. The model covered the extent of Maine, with Maine's 29 wildlife management districts as the experimental unit.

I. scapularis nymphal abundance was a nearly linear function of deer densities when densities ranged from 0 to ~13 deer/mi^2 whereas above 13 deer/mi^2 there was no relationship between nymphs and deer. This was consistent with the idea of a saturating relationship between *I. scapularis* and deer density (Kilpatrick et al. 2017). The findings of 13 deer/mi^2 threshold and below-average nymphal submission rates at <6 deer/mi^2 were consistent with empirical studies that suggested to lower *I. scapularis* abundance and hence Lyme disease, density of white-tailed deer should be lowered to below a threshold somewhere in the range of 8-13/mi^2 (Telford 1993, Telford 2002, Stafford et al. 2003, Stafford 2007, Kilpatrick et al. 2014). We emphasize that this study did not test the effect of lowering (or raising) deer density over time, but rather characterized a statistical association between nymphs and deer that was driven mainly by the south-to-north spatial gradient in deer density, in the presence of only moderate temporal changes in deer density in the southern tier (Chapter 1).

Our approach allowed us to consider the relationship between tick density and low-to-moderate deer density while accounting for effects of cold on *I. scapularis* abundance. The generalized additive model indicated that warmer winters and earlier degree-day accumulation conferred a slight increase in *I. scapularis* only where there were ~≥4-5 deer/mi^2 and maximum effect where deer densities ≥10 deer/mi2 (Fig. 2.10). As suggested in Chapter 1, low deer densities in the northern tier may have served as a check on gains in survival advantage conferred by climate change.

Our finding that nymph submission rate was above average where average winter low temperatures were above approximately -13°C was consistent with studies of cold hardiness, which showed increased lethality for *I. scapularis* below -18°C for nymphs (Burks et al. 1996, VanDyk et al. 1996, Brunner et al. 2012). Even though ambient temperatures are harsher than those under leaf litter and snow where *I. scapularis* would sequester during cold waves, we think -13°C is proxy to conditions that challenge *I. scapularis* at the cold end of their climate suitability envelope. Our finding that nymph submission rate was above average where at least ~1,320 degree-days >6°C had accumulated by the end of August was quite close to the average of 1,240 days to eclosion (SD 143.3, range 1,029 - 1,532) reported by Rand et al. (2004a) and confirms the importance of degree-day accumulation for larval eclosion. In the northern tier, in only 6 of the last 28 years >1,240 degree-days have been attained by the end of August (Chapter 1), indicating climate in the northern tier was still marginal for completion of the life cycle of *I. scapularis*, at least through the duration of the study (1990-2013).

Despite temporal uptrends in minimum winter temperature, degree-day accumulation and relative humidity in Maine, temporal variation in *I. scapularis* was best modeled through smooths of individual wildlife management districts over time. Temporal increases in *I. scapularis* were seen for the most part only in the northern districts, possibly representative of biological invaders moving into suitable (or marginally suitable) but unoccupied habitat.

In the northern tier, *I. scapularis* abundance was predicted to increase 1.2-fold given 1°C warming versus 5-fold given 1°C warming, deer managed to 10/mi^2 from the current ~5/mi^2. Due to uncertainties in the model this prediction should be construed qualitatively as "higher deer densities in the northern tier will likely result in more abundant *I. scapularis* than if we were subject to climate change alone."

2.5.1 Limitations of the Study

With regard to explanatory variables that did not enter the model, we note that lack of inclusion does not infer lack of importance. For example, longer, warmer falls in Maine were correlated with extension of *I. scapularis*' questing season later into fall (Chapter 1). Spring and fall minimum temperature did not enter the model, but warmer springs and falls co-occur with warmer, shorter winters, and greater tick abundance is associated with lengthening questing seasons (Chapter 1). Also, insignificance of forest cover type in the model reflected the fact that there is substantial forest cover in the northern tier of Maine that is deciduous or mixed. Suburbanization and presence of tick-associated invasive plants did not enter the models because they were concurve with deer, i.e., they co-occured with deer at the spatial scale used, but at the scale of the forest stand or old field the presence of tick-associated invasive plants are a key determinant of tick host abundance, tick abundance, and *B. burgdorfer*i infection prevalence (Williams and Ward 2010). We think that the scale selected for this analysis was appropriate for deer and climate, but a multi-scale model might capture more tick-associated variables. Also, model validation could be improved by testing the model against an independent passive tick surveillance dataset.

One might argue that any model of *I. scapularis* abundance is incomplete without information on the full suite of blood meal hosts, including passerine birds, as they are long-distance dispersers of ticks (Smith et al. 1996, Rand et al. 1998, Ogden et al. 2005, Ogden et al. 2006a,b, Ogden et al. 2008b, Clow et al. 2017, Leighton et al. 2012), and white-footed mice, as they are the most common rodent hosts of subadult *I. scapularis* and also highly reservoir competent for *B. burgdorferi* (e.g., Mather et al. 1989, Brunner et al. 2008). However, long-term datasets in Maine (2+ decades) are restricted to just two sites for birds (Rand et al. 1998, Elias et al. 2011) and two for small mammals (Rand et al. 1998, Elias et al. 2004, Wang et al. 2009, Ogawa et al. 2017). Still we know the white-footed mouse has a broad North American distribution (19-49°N 64-112°W, Wang et al. 2009, Bedford and Hoekstra 2015) including

Maine. The deer mouse (*P. maniculatus*) ranges farther north than but overlaps with the white-footed mouse in Maine, and is similar in terms of *I. scapularis* burdens, and *B. burgdorferi* reservoir competence (Rand et al. 1993, Garman et al. 1994, Oliver et al. 2006, Roy-Dufresne et al. 2013). The ubiquity of Peromyscus and other rodent hosts suggests small mammal blood meals are not a limiting factor in either the intact forest or peridomestic environments. In any case, adult *I. scapularis* do not feed on small mammals or birds, again highlighting the role of deer.

We thought that not including moose in the model could be problematic, but moose densities in Maine range from 0.2-0.6/mi^2 in the southern tier to 1.0-1.7/mi2 in the northern tier (Wattles and DeStefano 2011), much lower than even the lowest deer densities in the northern WMDs. Also, while infestation of moose by winter ticks (*Dermacentor albipictus*) is an area of active research (e.g. Jones et al. 2018), in a literature search we could find no reports on *I. scapularis* burdens on moose in North America.

Snow is a ground insulator that may promote I. *scapularis* survival, and Huntington et al. (2004) found that the ratio of snow to rain in northern New England has been declining in the months of December and March. Linske et al. (2019) found that snow cover may promote survival of *I. scapularis* during extreme cold, but due to variation in accumulation and duration, snow cover was an inconsistent insulator compared to leaf litter. Since deciduous and mixed deciduous-coniferous forests are core forest habitat for *I. scapularis* (Eisen et al. 2016), leaf litter may have a greater long-term, latent effect on emergence of *I. scapularis* than snow. Snow was not part of the PRISM gridded monthly dataset we used, but models that take timing of snowfall and snow depth into account would be an improvement.

Ecologists are motivated to capture meaningful spatial relationships while avoiding pseudo-replication (Hurlbert 1984), yet as Hodges and Reich (2010) warned "adding spatially correlated errors can mess up the fixed effect you love". Consistent with Wood (2017), we found high concurvity between the spatial random effect (the Markov random field) and spatial explanatory variables because they were at the same scale and so dropped the spatial random effect. The R package ngspatial (Hughes 2014), alleviates spatial confounding, so that a random spatial effect will account only for spatial variation not already explained by a covariate. We would like to have tried this, but ngspatial (at the time of this writing) did not allow a Tweedie response or the spatio-temporal covariance structures that mgcv gam did. Doubtless these issues will be resolved with development and refinements to modeling packages.

Notwithstanding limitations of the study, we think that the model's alignment with known relationships from the literature impart credibility to the findings.

2.6 Conclusions

In Lyme-endemic areas it is fair to ask whether we are promoting a healthy or pathogenic landscape (Lambin et al. 2010) through our land use policies and practices. The invasion of *I. scapularis* northward in Maine is partly a consequence of climate change and we may be able to mitigate this to some degree through balanced deer herd management. The Maine Department of Inland Fisheries and Wildlife northern tier goals for 2030 range from 10-15/mi^2 and southern tier goals from 15-20/mi^2 (MEIFW 2017). If the gist of this study is correct, in the northern tier of Maine there may be a unique opportunity to mitigate increases in *I. scapularis* due to climate change by keeping deer densities ≤10/mi^2.

A recommendation to lower deer densities to ≤10/mi^2 in the southern tier might not be reasonable given expectations for hunting opportunities, lands posted against hunting, and firearms bans in some towns, but we do suggest a goal of ≤15/mi^2 for the southern tier. Even if 15/mi^2 versus 20/mi^2 had no discernable effect on tick abundance and Lyme incidence, reduction of vehicle collisions, damage to landscaping, crops, and forests, and improved deer health (MEIFW 2017) would be beneficial.

The recommendation to cull deer has been met with the argument that even if deer reduction could measurably lower entomological risk, reduction to 8-13 deer/mi^2 is socially infeasible in most places, and logistically feasible only on islands and peninsulas (Jordan et al. 2007, Levi et al. 2015, Kugeler et al. 2016). However, as Telford (2017) has recommended, deer reduction as a tool should not be discarded wholesale because there are communities that may be in a position—culturally and geographically—to implement deer reduction. We can employ a number of other strategies to reduce ticks as well, such as mechanical reduction of tick habitat. Miller and McGill (2019) attributed moderate to severe tree regeneration debt in the southern and central, mid-Atlantic, and south regions of eastern US forests, to invasive plants and deer overabundance, and land use. Integrated tick management including deer and tick-associated invasive plant management will help prevent this future for Maine.

Other tick and tick-borne pathogen control strategies include acaricide application to tick habitat or tick hosts (e.g., Eisen and Dolan 2016, White and Gaff 2018), and host vaccination (Richer et al. 2014) and genetic modification (Eaves 2018). A human Lyme vaccine (Comstedt et al. 2017) should be available within several years, and anti-tick vaccines are in development. Even with some or all of these strategies in place, there is still no downside to managing the deer herd to a healthy level.

CHAPTER 3.

VIEWS ON LYME DISEASE AND DEER REDUCTION FROM THE OFFSHORE, UNBRIDGED ISLANDS OF MAINE, USA

3.1 Abstract

Lyme disease is caused by the bacterial spirochete *Borrelia burgdorferi*, which is transmitted through the bite of an infected blacklegged tick (*Ixodes scapularis*). Maine, USA, is a high Lyme disease incidence state, with rising incidence of Lyme and other tick-borne illnesses associated with a history of increasing *I. scapularis* abundance, including range expansion to the north. Lyme incidences on the 15 off-shore, unbridged islands of Maine are above the statewide average and at least on par with those seen on other offshore islands in Massachusetts and Rhode Island. Increasing *I. scapularis* abundance and Lyme incidence have been attributed to high deer densities by some residents of these island communities. Burgeoning deer densities on some of these islands have led to various deer management histories along with a good deal of conflict on how to manage deer populations. We summarized the burden of Lyme disease, entomological risk, and deer management histories on these islands. We also polled island residents in 2016 to quantify the level of concern about the Lyme disease problem and assess the level of support for deer herd reduction on their islands. A 2016 survey of island residents indicated that other deer-related problems, namely vehicle collisions and garden and forest damage, motivated support for deer reduction as much as Lyme disease. We recommended efforts to keep deer density ≤15/mi^2 and to remove invasive plant species--particular Japanese barberry—from the landscape. The benefits of these measures will extend beyond vector tick control to improved deer and forest health.

3.2 Introduction

Lyme disease is the most common tick-borne illness in the US, accounting for 69% of all tick- and mosquito-borne disease (Adams et al. 2016). Lyme disease is caused by the bacterial spirochete *Borrelia burgdorferi*, which is transmitted through the bite of an infected blacklegged tick (*Ixodes scapularis*) (Mead et al. 2015, Rosenberg et al. 2018). The first known case of Lyme disease in Maine was in 1986 (Rand et al. 2007) and the first reports of *I. scapularis* in Maine were published in the late 1980s (Anderson et al. 1987, Ginsberg and Ewing 1988). The increase in Lyme disease in Maine has been correlated in space and time with the range expansion of *I. scapularis* (Rand et al. 2007, Chapter 2: Fig. 2.1). The US Centers for Disease Control and Prevention define a high Lyme disease incidence state as average incidence of at least 10 confirmed cases per 100,000 persons for the previous three reporting years. Maine's three-year average incidence (2015-17) was 89.2 (range 74.7 – 106.6) and highest in the nation.

Maine has 15 unbridged, offshore islands with year-round communities; seven of these were coextensive with towns and had reportable Lyme case numbers across 2013-17. The seven-island, 2013-17 Lyme incidence average was 1,062 and ranged from 0 on the Cranberry Isles and Frenchboro to 3,972 on Islesboro (MECDC 2018a) compared to the statewide average of 89.2. Over the past three decades, several of Maine's offshore island communities have been interested in quantifying *I. scapularis* abundance and *B. burgdorferi* infection rates in *I. scapularis* on their islands. Beginning with Monhegan Island in 1989, representatives from various islands have invited our staff at the Maine Medical Center Research Institute's Vector-borne Disease Laboratory to collect ticks at sites around their islands.

Part of islanders' motivation for assessing entomological risk—density of infected *I. scapularis*—has been to inform their decisions about management of white-tailed deer (*Odocoileus virginianus*). On some of New England's offshore islands such as Monhegan Island in Maine, Block Island in Rhode Island, and Martha's Vineyard and Nantucket Island in Massachusetts, High Lyme incidence has been attributed to high densities of *I. scapularis* supported by hyper-abundant white-tailed deer (e.g., Rand et al. 2004b, RIDEM 2013, Greer et al. 2014). The white-tailed deer is the primary host of adult *I. scapularis* within its US range (e.g., Telford 2017), and is host to larval and nymphal *I. scapularis* as well (Watson and Anderson 1976). Following bans on white-tailed deer hunting on Maine's unbridged islands from the 1930's, several islands reinstituted a regular firearms season in the 1950's. Other islands maintained hunting bans, however, and deer numbers burgeoned in the absence of pressure from natural predators and hunting.

By the 1990s, deer densities of approximately 100 per square mile reached or exceeded island residents' tolerance for damage to vehicles, gardens, the landscape, and most recently, Lyme disease (Moore 2002). The Maine Department of Inland Fisheries and Wildlife (MEIFW) reported that white-tailed deer populations on the offshore islands were much higher than the 15/mi^2 goal called for by MEIFW (Lavigne 1997). In setting population goals for the state's 29 wildlife management districts, the MEIFW takes into consideration public demand for deer hunting and viewing, concerns over vehicle collisions, tick-borne disease, health of the deer, and damage to landscaping, orchards, and forests (MEIFW 2017). When deer densities in southern and central Maine exceeded 20/mi^2 during 1999-2001, MEIFW adjusted numbers back down through issuance of any deer permits (ADPs) during the regular firearms season (MEIFW

2017). However, MEIFW is unable to apply this approach in urban and suburban settings and on many of the offshore islands, where firearms discharge bans, safety concerns, and posted land have precluded firearms hunting.

In 2000, the Maine State Legislature granted authority to MEIFW to open islands previously closed by statute to deer hunting, which provided a formal mechanism for MEIFW and municipalities to coordinate controlled hunts. Thus, in cooperation MEIFW, those offshore islands without a regular firearms season have implemented controlled hunts to reduce (cull) deer numbers. However, ongoing debate over the need for further deer reduction and/or increased hunting pressure are part of the fabric of life on these islands (Rand 2017).

At the Vector-borne Disease Laboratory part of our mission is–through entomological surveys and invited outreach–to assist communities through the process of planning for integrated tick management. Over the years we have provided island communities with annual summaries of entomological data, but these data, as well as data on Lyme incidence and deer management history, and island residents' opinions on ticks and deer, have been available only through scattered sources.

Thus, our first aim was to review Lyme incidence, entomological risk, and history of white-tailed deer management on Maine's unbridged islands, from the late 1980s to present. The first aim provided an historical context for our second aim, which was to quantify islanders' support for deer reduction, through a survey we opened in 2016.

To understand bases of support for deer herd reduction, we asked islanders if they agreed, disagreed, or were neutral on whether Lyme disease was problematic on their islands. We then related the level of agreement to self-reported burden of tick bites and tick-borne disease, i.e., “burden of bite/TBD”. We graded burden of bite/TBD from high to low as self/extended family had acquired TBD, self only bitten (no TBD), and self never bitten. We also related degree of personal protection behaviors to burden of bite/TBD, to see if the degree to which Lyme was considered problematic and degree of health behaviors aligned. Then, we assessed the level of support for deer herd reduction in relation to problems associated with deer overabundance, including risk of Lyme disease. Our hypotheses were:

1. Odds that respondents will agree Lyme disease is a problem on their island will depend on the burden of tick bite/TBD, that is, be highest for those burdened by tick-borne disease (self/extended family), vs. intermediate for those only bitten (and never contracting TBD) vs. lowest for those never bitten.
2. Odds that respondents will use a given personal protection behavior will depend on the burden of tick bite/TBD, that is, be highest for those burdened by tick-borne disease (self/extended family), vs. intermediate for those only bitten (and never contracting TBD) vs. lowest for those never bitten.
3. Odds that respondents will agree that deer should be reduced on their island will be higher for those who attribute increased risk of Lyme disease to deer overpopulation on their island vs. those who have no problems with deer, and for those who experience additional problems with deer (increased risk of vehicle collisions, damage to yard, damage to forest) on their island vs. those who have no problems with deer.

We expected that the main variables of interest might interact with respondents’ demographics. For example, gender and age could modify personal protection behaviors, as seen in a Nantucket Island study where females and older people were more likely to take measures to prevent tick bites than men and younger people (Phillips et al. 2001). Also, support for deer reduction year-round versus seasonal residency and hunting tradition could modify support for deer herd reduction. For example, a year-round resident who hunts annually might view deer herd reduction as detrimental to her chances of obtaining venison for the freezer.

Following the central question on support for deer herd reduction we asked islanders for their views on methods of deer reduction, who should be responsible for tick control, and a question about pesticide application. To inform our outreach, we asked islanders if they felt they needed more information about tick control, about their trust in information about tick control from scientists and government, and what factors they thought were contributing to an increase in ticks in Maine. This last question was of interest because in the years leading up to and including 2016 there was substantial media coverage of white-footed mice and climate change as drivers of TBD, but little to no attention on the association between certain invasive plant species and tick abundance and *B. burgdorferi* infection prevalence. This led to our last hypothesis:

4. Given four choices of factors causing the tick problem in Maine (deer, rodents, climate change, invasive plants), significantly more respondents would omit than include invasive plants as a cause.

The historical summary and survey may help each island community see how it fits into an overall island narrative of tick control and deer herd management, and to draw the attention of a broader audience to Maine's offshore island communities as they grapple with these challenges.

3.3 Methods

3.3.1 Study Area

Maine, the most northeastern of the United States, encompasses 86,542 km^2 and 4.5° latitude (42.97-47.46°N, 66.95-71.08°W), and has 924 minor civil divisions (towns), 512 of which are populated. The majority of its human population of 1.3 million resides in its southern half, generally within an 80-km-wide coastal plain with elevations <150 m (Rand et al. 2007). *I. scapularis* range from established on the coast to emerging in the north.

The 15 unbridged, offshore Maine islands with year-round communities are depicted in Figure 3.1. These islands are accessible by boat (or aircraft) only and contain municipal centers focused around the town landing piers, as well as scattered rural distribution of homes. Successional upland meadows, and mowed fields (Rand et al. 1998) were scattered across generally forested landscapes. These forests were maritime spruce-fir (Picea and Abies spp.) forests and mixed, generally second-growth forests of red oak (*Quercus rubra*), red maple, (*Acer rubrum*), yellow birch (*Betula lutea*) and white pine, (*Pinus strobus*). The islands were variously infested with invasive honeysuckle (*Lonicera canadensis*), Japanese barberry (*Berberis thumbergii*), and oriental bittersweet (*Celastrus orbiculatus*). White-tailed deer densities have ranged from 0 to 114/mi^2 (Rand et al. 2004b). Coastal climate in summer is cooler and more humid, but warmer with less snow in winter than Maine’s inland.

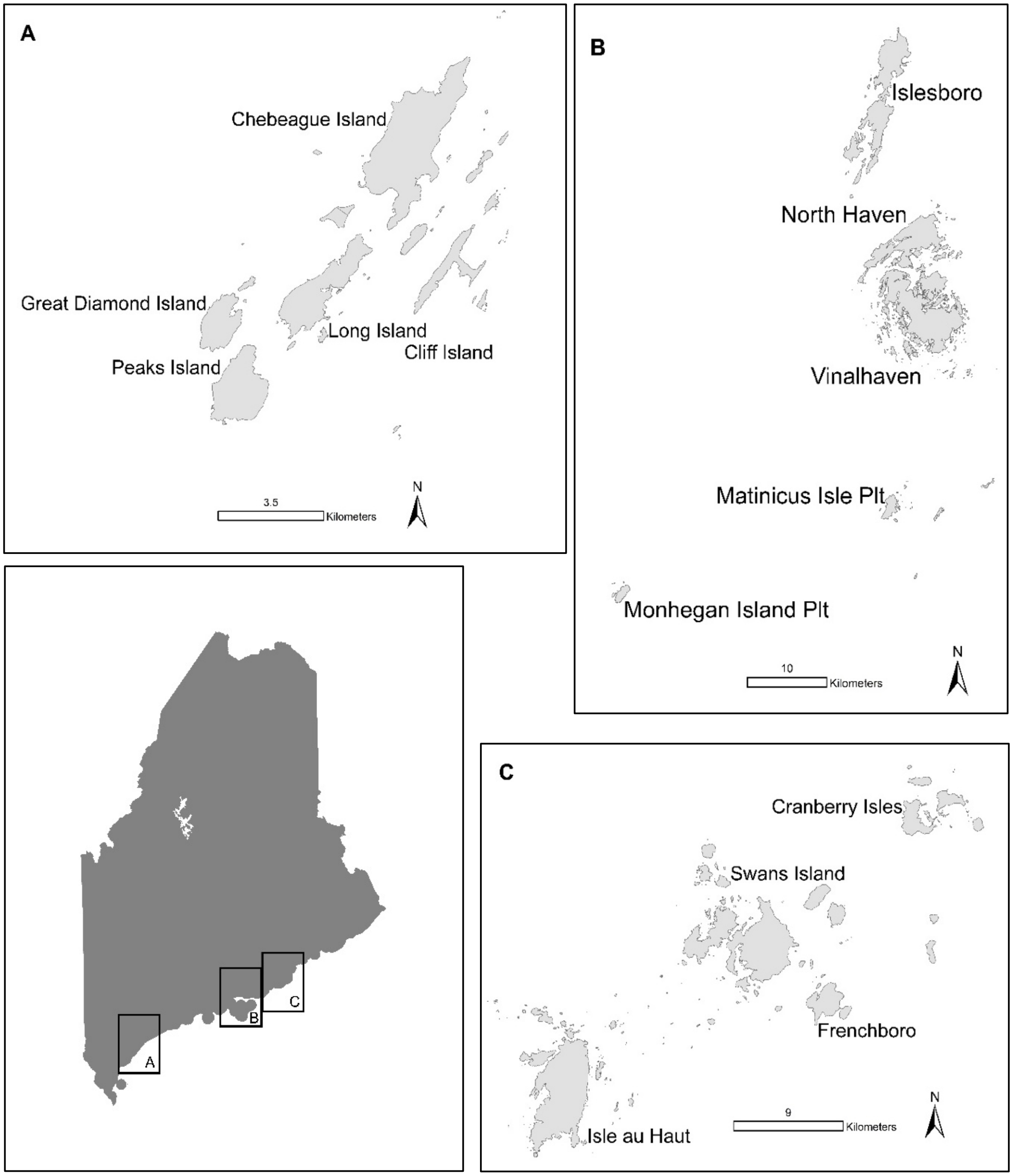

Figure 3.1. Maine's unbridged, offshore islands with year-round residents fall within Maine Department of Inland Fisheries and Wildlife administrative Regions A-C.

MEIFW regional deer biologists oversee deer herd management in eight administrative wildlife management regions (MEIFW 2007). Region A includes the Casco Bay islands of Chebeague Island (formerly part of the Town of Cumberland), Long Island (formerly part of the City of Portland) and Cliff Island, Great Diamond Island, and Peaks Island (City of Portland); Region B includes Islesboro, North Haven, Matinicus Isle Plantation, Monhegan Island Plantation, and Vinalhaven; Region C includes the Cranberry Isles, Frenchboro, Swans Island, and Isle-au-Haut (Fig. 3.1). Of the 15 unbridged Matinicus Isle Plantation, 23 miles offshore, never had deer; whereas Monhegan Island Plantation, 11 miles offshore, removed its white-tailed deer during the years 1997-1999 (Rand et al. 2004b). Many island towns include numerous smaller islands (Fig. 3.1), but data on Lyme incidence, ticks, and deer apply to the main island, where is found the municipal pier, the concentration of municipal buildings, and most of the human population. Within the town of Cranberry Isles there are two main islands, Great Cranberry and Islesford, where data refer to both islands collectively.

3.3.2 Datasets

3.3.2.1 Lyme Disease Incidence

We obtained cumulative Lyme disease case counts, cumulative population, and five-year incidence for the period 2013-17 from the Maine Center for Disease Control's Maine Tracking Network (MECDC 2018a). Seven of Maine's 15 unbridged, offshore islands were coextensive with towns and had reportable Lyme case numbers across 2013-17. Where cumulative population ≤2,000 and cases were between 1 and 5, MECDC reported "<6", so we assumed one cases and calculated a minimum incidence as 1/cases x 100,000. Cases are attributed to patients' home town and state. Thus, cases for island towns will not include cases acquired by summer residents. Island health centers keeping track of cases independently of the Maine CDC may or may not keep records for summer residents, but these data are generally not easily obtainable and may not meet CDC case definitions. Thus for standardization, we report only the cases reported by Maine CDC.

3.3.2.2 Questing Adult *I. scapularis* Abundance and *B. burgdorferi* Infection Prevalence

We collected ticks from transects averaging ~100m long at established (long-term) sites on the islands. These sites included hiking trails through forests, playing fields, the edges of school grounds, and private properties. We used 1m^2 flags consisting of light-colored corduroy attached to a 150cm pole, dragged over leaf litter and brush in the adult season (October- early November) when temperatures exceeded 10° C and vegetation was dry along transects at established sites on each island (e.g., Elias et al. 2006). Flags were inspected at approximately 5 min intervals, and ticks were placed in plastic vials for transportation to the laboratory for identification. After enumerating field-sampled ticks we calculated the number of adults per hour as an index to tick abundance. Flagging efficiency is higher for adult *I. scapularis* (Dantas-Torres et al. 2013) so our flagging produced far fewer nymphs during June/July than adults in October/November. To allow for comparisons across islands and years we therefore reported ticks per hour and infection rates for fall-flagged adults only.

Subsets of ticks from some samples were tested for *B. burgdorferi*. From 1989 through 2015 we tested for *Borrelia* by direct fluorescent antibody (DFA) as per Donahue et al. (1987). From 2016 through 2018 we tested for *B. burgdorferi* by polymerase chain reaction (PCR) using PCR primers targeting the OspA coding region as designed by Persing et al. (1990). PCR was performed using 2µL of sample DNA, 12.5µL of Platinum™ Green PCR 2x Master Mix

(Invitrogen, Waltham, MA), 1µL each of forward and reverse primers and 9µL of ultrapure water. Cycling conditions were 94°C for 3 minutes followed by 35 cycles of 94°C for 30, 55°C for 30 seconds and 72°C for 30 seconds and finally an infinite hold at 4°C. After testing we calculated *B. burgdorferi* infection prevalence (positive/tested).

3.3.2.3 Deer Management History

We described deer management history for each island by identifying, to the extent possible, the year or years of a controlled hunt (if applicable), the number of deer or deer density before the hunt, the number of deer taken in the controlled hunt, and the number of deer and deer density currently.

Historically, the Maine Department of Inland Fisheries and Wildlife (MEIFW) has used a sex-age-kill model to estimate deer/mi^2 for each of 29 wildlife management districts (WMDs), with inputs including a buck kill index and hunter effort (MEIFW 2007). This calculation has only rarely been used at the town level as there are insufficient numbers of deer harvested in any given town. Thus, other sampling methods were needed to estimate deer density on islands.

Census methods included aerial surveys and pellet group counts (MEIFW 2007). Islesboro has had two aerial surveys and one pellet group count; we obtained results from the town’s website. Maine’s news outlets have followed deer herd management across the decades, and reporters have contacted people “in the know” for their stories. These people may be the hunters holding permits to take deer during special hunts, the deer biologists for the districts in which the islands fall, and other on-island personnel (such as island health officers). We searched for these articles on island deer herd management on the internet. We also asked MEIFW biologists for their historical and current knowledge of deer herd management. Where an estimate of deer numbers was known, we used the island's land area to calculate deer/mi^2; if the estimate was given as deer/mi^2, then we back-calculated the number of deer. Deer densities and numbers were rough estimates.

3.3.2.4 Survey

We administered a 43-question survey using Qualtrics© web-based survey software (Table 3.1). Human subjects research was approved by the Maine Medical Center's Institutional Review Board (IRB #4789, Stakeholder Views on Deer Herd Reduction as a Method to Prevent Lyme Disease among Residents of Unbridged Maine Islands). We refer to the survey henceforth as the Island Survey. Year-round and seasonal residents alike were asked to participate. Seasonal (typically summer) residents own property and have a role in municipal policy formation. Questions pertaining to the aims and hypotheses of the study are listed in Table 3.1. Generally, questions about beliefs were scored on a 3-point Lickert scale (e.g., Agree, Disagree, Neutral). We opted for 3-point scale over a 5-point or higher scale because 1) our primary interest was in direction of response rather than intensity (Jacoby and Matell 1971), 2) we expected a modest number of respondents would require any scale >3 to be collapsed to three, a common situation that does not compromise reliability (Jacoby and Matell 1971), and 3) we wanted to avoid respondent fatigue and non-response (Lehmann and Hurlbert 1972). This latter consideration was key for the islands, which do not enjoy universal broadband internet and cell phone service (Tilson 2015).

Table 3.1. Questions asked in the 2016 Island Tick Survey. Respondents were year-round and seasonal residents of Maine's unbridged, off-shore islands. Respondents were not required to answer all questions so total number responding per question varied.

Category	Question	Options
Demographics	What island do you live on?	name of island
	What is your age?	18-24, 25-34, 35-44, 45-54, 55-64, 65+
	What is your gender?	male/female/oher
	What is your approximate household income?	<$25K, $25K to <$40K, $40K to <$55K, $55K to < $65K, $65K to $100K, >$100K
	What is the highest level of education you have completed?	some high school , high school/GED, some college, college, graduate/professional
	Are you a year-round or seasonal resident?	year-round, seasonal
	How long do you typically reside on the island?	days to a week, up to a month, more than a month
Importance of Lyme	Is Lyme disease a problem on your island?	agree, disagree, neither agree nor disagree
Burden of ticks and tick-borne disease	How many times have you been bitten by a deer tick on your island?	0, 1, 1 to 5, >5, not sure but more than once, don't know
	Do you find deer ticks on your dog or cat?	yes, no, does not apply
	Have you been treated for a tick-borne disease?	
	Lyme disease	yes, acquired on-island/yes, acquired off-island
	anaplasmosis	yes, acquired on-island/yes, acquired off-island
	babesiosis	yes, acquired on-island/yes, acquired off-island
	other	yes, acquired on-island/yes, acquired off-island
	Has anyone in your extended family been treated for a tick-borne disease?	
	Lyme disease	yes, acquired on-island/yes, acquired off-island
	anaplasmosis	yes, acquired on-island/yes, acquired off-island
	babesiosis	yes, acquired on-island/yes, acquired off-island
	other	yes, acquired on-island/yes, acquired off-island
Preventive health behaviors	How often would you say you protect yourself against tick bites when ticks are out?	
	avoid tick habitat	always, sometimes, never
	use personal repellent (bug spray)	always, sometimes, never
	tuck my pants into my socks	always, sometimes, never
	wear light-colored clothing	always, sometimes, never
	check myself for ticks after being outside	always, sometimes, never
Policy Support	Do you think there is a need to reduce the number of deer on your island?	agree, disagree, neither agree nor disagree
Deer values	Do you ever have problems with the deer on your island?	too many, Increased risk of a car collision, eat my garden plants and/or yard plantings, over-browse forest vegetation, increased risk of Lyme disease
	How do you benefit from the deer on your island?	I enjoy seeing deer, I value knowing deer are part of the landscape, I hunt deer, My family and/or friends hunt deer
Deer hunting approval	Do you approve of deer hunting?	
	in general	agree, disagree, neither agree nor disagree
	on your island	agree, disagree, neither agree nor disagree
Methods of reducing deer	To what extent do you agree or disagree with the following approaches to reducing deer on your island?	
	more doe permits	agree, disagree, neither agree nor disagree
	expanded archery season	agree, disagree, neither agree nor disagree
	expanded firearms season	agree, disagree, neither agree nor disagree
	a professional sharp-shooter	agree, disagree, neither agree nor disagree
	allow off-islanders to hunt only if family of islanders	agree, disagree, neither agree nor disagree
	allow any off-islanders to hunt	agree, disagree, neither agree nor disagree
	What would be acceptable ways to pay for a sharp-shooting program to reduce the deer herd?	state or federal funds, town budget, private funds
Responsibility	Who do you think should be responsible for tackling the issue of tick-borne disease on your island?	
	U.S. government	agree, disagree, neither agree nor disagree
	state government	agree, disagree, neither agree nor disagree
	town government	agree, disagree, neither agree nor disagree
	non-profit organizations	agree, disagree, neither agree nor disagree
	communities	agree, disagree, neither agree nor disagree
	small groups of individuals, or individuals	agree, disagree, neither agree nor disagree
Information seeking	How do you rate your knowledge of how to prevent tick bites?	none, some, a lot
	Do you think you need to learn more about how to prevent tick bites?	agree, disagree, neither agree nor disagree
Trust	Do you trust information on tick control given to you by scientists?	agree, disagree, neither agree nor disagree
	Do you trust information on tick control given to you by your town government?	agree, disagree, neither agree nor disagree
Causes of the Tick Problem	What would you say is causing the increase in deer ticks in some parts of Maine?	
	climate change	agree, disagree, neither agree nor disagree
	deer overpopulation	agree, disagree, neither agree nor disagree
	rodents	agree, disagree, neither agree nor disagree
	invasive plants	agree, disagree, neither agree nor disagree
Pesticide	Would you apply a pesticide on your property to kill ticks if the pesticide was harmless to other animals and people?	agree, disagree, neither agree nor disagree

Surveys could be taken via smart device, computer, or paper. We allowed more than one response from the same IP address to allow more than one response per household and per public (e.g., library) computer. We found no duplicates, i.e., where the same IP address appeared two or three times the respondents using the same computer had differing responses and appeared to be legitimate household members rather than one individual taking the survey twice. Advertising was through paper and an online news story in the Maine Island Institute's Working Waterfront (Groening 2016), island Facebook and website pages, by word-of-mouth, by laminated posters at ferry terminals, and by paper surveys left at town offices and libraries. The survey opened on May 1st, 2016 and closed December 31st, 2016.

The Island Survey was a convenience sample, a research strategy that allows people to opt-in, meaning that respondents self-select. Much survey research relies on convenience sampling due to the expense of population-based sampling (Mullinix et al. 2015). Convenience sampling can be biased, but allows for data collection over a short period of time at minimal expense compared to often infeasible population-based sampling. Rather than forgo any sampling at all, convenience sampling can generate data that can be interpreted in the presence of bias, where the bias can be described and inference can be constrained to the demographic of the sample (Kelley et al. 2003, Mullinix et al. 2015).

3.3.3 Analysis

We used SAS® (SAS 2018) for all analyses. We cross-tabulated categorical responses and reported frequencies of responses of island residents overall and by individual island. We used logistic regression models to address each of the three categories of hypotheses. The hypothesis 1 model tested level of agreement that Lyme disease was a problem (agree vs.

neutral/disagree) as a function of the burden of tick bites and disease. With regard to the response variable, very few respondents (*n* = 21, 3%) responded “disagree”, which resulted in cell counts as low as 2, violating the “rule of ten” and resulting in poorly estimated variances and confidence intervals (Hosmer and Lemeshow 2000), thus we pooled “disagree” with “neutral” so the model had a binomial response.

The series of hypothesis 2 models tested the nominal level (always vs. sometimes vs. never) of five specific behaviors to protect against tick bite as a function of the burden of tick bites and disease. We used a generalized logit to accommodate nonproportional odds in the multinomial models.

In the hypothesis 3 model, we tested the level of agreement that deer numbers should be reduced (agree, neutral, disagree) as a function of the predictor variable “increased risk of Lyme disease” plus a composite predictor variable “other deer problems”. Regarding the “increased risk of Lyme disease” few respondents (*n* = 32, 4%) responded “disagree”, which resulted in cell counts as low as 3, thus we pooled “neutral” and “disagree” resulting in two levels: “agree” and ”otherwise”. Among the non-Lyme deer problems there was some degree of internal agreement (Cronbachs alpha = 0.43) and, analogous to the situation of collinearity among continuous predictors, equally important predictors were pushing each other out of the model. We created a new composite predictor “other deer problems”. We scored the value “agree” if respondents answered “agree” to at least one of the variables “car collision”, “eat my garden”, “over-browse the forest”, otherwise we designated the response “otherwise”. This also resolved the problem of where some situations are non-issues, e.g., if a person doesn’t garden then garden destruction is a non-issue. Thus “other deer problems” was a measure of whether a respondent had at least one problem with deer not related to ticks. We used a generalized logit to accommodate the nonproportional odds in this multinomial model.

All models included the control variables gender, age class, education, and resident status (year-round or seasonal). The support for deer reduction model also contained hunting tradition (self and/or family/friends hunt) as a control variable. We tested for significant two-way interactions in all models between the main effect(s) of interest and these control variables. Because 97 respondents did not answer the income question, we did not include income as a control variable. Respondents were asked to write in their occupations if desired. As an approximation of risk of tick encounter, we categorized fishing, landscaping, gardening, or property management as outdoor. As 8.3% of respondents (n = 73) had outdoor occupations vs. 69.5% indoor vs. 22.2% unknown, we did not include occupation type as a control variable.

Differences of opinions by island relative to the overall opinions were of interest but, due to sparse data from islands with very small populations, we could not use island as a control variable in the logistic regression models. Further, no one island could logically serve as a reference island. Instead, we calculated the significance of the difference between the percent agreeing on an individual island versus the across-island percent agreeing for the two main outcome variables of interest (is Lyme disease a problem, is there a need for deer reduction) to serve as a reference to parties interested in the individual island responses.

To test whether significantly more respondents would omit than include invasive plants as a cause of the tick problem (hypothesis 4), we tallied the number of respondents that agreed to at least one cause among the choice of deer, rodents, and climate change, but not plants, vs.

those who included plants as a cause. We ran a chi-square test for equal proportions (1-3 causes not including plants vs. 1-4 causes including plants).

Our main interest was across-island results. But for the two major questions of the study (Is Lyme disease a problem on your island, is there a need to reduce deer on you island), we calculated the difference between the individual island percent agreeing versus the overall percent agreeing (vs. otherwise) and tested for significance (chi-square test for equal proportions, to see if any islands stood out relative to the overall averages.

3.4 Results

3.4.1 Island Summaries of Lyme incidence, Entomological Risk, and Deer Management History

Estimated minimum Lyme disease incidence across all of Maine's unbridged islands, 2013-17, was 848 cases per 100,000 (Table 3.2) and ranged from 0 to 3,972. The Cranberry Isles and Frenchboro had 0 reported cases. It can be seen for Isle au Haut, Matinicus, and Monhegan that the 5-year populations did not sum to a population that allowed reporting of the exact number of cases, so assuming at least one case, a minimum incidence for the 5-year period for these three islands ranged from 270 to 277. Three Casco Bay islands fall within the City of Portland and island-level case data thus were not available (Table 3.2).

Table 3.2. Government, population, area, and estimated Lyme disease incidence of Maine's 15 off-shore, unbridged islands. These islands have year-round residents. Case data were not available for City of Portland islands.

			Population		Area		2013-17 Lyme disease[a]			Minimum
Region[f]	Island	Government	Winter[b]	Summer[c]	mi^2	km^2	Cases	5-year pop	Incidence	Incidence[d]
A	Chebeague Island	Indep	341	1600	3.0	7.8	7	1742	402	402
A	Long Island	Indep	230	1000	1.3	3.3	7	1139	615	615
A	Cliff Island	City of Portland	71	200	0.5	1.2				
A	Great Diamond	City of Portland	91	200	0.7	1.7				
A	Peaks Island	City of Portland	864	2000	1.2	3.1				
B	Isle Au Haut	Indep	73	800	12.6	32.7	<6	370	*	270
B	Islesboro	Indep	566	1000	14.1	36.5	109	2744	3972	3972
B	Matinicus Isle Plt	LUPC	74	100	1.3	3.3	<6	361	*	277
B	Monhegan Island Plt	LUPC	69	250	0.8	2.1	<6	368	*	272
B	North Haven	Indep	355	1000	11.3	29.3	36	1827	1970	1970
B	Swans Island	Indep	332	1000	12.5	32.4	8	1678	4767	477
B	Vinalhaven	Indep	1165	2200	22.5	58.2	23	5859	393	393
C	Cranberry Isles[e]	Indep	110	850	1.6	4.0	0	696	0	0
C	Frenchboro	Indep	61	150	3.9	10.0	0	331	0	0
		Total	4402						Average Incidence	848

[a] From the Maine Center for Disease Control Tracking Network (MECDC 2018).

[b] US Census Bureau (2017).

[c] Colby Environmental Policy Group (2014).

[d] Calculated as (1/5-year population) x 100,000.

[e] The Cranberry Isles include the islands of Great Cranberry (population 40) and Islesford, aka Little Cranberry (population 70).

[f] Maine Department of Inland Fisheries and Wildlife administrative regions; a different deer biologist is assigned to each region.

Entomological data in Table 3.3 show that sampling effort over the years has varied substantially. Of the 15 islands, we have collected ticks on ten. There remain five islands on which we have not yet collected adult ticks in fall: Great Diamond, North Haven, the Cranberry Isles, and Frenchboro. Sampling has typically been done on an ad hoc basis in response to a request for assistance as there has been no comprehensive sampling program or funding beyond short-term grants for minimum surveillance. The exceptions were Monhegan and Isle au Haut, which were sampled frequently during the 1990s and 2000s given the intense interest in tick control on Monhegan and funding to conduct research on efficacy of control options (Isle au Haut was a reference island).

As seen on a decadal basis, adult tick abundance has increased on the islands. The exception was Monhegan, where deer were removed from 1997-99 and tick abundance and infection rates decreased (Rand et al. 2004b). Increases in *B. burgdorferi* infection prevalence can be seen as well (again excepting Monhegan). Cliff Island, Islesboro, and Swan's Island best illustrate increases in entomological risk over the years, with fall-flagged adults per hour increasing on Cliff Island from 10 to 37 (2000s to 2010s), on Islesboro from 0 to 37 to 43 (1990s to 2000s to 2010s), and Swans Island from <1 to 6 to 33 (1990s to 2000s to 2010s). Infection rates also increased: Cliff Island from 29 to 42% (2000s to 2010s), on Islesboro from <1 to 3 to 31 (1990s to 2000s to 2010s), and Swans Island from 0 to 19 to 25 (1990 s to 2000s to 2010s). In general, the entomological data in Table 3.3 should be interpreted with caution as number of years sampled per decade was as low as one in some cases, e.g., Chebeague Island. We note that since 1989, we have conducted outreach on all islands other than Great Diamond, Cranberry Isles, and Frenchboro.

Table 3.3. Summary of fall adult *I. scapularis* sampling, ticks flagged per hour, and percent positive for *B. burgdorferi*, 1990-2017.

		n (years)			adults per hour			*n* tested			% positive		
region	town	1990s	2000s	2010s	1990s	2000s	2010s	1990s	2000s	2010s	1990s	2000s	2010s
A	Chebeague Island	0	0	1			37.5			109			62.4
A	Cliff Island	0	7	4		10.0	37.4		154	171		29.3	41.6
A	Great Diamond Island												
A	Long Island	0	0	5			29.7	2		442			45.0
A	Peaks Island	3	0	0	0.4			4	0				
B	Isle Au Haut	8	5	0	12.4	20.7		920	745		17.7	24.1	
B	Islesboro	2	2	6	0.1	2.6	31.0	5	125	527	0.0	36.6	43.1
B	Matinicus Isle Plt	1	2	0		0.1		0		1			
B	Monhegan Island Plt	10	9	1	13.3	4.2		1602	554		37.0	33.4	
B	North Haven												
B	Vinalhaven	0	0	2			26.2			192			25.0
C	Cranberry Isles	0	0	0									
C	Frenchboro	0	0	0									
C	Swans Island	3	4	5	0.3	6.5	32.8	11	113	542	0.0	18.7	25.1

Table 3.4 shows known deer management histories on the islands. Four of the 14 islands that ever had deer never had culls: Chebeague, North Haven, and Vinalhaven, which have regular firearms seasons, and Isle au Haut, which includes part of Acadia National Park and has no deer hunting. Ten of the 14 islands that ever had deer had culls: the first known occurring 1992-95 on Great Diamond and the most recent 2012-14 on Islesboro. Pre- and post-cull deer density estimates were available for only four islands and were >85/mi^2 to 10-13/mi^2 for Cranberry Isles, were 60/mi^2 to 50/mi^2 for Islesboro, >100/mi^2 to 21-25/mi^2 for Peaks Island, and 114/mi^2 to 0 for Monhegan Island.

Monhegan was the one island that completely removed its deer herd (technically complete removal is not a cull). In 1959, for subsistence hunting, Monhegan islanders brought 6 white-tailed deer across 12 miles of water from the mainland to Monhegan (Rand 2017). By the early 1990s, deer had reached a density of 141/mi^2. The island became known for its high population of deer, blacklegged tick infestation, and what seemed a disproportionate number of human and canine Lyme disease cases. In 1995, islanders voted to remove all 113 deer permanently. Number of ticks per hour was reduced from 8 to 15/hour pre-removal to <1/hour post-removal, and number of larvae and nymphs on rats from 1 to 17 pre-removal to 0 post-removal (Rand et al. 2004b). As of this writing, permitted, special regulations hunts to control deer currently occur on five of the islands. Known, current deer densities ranged from 10 to 60 (Table 3.4).

Table 3.4. Summary of deer management history on the unbridged islands of Maine. Islands in bold implemented deer reduction hunts, i.e., culls, by way of controlled hunts or in a few instances by depredation hunt. The deer herd on Monhegan Island was entirely removed rather than culled.

				Deer Reduction History							
MEIFW		Land Area		Pre-hunt		Hunt		Number	Current		
Region	Island	mi^2	km^2	~n	~deer/mi2	Year(s)	Method(s)	Harvested	~n	~deer/mi2	Management[a]
A	Chebeague	3.0	7.8	n/a	n/a	none	n/a	n/a	unk	unk	Regular
A	Long	0.5	1.2	n/a	n/a	1999[b]	shotgun	<10[b]	20-30[c]	40-60[c]	Special
A	Cliff	0.7	1.7	unk	unk	2003[d], 2004[e]	sharpshooter	25[d]	25[e]	53	Special
A	Great Diamond	1.3	3.3	unk	unk	1992-95[e,f];1999-2001[b]	sharpshooter	unk; 37[b]	25[e]	38	Special
A	Peaks	1.2	3.1	274	100[d],200[e,g]	1999-2001[f]	sharpshooter	223-234[d,g]	25[e]-30[f]	21[e]-25[f]	Special
B	Islesboro	14.1	36.5	846	60[i]	2012-2014[h]	shotgun	124[h]	690	50[h]	Special
B	Matinicus Isle Plt	1.3	3.3	0	0				0	0	n/a
B	Monhegan Plt	0.8	2.1	90	141[i]	1996-1999[i]	sharpshooter	114[i]	0	0	n/a
B	North Haven	11.3	29.3	n/a	n/a	none	n/a		unk	unk	Regular
B	Vinalhaven	22.5	58.2	n/a	n/a	none	n/a		unk	unk	Regular
C	Isle au Haut	12.6	32.7	n/a	n/a	none	n/a		unk	unk	No hunting
C	Cranberry Isles	1.6	4.0	133-156	85-100[g]	1999-2001[f]	archery, shotgun	10[k]	15-20[k]	10-13[k]	Restricted
C	Frenchboro	3.9	10.0	unk	unk	2001[g]	archery, shotgun	unk	unk	unk	Restricted
C	Swans	12.5	32.4	unk	unk	2001-2003[f]	archery, shotgun	270[k]	188[l]	15[l]	Regular + Special

[a] Hunting under special regulations means the island is not open to the regular firearms season (except Swans Island), but rather has special hunting regulations by agreement between the municipality and the Maine Department of Inland Fisheries and Wildlife. Special regulations for some islands can be found in Maine's Statutes: www.mainelegislature.org/legis/statutes/12/title12sec11402.html. Restricted hunting on Cranberry Isles and Frenchboro means Regular with modifications.

[b] Bieber N. (pers. comm. 2018)

[c] Groening T. March 13, 2015. The Working Waterfront.

[d] Leath D.March 1, 2004. Deer control debated on islands. The Working Waterfront.

[e] Billings R. November 17, 2016. Shots heard 'round 3 Portland islands as annual culling of deer begins.

[f] MEIFW (2007)

[g] Moore B. June 1, 2002. Deer, islands, and people. The Working Waterfront.

[h] Fleming D. May 14, 2017. Portland Press Herald.

[i] Rand et al. (2004)

[j] Leven R. October 17, 2014. Other islands embrace changes in deer hunt. Mount Desert Islander.

[k] Edgecombe M. November 29-30, 2003. Islanders find relief in deer hunt. Bangor Daily News.

[l] MMCRI (2018). Swans Island deer density estimate 14.6/mi^2 (lower and upper 95% confidence limits 11.3,18.0) based on a 2018 deer pellet count.

3.4.2 Island Survey

3.4.2.1 Demographics

A total of 829 island residents responded with776 (93.6%) online responses and 53 (6.4%) paper responses (Table 3.5). Among respondents 70% were female, 72% were age 55+, and 76% percent had a 4-year college degree or higher (Table 3.5). Incomes were distributed evenly among <\$55,000; \$55,000 to 100K and >\$100,000. The split between year-round and seasonal residents was close to 50/50, with slightly more year-round residents (54%). Demographics of paper and online responses were not significantly different for gender, age, education, and income (chi-square test for equal proportions, all $P \geq 0.41$, and (\$55K up to 100K, >\$100K pooled due to low n for paper in each group). Excluding Monhegan (which had one respondent despite lack of deer on the island), percent of the year-round population responding ranged from 1% (Frenchboro) to 19% (Peaks Island). Responses from Frenchboro, the Cranberry Isles, Cliff, and Great Diamond were sparse as would be expected from islands with very small populations. The remainder of the results pertain to across-island summaries, but by-island responses can be found in Appendix C.

Table 3.5. Demographics of respondents to the 2016 Island Tick Survey. Respondents were year-round and season residents of Maine's unbridged, off-shore islands. Respondents were not required to answer all questions so total number responding per question varied.

Demographic	All Islands	Frenchboro	Cranberry_Isles	Swans	Isle_au_Haut	Islesboro	Monhegan	North_Haven	Peaks	Vinalhaven	Chebeague	Cliff	Great_Diamond	Long
age 55 and up	585 (72%)	8 (80%)	5 (38%)	51 (69%)	34 (69%)	72 (69%)	1 (50%)	31 (57%)	117 (78%)	53 (78%)	87 (82%)	12 (57%)	24 (69%)	76 (78%)
age 18 to 54	229 (28%)	2 (20%)	8 (62%)	23 (31%)	15 (31%)	33 (31%)	1 (50%)	23 (43%)	33 (22%)	15 (22%)	19 (18%)	9 (43%)	11 (31%)	22 (22%)
	*	NS	NS	*	*	*	NS	NS	*	*	*	NS	*	*
Graduate/Prof Degree	346 (43%)	5 (50%)	2 (17%)	34 (45%)	24 (51%)	50 (49%)	2 (100%)	20 (37%)	66 (45%)	32 (48%)	44 (43%)	11 (52%)	22 (63%)	25 (26%)
4-year College Degree	263 (33%)	1 (10%)	3 (25%)	18 (24%)	12 (26%)	32 (31%)		21 (39%)	61 (41%)	22 (33%)	30 (29%)	6 (29%)	9 (26%)	39 (40%)
Some College	133 (17%)	3 (30%)	5 (42%)	17 (23%)	7 (15%)	16 (16%)		9 (17%)	16 (11%)	4 (6%)	23 (22%)	3 (14%)	4 (11%)	19 (19%)
High School/GED	60 (7%)	1 (10%)	2 (17%)	6 (8%)	4 (9%)	5 (5%)		4 (7%)	4 (3%)	8 (12%)	6 (6%)	1 (5%)		15 (15%)
	*	NS	NS	*	*	*	.	*	*	*	*	*	*	*
Female	570 (70%)	5 (50%)	11 (85%)	53 (71%)	33 (67%)	64 (61%)	2 (100%)	38 (69%)	113 (74%)	45 (65%)	76 (74%)	17 (81%)	25 (71%)	66 (67%)
Male	248 (30%)	5 (50%)	2 (15%)	22 (29%)	16 (33%)	41 (39%)		17 (31%)	39 (26%)	24 (35%)	27 (26%)	4 (19%)	10 (29%)	33 (33%)
	*	NS	*	*	*	*	.	*	*	*	*	*	*	*
income $55K up to 100K	269 (37%)	4 (50%)	4 (44%)	24 (37%)	16 (35%)	24 (27%)	1 (50%)	20 (43%)	53 (40%)	27 (46%)	40 (41%)	8 (40%)	9 (26%)	32 (37%)
income >$100K	245 (34%)	2 (25%)	1 (11%)	24 (37%)	15 (33%)	48 (53%)		8 (17%)	39 (29%)	15 (25%)	24 (25%)	10 (50%)	22 (65%)	28 (33%)
income <$55K	208 (29%)	2 (25%)	4 (44%)	17 (26%)	15 (33%)	18 (20%)	1 (50%)	19 (40%)	41 (31%)	17 (29%)	33 (34%)	2 (10%)	3 (9%)	26 (30%)
	*	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS	*	NS
Year-round resident	446 (54%)	4 (40%)	12 (92%)	36 (48%)	14 (29%)	53 (50%)	1 (50%)	42 (76%)	110 (72%)	34 (49%)	61 (58%)	5 (24%)	10 (29%)	41 (42%)
Seasonal resident	373 (46%)	6 (60%)	1 (8%)	39 (52%)	35 (71%)	52 (50%)	1 (50%)	13 (24%)	42 (28%)	36 (51%)	44 (42%)	16 (76%)	25 (71%)	57 (58%)
	*	NS	*	NS	*	NS	NS	*	*	NS	NS	*	*	NS
Total Responses	829	10 (1%)	13 (2%)	75 (9%)	49 (6%)	105 (13%)	2 (0%)	55 (7%)	153 (19%)	70 (9%)	106 (13%)	21 (3%)	35 (4%)	99 (12%)
% pop responding		10 (1%)	13 (2%)	75 (9%)	49 (6%)	105 (13%)	2 (0%)	55 (7%)	153 (19%)	70 (9%)	106 (13%)	21 (3%)	35 (4%)	99 (12%)

3.4.2.2 Burden of Tick Bites and Tick-borne Disease

Eighty-three percent of island residents agreed that Lyme disease was a problem on their island whereas only 3% disagreed (Table 3.6). Twenty-three percent of islanders reported that they had contracted at least one case of Lyme disease on-island; and 27% of islanders reported that at least one extended family member had contracted Lyme disease on-island.

Our first hypothesis was that odds of respondents agreeing Lyme disease was a problem would depend on burden of bite/TBD. Among respondents, 58% reported themselves or family having had a tick-borne disease, 15% reported themselves bitten but not contracting a tick-borne disease, and 26% reported self not bitten. Bite/TBD burden was the only significant predictor of agreement that Lyme disease was a problem (n = 789, df = 2, Wald chi-square = 64.6, P <.0001, Table 3.7). Odds of respondents considering Lyme disease a problem on their island were nearly six times greater (OR 5.8, 95% CI 3.7-9.0) for those who had experienced tick-borne disease (through self, family, or friends) than those never bitten by a tick, and nearly four times greater (OR 3.8, 95% CI 2.1-7.0) for those bitten (but never ill) than those never bitten by a tick. There was no difference in odds between those experiencing TBD and bitten only (OR 1.5, 95% CI 0.8-2.9; Table 3.7). Control variables (gender, age class, education level) were not significant as main effects or as interactions with the effect of interest, bite/disease burden.

Table 3.6. Responses to the 2016 Island Survey of residents of Maine's unbridged, off-shore islands, 2016. An asterix denotes chi-square test for equal proportions $P \leq 0.05$.

Category	Question					
Importance of Lyme	Is Lyme disease a problem on your island?	**Agree**	**Disagree**	**Neutral**		*P*
		680 (83%)	21 (3%)	118 (14%)		*
Burden of ticks and tick-borne disease	Have you been bitten by a deer tick on your island?	**No**	**Yes**			
		421 (51%)	400 (49%)			NS
	Have you been treated for a tick-borne disease/where acquired?	**Off-island**	**On-island**	**Both**	**N/A**	
	Lyme disease	44 (5%)	187 (23%)	15 (2%)	575 (70%)	*
	anaplasmosis	4 (0%)	5 (1%)	1 (0%)	811 (99%)	*
	babesiosis	5 (1%)	11 (1%)	1 (0%)	804 (98%)	*
	other	2 (0%)	11 (1%)	2 (0%)	806 (98%)	*
	Has anyone in your extended family been treated for a tick-borne disease?	**Off-island**	**On-island**	**Both**	**N/A**	
	Lyme disease	115 (14%)	223 (27%)	31 (4%)	452 (55%)	*
	anaplasmosis	10 (1%)	10 (1%)	2 (0%)	799 (97%)	*
	babesiosis	16 (2%)	12 (1%)	2 (0%)	791 (96%)	*
	other	4 (0%)	4 (0%)	3 (0%)	810 (99%)	*
Preventive health behaviors	How often do you protect yourself against tick bites when ticks are out?	**Always**	**Never**	**Sometimes**		*
	avoid tick habitat	210 (26%)	150 (19%)	448 (55%)		*
	use personal repellent (bug spray)	180 (22%)	199 (25%)	425 (53%)		*
	tuck my pants into my socks	131 (16%)	349 (44%)	322 (40%)		*
	wear light-colored clothing	109 (14%)	171 (21%)	521 (65%)		*
	check myself for ticks after being outside	483 (60%)	27 (3%)	297 (37%)		
Policy Support	Do you think there is a need to reduce the number of deer on your island?	**Agree**	**Disagree**	**Neutral**		*
		483 (61%)	99 (12%)	211 (27%)		*
Deer issues/values	Do you ever have problems with the deer on your island?	**Agree**	**Disagree**	**Neutral**		
	vehicle collisions	321 (41%)	219 (28%)	244 (31%)		*
	garden damage	548 (69%)	116 (15%)	128 (16%)		*
	overbrowse the forest	301 (38%)	167 (21%)	317 (40%)		*
	risk of Lyme disease	653 (82%)	33 (4%)	108 (14%)		*
	How do you benefit from the deer on your island?	**Agree**	**Disagree**	**Neutral**		
	enjoy seeing deer	467 (59%)	153 (19%)	177 (22%)		*
	value deer presence	384 (48%)	191 (24%)	217 (27%)		*
Deer hunting approval/tradition	Do you approve of deer hunting?	**Agree**	**Disagree**	**Neutral**		
	in general	622 (78%)	55 (7%)	118 (15%)		*
	on your island	584 (74%)	102 (13%)	108 (14%)		*
	I hunt	48 (6%)	625 (80%)	108 (14%)		*
	My family/friends hunt	301 (38%)	387 (49%)	99 (13%)		*
Methods of reducing deer	Agreement with the following approaches to reducing deer on your island?	**Agree**	**Disagree**	**Neutral**		
	more doe permits	306 (62%)	69 (14%)	119 (24%)		*
	expanded archery season	295 (60%)	101 (20%)	97 (20%)		*
	expanded firearms season	193 (39%)	167 (34%)	132 (27%)		*
	a professional sharp-shooter	312 (63%)	104 (21%)	79 (16%)		*
	allow off-islanders to hunt only if family of islanders	144 (29%)	198 (40%)	147 (30%)		*
	allow any off-islanders to hunt	69 (14%)	315 (64%)	108 (22%)		*
	Acceptable ways to pay for a sharp-shooting program to reduce the deer herd?	**Any**	**Private**	**State/Federal**	**Town**	
		14 (4%)	28 (9%)	175 (54%)	108 (33%)	*
Responsibility	Responsibility for tackling the issue of tick-borne disease on your island?	**Agree**	**Disagree**	**Neutral**		
	U.S. government	308 (40%)	253 (33%)	210 (27%)		*
	state government	553 (71%)	114 (15%)	115 (15%)		*
	town government	615 (79%)	68 (9%)	97 (12%)		*
	non-profit organizations	267 (35%)	210 (27%)	288 (38%)		*
	communities	267 (35%)	231 (30%)	270 (35%)		NS
	small groups of individuals, or individuals	510 (66%)	98 (13%)	163 (21%)		*
Information seeking	How do you rate your knowledge of how to prevent tick bites?	**A lot**	**None**	**Some**		
		403 (50%)	12 (1%)	394 (49%)		*
	Do you think you need to learn more about how to prevent tick bites?	**Agree**	**Disagree**	**Neutral**		*
		388 (48%)	143 (18%)	277 (34%)		*
		Agree	**Disagree**	**Neutral**		
Trust	Do you trust information on tick control given to you by scientists?	598 (76%)	35 (4%)	150 (19%)		*
		Agree	**Disagree**	**Neutral**		
	Do you trust information on tick control given to you by your town government?	449 (57%)	83 (11%)	249 (32%)		*
Causes of the Tick Problem	What would you say is causing the increase in deer ticks in some parts of Maine?	**Agree**	**Disagree**	**Neutral**		
	climate change	368 (48%)	77 (10%)	329 (43%)		*
	deer overpopulation	622 (79%)	44 (6%)	125 (16%)		*
	invasive plants	206 (27%)	146 (19%)	414 (54%)		*
	rodents	483 (62%)	41 (5%)	255 (33%)		*
		Agree	**Disagree**	**Neutral**		
Pesticide	Would you apply a pesticide on your property to kill ticks if otherwise harmless?	475 (59%)	172 (21%)	157 (20%)		

Table 3.7 Logistic regression models relating importance of Lyme disease and personal protective behaviors taken versus burden of tick bite and tick-borne disease, and support for deer herd reduction versus issues with deer, asked in a survey of residents of Maine's unbridged, off-shore islands, 2016.

	Type 3 Analysis of Effects								
		Significant		Wald		Odds Ratio Estimates			
Category	Model	Effect(s)	DF	Chi-Sq	*P*	Contrasts	OR	LCL	UCL
Importance of Lyme disease in response to burden of ticks/TBD	Is Lyme disease a problem on your island? (agree, neutral/disagree) *n* = 789								
		burden	2	64.6	<.0001	TBD vs. bitten only	1.5	0.8	2.9
						TBD vs. not bitten	**5.8**	**3.7**	**9.0**
						bitten only vs. not bitten	**3.8**	**2.1**	**7.0**
Behavioral response to burden of ticks/TBD	Check myself for ticks after being outside (*n* = 773)								
		burden	2	23.48	<.0001	Tick check always: TBD vs. only bitten	**1.5**	**1.0**	**2.3**
						Tick check always: TBD vs. not bitten	**2.3**	**1.7**	**3.3**
						Tick check always: only bitten vs. not bitten	1.5	1.0	2.4
		gender	1	9.4	0.002	Tick check always: female vs. male	**1.7**	**1.2**	**2.3**
		resident	1	4.7	0.03	Tick check always: seasonal vs. year-round	**1.4**	**1.0**	**1.9**
	How often would you say you protect yourself against tick bites when ticks are out? (always, sometimes, never)								
	Avoid tick habitat (*n* = 756)								
		gender	2	32.2	<.0001	AvoidHab Always: Female vs Male	**3.9**	**2.4**	**6.3**
						AvoidHab Sometimes: Female vs Male	**2.2**	**1.5**	**3.3**
	Use personal repellent (*n* = 775)								
		resident	2	36.9	<.0001	Use repellent always: seasonal vs. year-round	**3.9**	**2.5**	**6.1**
						Use repellent sometimes: seasonal vs. year-round	**1.9**	**1.3**	**2.8**
	Tuck my pants into my socks (*n* = 776)								
		burden	4	10.5	0.03	Tuck pants always: TBD vs only bitten	**2.2**	**1.0**	**4.5**
						Tuck pants sometimes: TBD vs only bitten	1.0	0.6	1.5
						Tuck pants always: TBD vs not bitten	1.0	0.6	1.7
						Tuck pants sometimes: TBD vs not bitten	1.5	1.0	2.2
						Tuck pants always: only bitten vs. not bitten	0.5	0.2	1.1
						Tuck pants sometimes: only bitten vs. not bitten	1.5	0.9	2.6
		gender	2	28.2	<.0001	Tuck pants always: female vs. male	**3.2**	**1.9**	**5.4**
						Tuck pants sometimes: female vs. male	**2.1**	**1.5**	**2.9**
		age	2	15.2	0.0005	Tuck pants always: >55 vs. 18-≤55	**3.3**	**1.8**	**6.0**
						Tuck pants sometimes: >55 vs. 18-≤55	1.2	0.9	1.8
		resident	2	6.2	0.04	Tuck pants always: seasonal vs. year-round	**1.5**	**1.0**	**2.4**
						Tuck pants sometimes: seasonal vs. year-round	**1.4**	**1.0**	**2.0**
	Wear light-colored clothing (*n* = 759)								
		gender	2	23.5	<.0001	Light-colored always: female vs. male	**3.2**	**1.8**	**5.7**
						Light-colored sometimes: female vs. male	**2.1**	**1.4**	**3.0**
		age	1	9.4	0.002	Light-colored pants always: >55 vs. 18-≤55	**2.0**	**1.1**	**3.7**
						Light-colored pants sometimes: >55 vs. 18-≤55	**1.5**	**1.0**	**2.2**
		resident	1	4.7	0.03	Light-colored always: seasonal vs. year-round	**2.6**	**1.6**	**4.4**
						Light-colored sometimes: seasonal vs. year-round	**1.5**	**1.0**	**2.2**
Policy support in relation to problems with deer	Do you think there is a need to reduce the number of deer on your island? (*n* = 760)								
		risk of Lyme	4	72.5	<.0001	Reduce deer agree: Lyme risk agree vs. otherwise	**13.5**	**7.1**	**25.5**
						Reduce deer neutral: Lyme risk agree vs. otherwise	**3.1**	**1.8**	**5.3**
		additional deer issues	4	87.9	<.0001	Reduce deer agree: other deer problems agree vs. otherwise	**13.5**	**7.4**	**24.6**
						Reduce deer neutral: other deer problems agree vs. otherwise	**2.1**	**1.2**	**3.7**
		resident	2	7.8	0.02	Reduce deer agree: resident seasonal vs. year-round	1.5	0.9	2.7
						Reduce deer neutral: resident seasonal vs. year-round	**2.1**	**1.2**	**3.6**
						Reduce deer agree: no hunting tradition vs. hunting	**2.3**	**1.3**	**4.0**
						Reduce deer neutral: no hunting tradition vs. hunting	1.7	1.0	2.8

3.4.2.3 Personal Protective Behaviors

Among behaviors to protect against tick bite, the tick check was the one always performed by more than half the respondents (60%) and was always/sometimes performed by 97% of respondents (Table 3.6). In contrast, always/sometimes use of other protective measures ranged from 56% (tuck pants into socks) to 81% (avoid tick habitat).

Bite/disease burden was a significant predictor of always/sometimes tick checks (*n* = 773, df = 2, Wald chi-square = 12.1, *P* = 0.002, Table 3.7). Odds of respondents who had experienced tick-borne disease (through self, family, or friends) were higher than those who had bitten only or never bitten (OR 1.5, 95% CI 1.0-2.3; OR 2.3, 95% CI 1.7-3.3, respectively, Table 3.7) However, respondents bitten but never ill were no more likely to conduct a tick check than those never bitten by a tick. Thus our results were only partially consistent with hypothesis 2., because we expected bitten respondents to be more likely than non-bitten respondents to conduct tick checks. Odds of women performing tick checks were greater than for men (OR 1.7, 95% CI 1.2-1.9), as were odds of seasonal residents compared to year-round residents (OR 1.4, 95% CI 1.0-1.9).

Women were more likely to avoid tick habitat than men, both always and sometimes (OR 3.9 95% CI 2.5-6.3; OR 2.2 95% CI 1.5-3.3, respectively). Seasonal residents were more likely to use personal repellent than year-round residents, both always and sometimes (OR 3.9 95% CI 2.5-6.1; OR 1.9 95% CI 1.2-3.8, respectively). Respondents were more likely to always tuck their pants into their socks if they had experienced TBD, female, >55 years of age, and seasonal residents, and more likely to always or sometimes wear light-colored clothing if they were female, >55 years of age, and seasonal residents (ORs ranging from 1.4 to 3.3, Table 3.7). In summary, only the tick check was both universally adopted and associated with bite/disease burden.

3.4.2.4 Support for Deer Herd Reduction

Sixty-one percent of respondents agreed there was a need to reduce deer on their island, compared to 12% who disagreed and 27% who were neutral (Table 3.6). Agreement with various deer problems ranged from increased risk of Lyme (82%) to eat my garden plants (69%) to too many, car collision, and over-browse forest vegetation (55%, 41%, 38%, respectively, Table 3.8). There was agreement with positive values as well: enjoy seeing deer (59%), value presence (48%). Only 6% of respondents hunted themselves but 38% had friends/family that were hunters.

Consistent with hypothesis 3., odds respondents supported deer herd reduction were 13 times higher for those who agreed that deer overabundance increased risk of Lyme disease (OR 13.5 95% CI 7.1-25.5) than for those who were neutral or disagreed (Table 3.7). Even those neutral on deer herd reduction were more likely to agree deer overabundance increased risk of Lyme disease (OR 3.1 95% CI 1.8-5.3).

Also consistent with hypothesis 3., Odds of respondents supporting deer herd reduction were 13 times higher for those who agreed overabundant deer caused at least one other problem (apart from Lyme disease) than for those who disagreed (OR 13.5 95% CI 7.4-24.6, Table 3.7). Even those neutral on deer herd reduction were more likely to agreed deer overabundance caused at least one other problem (OR 2.1, 95% CI 1.2-3.7).

Odds of neutrality on deer herd reduction were higher for seasonal residents than for year-round residents (OR 2.1, 95% CI 1.2-3.6, Table 3.7). Odds of support for deer herd reduction where higher for those who did not hunt and had no family and friends who hunted (OR 2.3 CI 1.3-4.1). Removal of Islesboro respondents did not change these patterns. There were no interactions among effects in the deer herd reduction support model.

3.4.2.5 Methods of Deer Herd Reduction

Seventy-eight percent of respondents approved of deer hunting in general (island detail is in Appendix C) and 74% approved of deer hunting on their islands (Table 3.6). Sixty-two percent approved of doe permits and 60% of an expanded archery season as hunting methods to reduce deer. Only 39% of respondents approved of an expanded firearms season to reduce deer. Sixty-three percent of respondents approved of sharpshooting as a method of deer reduction.

More islanders disagreed (40%) than agreed (29%) that off-islanders should be allowed to hunt on-island if family. Across islands, more disagreed (64%) than agreed (14%) that anyone should be allowed to hunt on island; more islanders thought sharpshooting should be paid for by state or federal funds (54%) than town (33%) or private funds (9%).

3.4.2.6 Responsibility for Municipal Tick Control

In terms of who should be responsible for managing tick control, more respondents agreed the town had responsibility (79%) with the state following in 2nd (71%) and the community (i.e., unit smaller than the town, such as a neighborhood) in third (66%). Percent agreeing that responsibility lie with the federal government, non-governmental organizations, or individuals ranged from 35 to 40%. Fifty-nine percent of respondents agreed they would apply a pesticide to control ticks if it were harmless to other animals and people.

3.4.2.7 Causes of the Tick Problem

Seventy-nine percent of respondents attributed increased tick abundance to deer, 62% to rodents, 48% to climate change, and 27% to invasive plant species (Table 3.6). Among 744 respondents agreeing to one or more factors contributing to increased tick abundance, 22.0% (*n* = 169) agreed to one, 40.3% (*n* = 300) to two, 23.7% (*n* = 176) to three, and 13.3% (*n* = 99) to all four factors. Few picked just deer 13.4% (*n* = 100), just rodents 3.5% (*n* = 27), just climate change, 5.0% (*n* = 37) or just invasive plants 0.7% (*n* = 5). Consistent with hypothesis 4., three times as many respondents agreed to 1-3 causes not including invasive plants 72.0% (n = 536) than did those agreeing to 1-4 causes including invasive plants (28%, *n* = 208, df = 1, chi-square =150.0, *P* < 0.0001).

3.4.2.8 Individual Island Opinions on Lyme Disease and Deer

Differences between individual island percent agreeing versus the overall percent agreeing Lyme disease is a problem (83.6%) and overall percent agreeing there is a need to reduce the number of deer (60.8%) are found in Table 3.8. Great Diamond Island, the Cranberry Isles and Frenchboro stood out has having below 50% agreement on Lyme disease as a problem though only Great Diamond and the Cranberry Isles fell below 50% agreement on deer reduction. Reponses for each island by question are in Appendix C, Tables C.1-C.7.

Table 3.8. Differences between individual island percent agreeing versus the overall percent agreeing Lyme disease is a problem (83.6%) and overall percent agreeing there is a need to reduce the number of deer (60.8%).

	Is Lyme disease a problem?				Need to reduce deer?			
Island	All islands (%)	%	difference$_{\text{Lyme}}$	*P*	All islands (%)	%	difference$_{\text{deer}}$	*P*
Cliff	83.7	100.0	16.3	*	60.8	61.9	1.1	
Long	83.7	99.0	15.3	*	60.8	81.3	20.5	*
Swans	83.7	96.0	12.3	*	60.8	57.5	-3.3	
Isle	83.7	95.9	12.3	*	60.8	54.5	-6.2	
Chebeague	83.7	93.3	9.7	*	60.8	56.7	-4.1	
Vinalhaven	83.7	90.0	6.3		60.8	75.4	14.6	*
Islesboro	83.7	86.7	3.0		60.8	69.3	8.5	
North	83.7	78.2	-5.5		60.8	61.5	0.8	
Peaks	83.7	68.4	-15.2	*	60.8	54.4	-6.4	
Great	83.7	42.9	-40.8	*	60.8	18.2	-42.6	*
Frenchboro	83.7	40.0	-43.7	*	60.8	60.0	-0.8	
Cranberry	83.7	30.8	-52.9	*	60.8	15.4	-45.4	*

3.5 Discussion

The intent of this study was two-fold: first, to assemble data on Lyme incidence, entomological risk, and deer herd management history for the unbridged islands of Maine, and second, to poll the residents of the islands to quantify their perceptions of Lyme risk and support for deer herd reduction on their islands. On Maine's offshore islands, deer densities have episodically exceeded social carrying capacity for deer, and the Island Survey indicated that risk of Lyme disease, in conjunction with other deer-related problems, were motivators of support for deer reduction at the time of the 2016 survey.

3.5.1 Island Lyme Incidence, Entomological Risk, and Deer Management History

The offshore islands of Massachusetts and Rhode Island are known for their burdens of tick-borne diseases (TBDs), and this study brings the collective burden of TBD on Maine's offshore islands into a similar focus. During 2010-14, incidences on the islands of Martha's Vineyard (coextensive with Dukes County) and Nantucket Island (coextensive with Nantucket County), MA, were 318 and 495 cases per 100,000, respectively compared to the five-year state average of 62 (MADPH 2018). Incidence was 590 in Block Island (Town of New Shoreham, RI) compared to the statewide average of 87 (RIDPH 2018). In comparison, 2013-17 Lyme incidence in Maine's island municipalities averaged 848 (range 0 to 3,972) compared to the state average of 89 cases/100,000. Where available, our entomological data showed decadal shifts from lower to higher *I. scapularis* density and infection rates. The exception was on Monhegan Island, where deer were eliminated during 1997-1999.

We could not reconstruct pre- and post-cull deer density estimates for most islands, but agency and media reports indicated overabundance led to the culls (Lavigne 1997, Moore 2003, Edgecombe 2003, Leath 2004, MEIFW 2007, Billings 2016, Fleming 2017, MEIFW 2017). Over the years, the print media have documented the narrative of deer abundance exceeding social carrying capacity for deer on the islands. The following observations of MEIFW biologists and islanders on impact of deer overabundance is illustrated through quotes from several news articles:

> Maine Department of Inland Fisheries and Wildlife biologist Gerry Lavigne: "In the 1980s people on Cranberry and Swan's Island began to complain about too many deer…island people probably got comfortable with having a lot of deer around, perhaps even growing accustomed to not having a garden and not seeing native vegetation, because it was a gradual change. Then Lyme Disease changed all that…It wasn't until the emergence of Lyme disease as a human risk that people began thinking seriously about controlling deer…It's why people on Monhegan, and Casco Bay island residents, voted to reduce their deer herds" (Moore 2002).

> MEIFW biologist Thomas Schaeffer: “They [deer] decimate everything in sight…Native grasses and wildflowers disappeared, ornamentals disappeared. You go out there and it seems like a prison – everything is in an enclosure just to protect it from deer…Going from one end of Great Cranberry to another, it wasn’t unusual to see 50 deer standing on lawns” (Moore 2002).

> Randy Billings, Portland Press Herald writer: “when Peaks Island became overrun with deer…The deer herds were so large that deer were starving to death and island residents could not maintain gardens” (Billings 2016).

Whereas the residents of Monhegan ultimately were able to agree on a deer herd management program (elimination in this case), Islesboro has followed a much different trajectory. A group of Islesboro residents formed a tick control committee in the mid-2000s, and the town spent $20,000 out of the town budget to census deer (65/mi^2 in 2012). A reduction program from 2012-14 resulted in little reduction of numbers (50/mi^2 in 2015). A group consisting mostly of summer residents (Concerned Citizens of Islesboro) offered to put $350,000 towards deer reduction by sharpshooter (Town of Islesboro Deer Reduction Committee 2018), but in 2015 the town voted down the sharpshooting option 2 to 1 against. In 2016 the town voted against going to a regular firearms season from the current expanded archery season. The community became polarized and the tick control committee was dismantled (Fleming 2017):

> Sandy Oliver, Islesboro Board of Selectmen: “The problem is everywhere. And it’s incredibly divisive. It’s pitted some of the summer population against some of the year-round residents” (Fleming 2017).

> Linda Gillies, Islesboro Deer Reduction Committee (defunct): “In 2014 and 2015 when the sharpshooting option came up, the community was fractured…People took sides and didn’t speak to each other” (Fleming 2017).

Thus, for Islesboro a workable formula has not been developed yet.

On Swans Island, the 2001-03 reduction hunt that took nearly 270 deer may have been temporarily successful but in 2018 some residents and officials began to discuss another special reduction hunt. In 2018, our lab conducted a pellet group count and estimated 15 deer/mi^2, certainly not as high as numbers on Islesboro, but perhaps still high enough to raise concern among residents. As of this writing Swans Island may reinstate an expanded firearms season to special permit holders (S. Bard, MEIFW wildlife biologist, email communication, January 2019). The City of Portland islands (Cliff, Great Diamond, and Peaks) as well as Long Island have special hunts to apply downward pressure to deer numbers, but rather high densities (~21 to 60) suggest goals are not being met. In summary, most islands with deer have either regular or special hunts, and most are struggling to some extent to keep deer numbers down.

Without accurate data on island-acquired cases of Lyme disease and deer density it would not be appropriate to attempt to correlate Lyme incidence with entomological risk and deer density. However, it can be noted that on the Cranberry Isles and Frenchboro, the culls of 1999-2001 with subsequent hunting pressure apparently have maintained deer at levels satisfactory to residents. Evidence for this is 1) very few survey responses compared to islands with similar populations, 2) survey results indicating well below average concern over Lyme and deer, and 3) lack of news articles compared to the other islands.

The emphasis of this study was not to show that deer densities on islands increased ticks and TBD on Maine's offshore islands, but rather that deer densities have episodically exceeded social carrying capacity for deer. The Island Survey indicated that risk of Lyme disease has been a primary motivator for deer reduction in conjunction with other deer-related problems.

3.5.2 Island Survey

In the Island Survey, 83% of island residents agreed that Lyme disease was a problem on their island whereas only 3% disagreed. Hypothesis 1. was that odds island residents would consider Lyme a problem would be greater for those who had experienced TBD followed by those bitten only, followed by those not bitten, i.e., TBD > bitten only > not bitten. Instead, we found TBD = bitten only > not bitten. Odds of respondents agreeing Lyme disease was a problem on their island were at least four times higher for those who had experienced tick-borne disease (self/family) or tick bite (self/family) versus those never bitten. We interpret this to mean a tick bite elevated perception of risk of contracting Lyme disease to the same level as actually having contracted the disease. None of the control variables--gender, age class, education level—was a significant predictor, suggesting a lack of discrimination on the part of the vector tick based on these demographics. Finding a tick crawling or attached to oneself, family, member, or even pet may immediately shift a person's subjective assessment of risk, i.e., perception of risk, from low to high. Affective reactions to a hazard are fast and automatic (Bodemer and Gaissmaier 2015). Certainly immediate feelings of disgust and fear may attend discovery of a tick on one's body. During and soon after a tick encounter, for most people there may no longer be room for optimistic bias ("it won't happen to me", Bodemer and Gaissmaier 2015, p. 7).

Among protective behaviors, the tick check was by far the most commonly used behavior, compared to avoidance of tick habitat, use of tick repellent, and clothing strategies (tucking pants into socks, wearing light-colored clothes). The tick check was the only protective behavior unequivocally associated with burden of TBD, however, people only bitten were no more likely to perform a tick check than by those never bitten. This was contrary to our expectations (hypothesis 2.) and out of alignment with the result of the first model, which showed bitten-only persons felt Lyme disease was a problem on their island to the same extent as those who had experienced TBD.

Misalignment between knowledge of risk and health behaviors is to be expected and is the topic of a massive body of research on health-related behavior (e.g., Kelly and Barker 2016). What might appear to be an irrational decision might be rational given the social, economic, and political context of the decision (Kelly and Barker 2016). For example, one might not want to go about looking rather silly with one's pants tucked into one's socks. Or, skipping a protective behavior could be a manifestation of optimism bias, whereby personal risk is discounted, to deliver in the moment a feeling of being safe (Weinstein 1989, Bodemer and Gaissmaier 2015). For example, a person going out to the garden might think they are too far from the woods to get a tick. A return of optimistic bias is probably inevitable as time since the last tick encounter increases, since people's perceptions of risk appear to decrease most rapidly during the initial phase of a crisis and then begin to level off (Burns et al. 2012). Alternatively, optimistic bias could manifest if tick encounters are frequent but rapid tick removal has prevented TBD transmission.

Health behaviors varied by certain demographics. Women, people 55 years of age and over, and seasonal residents had a greater propensity to perform behaviors to protect against tick bites than men, younger people, and year-round residents. The gender difference was consistent with the study of Phillips et al. (2001) of residents of Nantucket Island, Massachusetts in which females practiced protective behaviors more frequently.

The behavior unique to seasonal residents was the use of personal repellent. Seasonal residents may arrive at their summer homes with a heightened awareness of the potential for a tick encounter, whether or not they come from a high Lyme incidence state. Initially at least, seasonal residents may find the hazard of TBD more proximal than year-rounders but can improve their sense of control over the risk (Slovic 1987) by applying repellents. This is only conjecture, however.

It was noteworthy that the tick check was the only protective behavior associated with having had TBD or a tick bite. Other protective behaviors were associated with individual demographics but not exposure. Similarly, Slunge and Boman (2018) found a strong positive association between exposure and tick checks but a weak association between exposure and other protective measures. It may be that people feel the tick check is the only effective (or the best) protective measure (Connally et al. 2009), while those who have lowest tolerance for risk are those who take the extra measures.

In the 2016 Island Survey, 61% of respondents agreed there was a need to reduce deer on their island. By contrast, in a 2016 random telephone poll of Maine residents conducted on behalf of MEIFW, only 8% of the general population (n = 301) and 5% of hunters (n = 131) supported a decrease in deer abundance in the southern Maine area (Responsive Management 2016) where deer density is highest (MEIFW 2017). Indeed, 13% and 23% of the general population and hunters, respectively, supported an *increase* in deer abundance. A salient issue is by definition prominent, i.e., of notable significance or relevance. If an issue appears "unrelated to any immediate, obvious personal difficulties" there is no incentive to act; people will pay more attention to pressing issues such as "family, finances, or localized environmental issues" (Yang et al. 2014, p. 301). This study indicated that deer overabundance is a salient localized environmental issue for many Maine islanders. High salience leads to policy support (Yang et al. 2014). Clearly, survey respondents' policy support for deer reduction was much stronger than that of mainlanders'. Still, mainlanders' support for deer reduction increased when negative ecological consequences included poorer deer health and wildlife habitat quality, and increased risk of Lyme disease (Responsive Management 2016). This was consistent with a study of New Jersey residents that found support for deer reduction to prevent negative ecological consequences of not reducing deer (Johnson 2014).

Those with no hunting tradition (self/family/friends) were more likely to support deer herd reduction. It may be that non-hunters feel the only solution is a cull, whereas some hunters maybe believe regular hunting pressure is sufficient to keep deer numbers in check. It also could mean that people with a hunting tradition may prefer higher deer densities for more productive hunting. Stafford et al. (2017) and Williams et al. (2018b) found that a hunter group in Connecticut successfully campaigned against a proposed deer cull as part of a larger integrated tick management (ITM) program that would have brought numbers down below 13/mi^2 (5/km^2) (Williams et al. 2018b). Demographic nuances certainly have and will continue play a role in policy making from one island to the next.

Those opining on deer reduction methods favored, not surprisingly, doe permits and expanded archery over expanded firearms. Take of does is more effective in population control than buck-only take (MEIFW 2007), and archery probably is considered safer on islands than firearms, although four islands do have regular firearms seasons at this time. While these are good options for deer herd reduction, the trick is to apply enough hunting pressure, since most islanders prefer not to bring in even off-island family to increase hunting pressure. Islanders seem comfortable with special permitees, but getting enough of these permitees remains the challenge. Support for sharpshooters was over 50%, but sharpshooters cost money and there was little enthusiasm for taking that from town budgets. Nevertheless, respondents felt responsibility for tick control fell to the town for the most part, ostensibly in partnership with the state. As for who should be responsible for tick control, responses represented a middle ground with respondents feeling federal government should not bear much responsibility, nor should the individual. This is reasonable since even if an individual could treat her or his yard, it would fall to the town to treat trails, school grounds, and other common lands. This and the formation of various tick and deer control committees on various islands indicate a sense of a shared responsibility for community health improvement (LaBonte 1988, IOM 1997).

Many respondents felt they knew a lot about ticks, and desire to learn more was perhaps less than enthusiastic or at least middle-of-the-road. This was not surprising given that *I. scapularis* have been invading the islands since at least the early 1990s, that many islands have received entomological data and outreach from our lab. Certainly, the media has produced a disproportionately high volume of articles on ticks and TBD over the years compared to disease conditions that cause more hospitalizations and deaths, such as seasonal influenza, HIV, hepatitis B and C (Smith et al. 2019b). It may be that the best information for islanders (and the public at large) is cutting-edge information integrated with older information in a way that is balanced, holistic, and to the extent possible, based on scientific studies that are locally applicable.

We were interested in the relative importance islanders ascribed to four factors influencing distribution of *I. scapularis* abundance in Maine, especially the extent to which islanders emphasized one cause, or omitted invasive plant species as a cause. Interestingly, only 22% ascribed the tick problem to any one cause, and only 13% ascribed the tick problem to just deer. Considering the focus of the survey was deer herd reduction, we thought it significant that 64% selected two or three causes. This showed a majority of islanders ascribed Maine's tick problem to multiple causes.

On the other hand, and consistent with our 4th and last hypothesis, only 27% ascribed the tick problem to invasive plant species, with nearly three times as many respondents agreeing to 1-3 causes not including invasive plants vs. agreeing to 1-4 causes including invasive plants. One reason could be lack of media attention to the association between blacklegged ticks and invasive plants. A Nexis Uni® database search of media coverage between January 1, 2010 and December 31, 2018 that included the key phrases “Maine” and “deer ticks” resulted in 161 articles. Adding the key phrase “Japanese barberry” resulted in one article (Curtis 2018) and was the result of an interview with the author. The first evidence *I. scapularis* abundance was elevated in dense growths of Japanese barberry, Asiatic bittersweet and Japanese honeysuckle in Maine was published in the mid-2000s (Lubelczyk et al. 2004, Elias et al. 2006). Soon thereafter in Connecticut, Ward et al. (2009), and Williams and Ward (2010) confirmed higher *I. scapularis* abundance and *B. burgdorferi* infection prevalence in Japanese barberry than in native vegetation. Williams et al. (2017) have demonstrated that Japanese barberry can be suppressed with aggressive management. As Japanese barberry is invading many island and mainland landscapes, this is a key component to include in outreach on tick ecology and integrated tick management.

The “One Health” concept holds that human, veterinary, and wildlife health depend on the health of the landscape (CDC 2018c). We think the more the townspeople can be encouraged to take an ecosystem-based view of a vector-borne infectious disease system (Lambin et al. 2010), the more they can customize integrated tick management solutions for their own towns. A mosaic of characteristics contributes to high densities of *I. scapularis* in a given landscape, including distribution and abundance of suitable deer and rodent hosts, and presence of suitable tick and host habitat, and warming average climate change at the northern edge of the *I. scapularis* range (Eisen et al. 2014). This survey has given us impetus to think about using the One Heath concept as a framework for holistic communication about tick-borne disease risk (e.g., Decker et al. 2011). Residents would benefit their communities by becoming adept at diagnosing the health of the landscape in which they live. There exists a wide array of tools in the integrated pest management (IPM) toolbox (Stafford et al. 2017) available to communities for tick control. Even if people inadvertently have created a mosaic of policies that optimize landscape pathogenicity, they might be able to restore their landscapes to health. Holistic, One Health thinking (e.g., Stafford et al. 2017) may help communities mired in controversy over deer reduction to think of alternative ITM strategies.

3.5.3 Shortcomings of the Study

Challenges in this study included 1) assessment of the burden of Lyme disease, 2) incomplete data on entomological risk, 3) incomplete data on deer herd management histories, and 4) unknown bias associated with convenience sample.

First, a major challenge is assessing the true burden of tick-borne disease for towns with small populations. When the population of an island is, for example, 70, just one case of Lyme disease attributed to the island municipality raises the incidence from zero to 300, over the three times the state average, notwithstanding travel history of the case. Nevertheless, by aggregating across years and islands we had reasonable confidence in the figures from the Maine Center for Disease Control.

Second, due to the vagaries research funding, and it was not possible to accrue consistent entomological data over time for most islands. But by summarizing to the decadal level, we were able to provide reasonable evidence that *I. scapularis* and *B. burgdorferi* infection prevalence have increased over time (with the exception of Monhegan Island).

Third, deer management histories were partial, but the summary we assembled was deemed reasonably complete by MEIFW biologists (N. Bieber, and K. Kemper, email communication, December 2018; S. Lindsay, H. Jones, S. Bard, email communication, January 2019).

Fourth, the island survey was a convenience sample. In the 2016, Maine Inland Fisheries and Wildlife conducted a random sample survey of Maine residents' opinions on big game management by telephone. Demographics of respondents were 52% women, 37% 55+ years of age, and 42% with college degrees or higher, and 14% with post-graduate degrees (Responsive Management 2016). By contrast, in the Island survey respondents were 70% women, 72% 55+ years of age, 76% with college degrees or higher, and 42% with post-graduate degrees. It may be that we heard from more women than men because women are more likely to be health care managers of the household (Grant et al. 2004, U.S. Department of Labor 2005), and the focus of our survey was on health risk, not big game management. Perhaps older women with more education and household income had more time and opportunity to take surveys. Twenty-one percent of respondents were females age 55+ with a post-graduate degree and incomes $55,000 or higher. When we ran the models without this group, odds ratios varied slightly from the original models, but the relationships did not change, e.g., odds of respondents agreeing Lyme disease was a problem on their island higher for those who had experienced tick-borne disease (self/family) or tick bite (self/family) versus those never bitten. Still, people who don't have problems with ticks or no time for surveys were probably less likely to take the survey and we recognize this as a source of bias. Despite the survey's biases, the deer herd management history of the islands corroborated the survey finding that Lyme disease and deer overabundance are salient issues on most islands. Furthermore, even a random sample would have represented a snapshot in time. The best up-to-date metric of public opinion is the town vote.

3.5.4 Recommendations

First, we recommend that island communities keep tabs on their deer densities by way of censuses, perhaps every five years. Aerial census is expensive, but deer pellet group counts can be done for less money or even by volunteer effort. That way, if a community commits to a cull followed by an aggressive maintenance plan, effectiveness of the program can be assessed. What should be the target deer density? In 2002, MEIFW biologist Gerry Lavigne stated "If you really want the complete mix of native flora, you have to keep deer below 20. Not many have that low a density." Moore (2002). To suppress *I. scapularis* and Lyme disease, it has been suggested that density of white-tailed deer should be lowered to below a threshold in the range of 8-13/mi^2 (Telford 1993, Telford 2002, Stafford et al. 2003, Stafford 2007, Kilpatrick et al. 2014, Telford 2017, Chapter 2). MEIFW expresses deer density goals in increments of five, with current goals of 10/mi^2, 15/mi^2, 20/mi^2, for the northernmost, southernmost, and central wildlife management districts (WMDs), respectively (MEIFW 2017). We recommend that deer density goals not exceed 15/mi^2 on the islands and that islanders consider goals below this where culturally acceptable. Deer density estimates are only one way to assess deer abundance and measurable goals. Systems that measure deer and landscape health could corroborate or supplant deer censuses.

The second recommendation is that communities organize efforts to inventory and remove invasive plant species associated with ticks, namely, oriental bittersweet, and Japanese honeysuckle, and especially, Japanese barberry. Peaks Island has conducted at least two rounds of invasive plant species removal to restore native vegetation, and the Town of Falmouth has a budget to remove its invasive plants (Town of Falmouth 2018). If deer herd reduction is a polarizing issue, as it was in Islesboro, a community might focus on other tick control methods. Invasive plant species removal is never easy, but is relatively non-controversial, and actionable on a community and individual level, which is empowering (Witte 1994). Invasive plant removal is money and time well spent, because it allows restoration of native plants and wildlife species in addition eliminating *I. scapularis* habitat. The sale of Japanese barberry and other invasive plants was banned in Maine in 2017; information on identification, removal, and replacement can be found with the Maine Invasive Species Network (https://extension.umaine.edu/invasivespecies) and the Maine Natural Areas Program (https://www.maine.gov/dacf/mnap/features/invasive_plants/invasives.htm).

The third set of recommendations is for communicators involved in outreach on tick ecology and integrated tick management. Communicators can be town officials, natural resource managers, vector ecologists, public health officials, lay persons, and others. First, communicators will benefit from a fundamental knowledge of risk communication principles. For an overview of psychological underpinnings and methods of risk communication we recommend Bodemer and Gaissmaier (2015). The style of outreach should gain trust, establish common values, be procedurally fair, and empowering (Slovic 1993, Witte 1994, Siegrist and Cvetkovich 2000, Poortinga and Pidgeon 2006, McComas et al. 2007, Besley and McComas 2013, Webler 2013). Second, communicators should have a thorough, current, and holistic grasp of the body of research findings and the array of integrated tick management options. Here we have emphasized deer and invasive plant management, but other current (e.g., rodent bait boxes) or future ITM options (e.g., commercially available entomopathogenic fungus, Metarhizium spp.) may be feasible. Communicators also should be sensitive to the locale, history and culture(s) of their audiences. For example, in a coastal fishing community, deer reduction might be feasible, but pesticide application may be completely out of the question, whereas the opposite could be true inland. Outreach also needs to apply research findings with awareness of where the research was conducted. For example, the ecology of Lyme disease in a state such as New York may differ from a state such as Maine because of the varying cultural and ecological contexts, leading to differing policy solutions. Third, communicators should consider framing their outreach in terms of landscape health, i.e., use the One Health framework. This requires awareness of what the current media focus is, and ability to steer stakeholders away from single-issue thinking. A case in point was the Washington Post article “Why this adorable mouse is to blame for the spread of Lyme disease” (Bever 2017). This article focused solely on mice without addressing the larger ecological context of Lyme disease and it also failed to mention how important mice are as prey to many species of wildlife. As Dr. Alessio Mortelitti, University of Maine Professor of Wildlife Ecology has said: “small mammals are the sandwiches of the forest”. Unfortunately, the Bever (2017) article took a “blame wildlife” stance (Roh et al. 2015). Lu et al. (2016) found that acknowledging the benefits of bats (insect control) along with the health risks (rabies) led to greater intentions on the part of national park visitors to report odd bat behavior to park rangers. In conversations about the role of native wild mammal and bird species in the ecology of Lyme disease, we suggest communicators balance discussions by including the benefits of these species. Healthy balance is the essence of the OneHealth concept.

3.6 Conclusions

Communities and natural resource management agencies and public health institutions have wrestled with the controversial issue of deer reduction to control ticks, reduce vehicle collision rates and damage to orchards and peridomestic landscaping, and to improve forest health and health of the deer herd (e.g., Beguin et al. 2009, McShea 2012, Telford 2017). The process of deciding on how to control ticks, including deer herd management, can be lengthy, difficult, and divisive for a community. Our motivation was to assist by providing information to island residents and their collaborators, such as town and city administrators, natural resource managers, public health officials, and vector-borne disease ecologists. As a matter of public policy, MEIFW already considers the relationship between deer and *I. scapularis* important when setting goals for big game species in Maine's wildlife management districts (MEIFW 2017). Since Maine islands have a tradition of awareness of deer overabundance and deer herd management strategies, we think the role of the scientific and public health community is to affirm these efforts and assist with specific recommendations, when requested. Recommendations should suit local environmental conditions and cultural norms. Our bottom-line recommendation for the island communities is to keep deer $\leq 15/\text{mi}^2$ and remove invasive vegetation. Even when Lyme vaccine and anti-tick vaccines come to market, deer herd management and invasive plant species removal will have benefits that extend beyond vector tick control.

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APPENDIX A: CONVERSION OF BUCK KILL INDEX TO DEER PER SQUARE MILE

Table A.1 Regression equations used by the Maine Department of Inland Fisheries and Wildlife to convert buck kill index (BKI) to deer per square mile for each wildlife management district (WMD).

WMD	Equation	Equation type	R^2
1	0.2225*(BKI^0.9722)	curvilinear	0.63
2	(0.0044*(BKI^2))+(0.1365*BKI)+0.0296	polynomial	0.96
3	(0.1726*BKI)-0.1351	linear	0.79
4	0.4344*(BKI^0.7761)	curvilinear	0.87
5	0.2409*(BKI^0.9677)	curvilinear	0.93
6	(0.0127*(BKI^2))-(0.3202*BKI)+4.2234	polynomial	0.87
7	0.2022*(BKI^0.9796)	curvilinear	0.82
8	(-0.0026*(BKI^2))+(0.2789*BKI)-1.2221	polynomial	0.83
9	(0.0039*(BKI^2))-(0.0622*BKI)+3.2201	polynomial	0.59
10	0.3617*(BKI^0.7469)	curvilinear	0.86
11	(0.0023*(BKI^2))-(0.0546*BKI)+4.5121	polynomial	0.93
12	0.0921*(BKI^1.1448)	curvilinear	0.87
13	(0.1816*BKI)-2.0124	linear	0.90
14	2.9123*EXP(0.018*BKI)	curvilinear	0.52
15	2.0846*EXP(0.0171*BKI)	curvilinear	0.92
16	0.0128*(BKI^1.4442)	curvilinear	0.92
17	0.3932*(BKI^0.7984)	curvilinear	0.75
18	0.5174*(BKI^0.663)	curvilinear	0.73
19	(0.0042*(BKI^2))-(0.082*BKI)+3.0274	polynomial	0.82
20	0.0065*(BKI^1.5654)	curvilinear	0.58
21	0.039*(BKI^1.1482)	curvilinear	0.95
22	0.0083*BKI^1.4992	curvilinear	0.92
23	(0.171*BKI)-10.466	linear	0.74
24	0.0295*(BKI^1.2001)	curvilinear	0.83
25	(0.1629*BKI)-6.5855	linear	0.73
26	(0.1759*BKI)-7.3442	linear	0.88
27	0.2004*(BKI^0.906)	curvilinear	0.78
28	(-0.0011*(BKI^2))+(0.1674*BKI)+0.8594	polynomial	0.70
29	0.2083BKI^.8289	power	0.78
		Average R^2:	0.81

APPENDIX B: DETAILS OF GENERALIZED ADDIVITE MODELS

Nonlinear smoothing of covariates is a major aspect of GAMMs. A second major aspect of GAMMs is they combine the results of each predictor variable additively (Fig. B.1), although terms for interaction can also be added and tested for significance in a way analogous to ANOVA (Wood 2017).

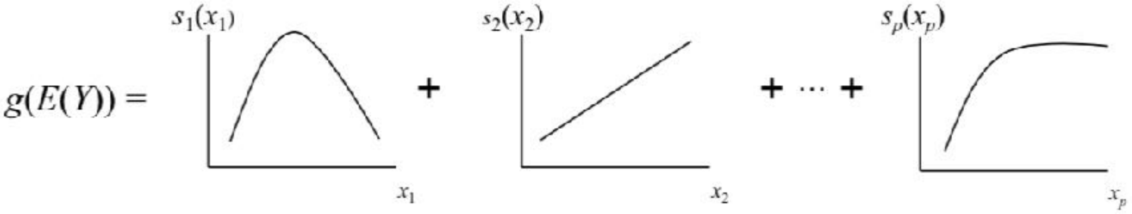

Figure B.1. Generalized additive models combine the results of each predictor variable additively. That is, the additive effect of $\boldsymbol{s}(\boldsymbol{x})$ + $\boldsymbol{s}(\boldsymbol{x})$ leads to $\boldsymbol{s}(\boldsymbol{x})$ + $\boldsymbol{s}$ $(\boldsymbol{x})$ (Larsen 2015).

A GAMM (or GAM) reflects a prior belief that the appropriate model structure would describe the response as a smooth, rather than linear, function of one or more predictors (Wood 2001). A smooth function *f* is composed by the sum of its basis functions *b* and their corresponding regression coefficients β, written as:

$$s(x) = \sum_{k=1}^{K} kbk(x)$$

where k is the basis dimension (Wood et al. 2016). A way to think of this is that for any predictor variable, a number of basis functions are combined to make one overarching smooth function. Generally, GAMs divide the data into sections with knots at the ends of the sections. A low order spline function is fit to the data in the section, with the derivative of the function at the knots constrained to be the same for sections sharing a knot to ensure a smooth and continuous line.

The smooth function is estimated by minimizing the penalized sum of squares

$$\sum_{i=1}^{n}(y_i - f(x_i))^2 + \lambda\int (s''(x))^2$$

where the residual sum of squares term (left of the + sign) ensures fit while the penalty term (right of the + sign) ensures smoothness. The penalty term imposes smoothness by calculating the integrated square of the second derivatives. Since the second derivative measures the slopes of the slopes, a wiggly curve will have large second derivatives, while a straight line will have second derivatives of 0; adding up the squared second derivatives measures the wiggliness of the curve.

Integrated derivatives of the smooth can be written as $\beta^T S\beta$, where S is the penalty matrix. The wigglyness ($\beta^T S\beta$) of the smooth, i.e., closeness to the data, is penalized through a smoothing parameter, λ, thus $\lambda\beta^T S\beta$ represents a trade-off between wiggliness and smoothness that maximizes the likelihood (Wood et al. 2016, Wood 2017).

Figure B.2 illustrates the choice of smooth on the best value of λ versus no penalty (λ = 0) versus a complete smooth (λ ≥ 1), with the correct smooth in blue and the effect of lambda in dark gray. With no penalty (λ = 0), the smooth resembles a very high order polynomial, goes through nearly every data point, and is excessively “wiggly”, whereas a straight line (λ ≥ 1) over-smooths. GAMs have degrees of freedom depending on number of knots, i.e., effective degrees of freedom. GAMs attempt parsimony by balancing the minimal residual deviance on the fewest possible degrees of freedom.

GAMMs allow treatment of “autocorrelation and repeated measures situations” (Wood 2006). In a study with repeated measurements on subjects (in this case, WMDs), subjects’ individual smooths may vary from the global smooth trend over time. Subject random effects may be incorporated into a GAMM by allowing a “factor smooth interaction”, which allows a separate temporal smooth for each factor (i.e., subject), and informs the model that there are repeated measures on *n* subjects.

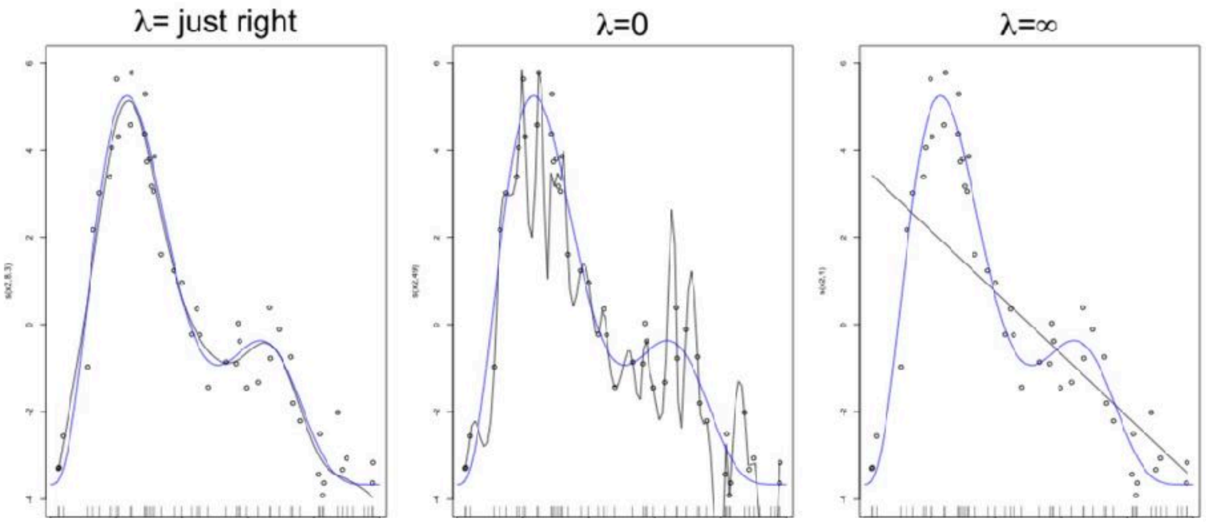

Figure B.2. Effect of choice of smoothing parameter, λ, on wiggliness of smooth (Miller 2016). In all plots, a blue line represents the smooth where λ is just right. Where λ is too “wiggly” the smooth (black line, midde panel) essentially connects the data points and where λ is infinity the smooth (black line, right panel) is a straight line.

With areal spatial data, values for the response can be correlated with values in neighboring units. Areal spatial correlation can be modeled as smooth random spatial effect known as a Markov random field (MRF). The smooth has a coefficient, γ_i for region i. The neighboring areal units of each unit are identified, and a quadratic penalty constructed. If N_i is the set of neighbors of unit i, then the penalty is

$$\sum_i (\sum_{j \in N_i} (\gamma_i - \gamma_j))^2$$

The MRF defines a spatial effect such that the effect of the MRF for any unit varies smoothly over the neighbors of that unit. Smoothness depends on the rank of the MRF. A full-rank (number of knots = the number of spatial units) MRF would result in a “wiggly” or “rough” smooth with essentially one coefficient per unit whereas a low-rank MRF (knots < number of spatial units) the results in a smoother field. For a fully spatiotemporal random effects model, the MRF is allowed to vary over time.

The R code (using “nymphs” as shorthand for nymph submission rate) was as follows:

1. Temporal “factor smooth” random effect

```
gam(sqrt(nymphs) ~ s(year) + [additional main effects] +
  ti(year, WMD, bs = c("fs"), m = 1),
  family=tw(), data=data)
```

where the “ti” syntax specifies the tensor product, bs="fs" requested the factor smooth, and m=1 allowed for more flexibility of the random smooths over the default of m=2 (Sóskuthy 2017, Baayen et al. 2018).

2. Spatial Markov random field random effect

```
gam(sqrt(nymphs) ~ [main effects] +
  s(WMD, bs = "mrf", list(nb = neighborlist)),
  family=tw(), data=data)
```

where “mrf” specified the smoothing basis for the spatial autocorrelation, and “nb” specified the object “neighborlist” with a queen neighbor structure for the WMDs (Wood 2017).

3. Additive temporal-spatial random effect

```
gam(sqrt(nymphs) ~ s(year) + [additional main effects] +
  ti(year, WMD, bs = c("fs"), m = 1) +
```

```
  s(WMD, bs = "mrf", list(nb = neighborlist)),

  family=tw(), data=data).
```

4. Interacting temporal-spatial random effect

```
gam(sqrt(nymphs) ~ [main effects] +

  te(year, WMD, bs = c("fs", "mrf"),

  xt = list(year = NULL, id = list(nb = neighborlist))),

  family=tw(), data=data.
```

APPENDIX C. ISLAND SURVEY RESULTS BY ISLAND

Table C.1. Responses to questions about the importance of Lyme disease and burden of tick bites and tick-borne disease (TBD) asked in a survey of residents of Maine's unbridged, off-shore islands, 2016. An asterix denotes chi-square $P \leq 0.05$.

Category	Question	Responses	All Islands	Frenchboro	Cranberry_Isles	Swans	Isle_au_Haut	Islesboro	North_Haven	Peaks	Vinalhaven	Chebeague	Cliff	Great_Diamond	Long
Importance of Lyme Disease	Is Lyme disease a problem on your island?	Agree	680 (83%)	4 (40%)	4 (31%)	72 (96%)	47 (96%)	91 (87%)	43 (78%)	104 (68%)	63 (90%)	98 (93%)	21 (100%)	15 (43%)	98 (99%)
		Disagree	21 (3%)		5 (38%)			4 (4%)	2 (4%)	4 (3%)	1 (1%)			4 (11%)	1 (1%)
		Neutral	118 (14%)	6 (60%)	4 (31%)	3 (4%)	2 (4%)	10 (10%)	10 (18%)	44 (29%)	6 (9%)	7 (7%)		16 (46%)	
			*	NS	NS	*	*	*	*	*	*	*	.	*	*
Burden of tick bites	Ever bitten by a tick?	N	421 (51%)	9 (90%)	11 (85%)	49 (65%)	10 (20%)	46 (44%)	21 (38%)	98 (64%)	32 (46%)	50 (47%)	12 (57%)	25 (71%)	45 (45%)
		Y	400 (49%)	1 (10%)	2 (15%)	26 (35%)	39 (80%)	59 (56%)	34 (62%)	55 (36%)	38 (54%)	56 (53%)	9 (43%)	10 (29%)	54 (55%)
			NS	*	*	*	*	NS	NS	*	NS	NS	NS	*	NS
Burden of tick-borne disease	Dx Lyme	off-island	44 (18%)	1 (100%)		3 (21%)	5 (24%)	6 (16%)	3 (17%)	11 (28%)	8 (32%)	4 (12%)	1 (10%)	1 (25%)	
		on my island	187 (76%)		1 (100%)	10 (71%)	15 (71%)	29 (76%)	15 (83%)	27 (69%)	15 (60%)	28 (82%)	7 (70%)	3 (75%)	29 (91%)
		Both	15 (6%)			1 (7%)	1 (5%)	3 (8%)		1 (3%)	2 (8%)	2 (6%)	2 (20%)		3 (9%)
			*	.	.	*	*	*	*	*	*	*	*	NS	*
	Dx Anaplamosis	off-island	4 (40%)				1 (100%)	1 (50%)	1 (100%)	1 (33%)					
		on my island	5 (50%)					1 (50%)		1 (33%)		3 (100%)			
		Both	1 (10%)							1 (33%)					
			NS				.	NS	.	NS		.			
	Dx Babesiosis	off-island	5 (29%)						1 (100%)	1 (100%)	3 (75%)				
		on my island	11 (65%)				1 (50%)	1 (100%)			1 (25%)	4 (100%)	2 (100%)		2 (100%)
		Both	1 (6%)				1 (50%)								
			*				NS	.	.	.	NS	.	.		.
	Dx other TBD	off-island	2 (13%)								1 (50%)	1 (25%)			
		on my island	11 (73%)			1 (100%)		2 (67%)	1 (100%)	1 (100%)	1 (50%)	3 (75%)			1 (100%)
		Both	2 (13%)				1 (100%)	1 (33%)							
			*			.	.	NS	.	.	NS	NS			.
	Dx Lyme - Family	off-island	115 (31%)	3 (75%)		11 (34%)	4 (13%)	9 (17%)	5 (19%)	38 (66%)	13 (41%)	14 (29%)		4 (57%)	10 (20%)
		on my island	223 (60%)	1 (25%)		21 (66%)	23 (77%)	37 (70%)	21 (78%)	18 (31%)	17 (53%)	28 (57%)	7 (64%)	3 (43%)	37 (74%)
		Both	31 (8%)				3 (10%)	7 (13%)	1 (4%)	2 (3%)	2 (6%)	7 (14%)	4 (36%)		3 (6%)
			*	NS		NS	*	*	*	*	*	*	NS	NS	*
	Dx Anaplamosis - Family	off-island	10 (45%)			1 (50%)	1 (100%)	1 (20%)	2 (100%)	4 (100%)		1 (33%)			
		on my island	10 (45%)			1 (50%)		3 (60%)				1 (33%)			4 (100%)
		Both	2 (9%)					1 (20%)				1 (33%)			
			NS			NS	.	NS	.	.		NS			.
	Dx Babesiosis - Family	off-island	16 (53%)						3 (100%)	6 (86%)	2 (100%)	4 (44%)			
		on my island	12 (40%)			1 (100%)		1 (50%)		1 (14%)		4 (44%)	1 (100%)		3 (100%)
		Both	2 (7%)					1 (50%)				1 (11%)			
			*			.		NS	.	NS	.	NS	.		.
	Dx other TBD - Family	off-island	4 (36%)		1 (100%)		1 (50%)			2 (67%)					
		on my island	4 (36%)					1 (50%)		1 (33%)					1 (100%)
		Both	3 (27%)			1 (100%)	1 (50%)	1 (50%)							
			NS		.	.	NS	NS		NS					.
Burden of tick bites and disease		Tick-borne disease	480 (58%)	4 (40%)	2 (15%)	42 (56%)	37 (76%)	71 (68%)	31 (56%)	76 (50%)	40 (57%)	69 (65%)	16 (76%)	9 (26%)	63 (64%)
		only bitten	127 (15%)		1 (8%)	12 (16%)	10 (20%)	12 (11%)	12 (22%)	21 (14%)	13 (19%)	16 (15%)	2 (10%)	7 (20%)	17 (17%)
		not bitten	214 (26%)	6 (60%)	10 (77%)	21 (28%)	2 (4%)	22 (21%)	12 (22%)	56 (37%)	17 (24%)	21 (20%)	3 (14%)	19 (54%)	19 (19%)
			*	NS	*	*	*	*	*	*	*	*	*	*	*

Table C.2 Responses to questions about personal behaviors taken to prevent ticks bites, asked in a survey of residents of Maine's unbridged, off-shore islands, 2016.

Question	Method	Responses	All Islands	Frenchboro	Cranberry_Isles	Swans	Isle_au_Haut	Islesboro	North_Haven	Peaks	Vinalhaven	Chebeague	Cliff	Great_Diamond	Long
How often would you say you protect yourself against tick bites when ticks are out?	Avoid tick habitat	Always	210 (26%)	1 (10%)	2 (17%)	10 (14%)	8 (17%)	35 (33%)	10 (19%)	52 (34%)	10 (14%)	30 (29%)	10 (48%)	10 (29%)	28 (28%)
		Never	150 (19%)	3 (30%)	6 (50%)	19 (26%)	8 (17%)	20 (19%)	9 (17%)	30 (20%)	16 (23%)	15 (14%)	2 (10%)	7 (21%)	12 (12%)
		Sometimes	448 (55%)	6 (60%)	4 (33%)	45 (61%)	31 (66%)	50 (48%)	35 (65%)	69 (46%)	43 (62%)	59 (57%)	9 (43%)	17 (50%)	59 (60%)
			*	NS	NS	*	*	*	*	*	*	*	NS	NS	*
	Use repellent	Always	180 (22%)	1 (10%)	1 (8%)	14 (19%)	17 (35%)	26 (25%)	10 (19%)	31 (21%)	16 (24%)	22 (21%)	1 (5%)	6 (18%)	29 (30%)
		Never	199 (25%)	2 (20%)	4 (33%)	18 (24%)	8 (17%)	30 (29%)	18 (34%)	37 (25%)	16 (24%)	30 (29%)	6 (29%)	11 (32%)	15 (15%)
		Sometimes	425 (53%)	7 (70%)	7 (58%)	42 (57%)	23 (48%)	49 (47%)	25 (47%)	82 (55%)	35 (52%)	52 (50%)	14 (67%)	17 (50%)	54 (55%)
			*	*	NS	*	*	*	*	*	*	*	*	NS	*
	Tuck pants into socks	Always	131 (16%)	1 (10%)	1 (8%)	9 (12%)	10 (21%)	16 (15%)	8 (15%)	23 (15%)	16 (24%)	18 (17%)	2 (10%)	3 (9%)	17 (17%)
		Never	349 (44%)	7 (70%)	7 (58%)	35 (47%)	20 (43%)	54 (52%)	31 (58%)	67 (45%)	23 (34%)	38 (36%)	8 (38%)	21 (62%)	31 (32%)
		Sometimes	322 (40%)	2 (20%)	4 (33%)	30 (41%)	17 (36%)	34 (33%)	14 (26%)	59 (40%)	28 (42%)	49 (47%)	11 (52%)	10 (29%)	50 (51%)
			*	*	NS	*	NS	*	*	*	NS	*	*	*	*
	Wear light-colored clothing	Always	109 (14%)		1 (9%)	7 (9%)	10 (21%)	18 (17%)	8 (15%)	17 (11%)	8 (12%)	16 (15%)	2 (10%)	4 (12%)	15 (15%)
		Never	171 (21%)	4 (40%)	3 (27%)	14 (19%)	7 (15%)	20 (19%)	18 (35%)	39 (26%)	13 (20%)	18 (17%)	4 (19%)	9 (26%)	16 (16%)
		Sometimes	521 (65%)	6 (60%)	7 (64%)	53 (72%)	31 (65%)	67 (64%)	26 (50%)	93 (62%)	45 (68%)	71 (68%)	15 (71%)	21 (62%)	67 (68%)
			*	NS	NS	*	*	*	*	*	*	*	*	*	*
	Perform a tick check	Always	483 (60%)	2 (20%)	5 (38%)	39 (53%)	40 (83%)	63 (60%)	31 (57%)	70 (47%)	47 (70%)	68 (65%)	11 (52%)	16 (47%)	70 (71%)
		Never	27 (3%)	2 (20%)	2 (15%)	1 (1%)		3 (3%)		14 (9%)	2 (3%)	1 (1%)		2 (6%)	
		Sometimes	297 (37%)	6 (60%)	6 (46%)	34 (46%)	8 (17%)	39 (37%)	23 (43%)	65 (44%)	18 (27%)	36 (34%)	10 (48%)	16 (47%)	29 (29%)
			*	NS	NS	*	*	*	NS	*	*	*	NS	*	*

Table C.3. Responses to questions about the need to reduce white-tailed deer and deer-related issues and values, asked in a survey of residents of Maine's unbridged, off-shore islands, 2016.

Category	Question	Responses	All Islands	Frenchboro	Cranberry_Isles	Swans	Isle_au_Haut	Islesboro	North_Haven	Peaks	Vinalhaven	Chebeague	Cliff	Great_Diamond	Long
Policy	Is there a need to	Agree	483 (61%)	6 (60%)	2 (15%)	42 (58%)	24 (55%)	70 (69%)	32 (62%)	81 (54%)	52 (75%)	59 (57%)	13 (62%)	6 (18%)	78 (81%)
support	reduce deer on	Disagree	99 (12%)		8 (62%)	9 (12%)	3 (7%)	11 (11%)	3 (6%)	30 (20%)	3 (4%)	13 (13%)	1 (5%)	10 (30%)	4 (4%)
	your island?	Neutral	211 (27%)	4 (40%)	3 (23%)	22 (30%)	17 (39%)	20 (20%)	17 (33%)	38 (26%)	14 (20%)	32 (31%)	7 (33%)	17 (52%)	14 (15%)
			*	NS	NS	*	*	*	*	*	*	*	*	NS	*
Deer	car collision	Agree	321 (41%)	3 (33%)		41 (57%)	17 (38%)	69 (68%)	37 (71%)	32 (22%)	43 (65%)	40 (39%)	1 (5%)	2 (6%)	20 (21%)
values		Disagree	219 (28%)	3 (33%)	12 (92%)	7 (10%)	8 (18%)	9 (9%)	3 (6%)	70 (48%)	4 (6%)	27 (26%)	12 (57%)	26 (79%)	33 (34%)
		Neutral	244 (31%)	3 (33%)	1 (8%)	24 (33%)	20 (44%)	24 (24%)	12 (23%)	43 (30%)	19 (29%)	35 (34%)	8 (38%)	5 (15%)	43 (45%)
			*	NS	*	*	NS	*	*	*	*	NS	*	*	*
	eat my garden plants/	Agree	548 (69%)	10 (100%)	7 (54%)	51 (71%)	36 (80%)	77 (75%)	42 (81%)	79 (53%)	53 (79%)	68 (65%)	15 (71%)	11 (33%)	82 (85%)
	yard plantings	Disagree	116 (15%)		2 (15%)	8 (11%)	6 (13%)	9 (9%)	3 (6%)	41 (28%)	7 (10%)	18 (17%)	3 (14%)	11 (33%)	5 (5%)
		Neutral	128 (16%)		4 (31%)	13 (18%)	3 (7%)	16 (16%)	7 (13%)	28 (19%)	7 (10%)	18 (17%)	3 (14%)	11 (33%)	10 (10%)
			*	.	NS	*	*	*	*	*	*	*	*	NS	*
	over-browse	Agree	301 (38%)	4 (44%)	2 (17%)	26 (37%)	21 (47%)	55 (54%)	17 (33%)	61 (41%)	20 (31%)	29 (28%)	8 (38%)	10 (30%)	38 (40%)
	forest vegetation	Disagree	167 (21%)		7 (58%)	18 (25%)	6 (13%)	13 (13%)	5 (10%)	45 (30%)	14 (22%)	27 (26%)	3 (14%)	13 (39%)	12 (13%)
		Neutral	317 (40%)	5 (56%)	3 (25%)	27 (38%)	18 (40%)	34 (33%)	29 (57%)	43 (29%)	31 (48%)	47 (46%)	10 (48%)	10 (30%)	46 (48%)
			*	NS	NS	NS	*	*	*	NS	*	*	NS	NS	*
	increased risk of	Agree	653 (82%)	6 (67%)	6 (46%)	64 (86%)	41 (91%)	77 (75%)	43 (83%)	115 (77%)	60 (91%)	87 (84%)	19 (90%)	20 (61%)	92 (94%)
	Lyme disease	Disagree	33 (4%)		1 (8%)	2 (3%)	1 (2%)	7 (7%)	1 (2%)	14 (9%)		2 (2%)		4 (12%)	1 (1%)
		Neutral	108 (14%)	3 (33%)	6 (46%)	8 (11%)	3 (7%)	18 (18%)	8 (15%)	20 (13%)	6 (9%)	15 (14%)	2 (10%)	9 (27%)	5 (5%)
			*	NS	NS	*	*	*	*	*	*	*	*	*	*
	too many	Agree	438 (55%)	8 (80%)	2 (15%)	35 (49%)	27 (60%)	66 (65%)	36 (69%)	66 (44%)	45 (66%)	49 (48%)	15 (71%)	9 (27%)	63 (65%)
		Disagree	142 (18%)		9 (69%)	13 (18%)	5 (11%)	10 (10%)	3 (6%)	46 (31%)	5 (7%)	20 (19%)	3 (14%)	16 (48%)	7 (7%)
		Neutral	212 (27%)	2 (20%)	2 (15%)	23 (32%)	13 (29%)	26 (25%)	13 (25%)	37 (25%)	18 (26%)	34 (33%)	3 (14%)	8 (24%)	27 (28%)
			*	NS	*	*	*	*	*	*	*	*	*	NS	*
	enjoy seeing	Agree	467 (59%)	5 (63%)	10 (83%)	43 (58%)	22 (47%)	55 (55%)	29 (55%)	85 (56%)	34 (50%)	66 (63%)	12 (57%)	29 (85%)	60 (62%)
		Disagree	153 (19%)	2 (25%)	1 (8%)	11 (15%)	12 (26%)	21 (21%)	7 (13%)	39 (26%)	15 (22%)	17 (16%)	6 (29%)	2 (6%)	18 (19%)
		Neutral	177 (22%)	1 (13%)	1 (8%)	20 (27%)	13 (28%)	24 (24%)	17 (32%)	27 (18%)	19 (28%)	21 (20%)	3 (14%)	3 (9%)	19 (20%)
			*	NS	*	*	NS	*	*	*	*	*	*	*	*
	value presence	Agree	384 (48%)	4 (44%)	8 (67%)	38 (51%)	19 (40%)	49 (49%)	28 (53%)	77 (52%)	31 (46%)	48 (48%)	10 (48%)	23 (68%)	34 (35%)
		Disagree	191 (24%)	2 (22%)	1 (8%)	15 (20%)	14 (30%)	24 (24%)	10 (19%)	45 (30%)	17 (25%)	22 (22%)	8 (38%)	4 (12%)	25 (26%)
		Neutral	217 (27%)	3 (33%)	3 (25%)	21 (28%)	14 (30%)	26 (26%)	15 (28%)	27 (18%)	20 (29%)	31 (31%)	3 (14%)	7 (21%)	38 (39%)
			*	NS	*	*	NS	*	*	*	NS	*	NS	*	NS
	I hunt deer	Yes	48 (6%)	1 (11%)	5 (42%)	7 (10%)	1 (2%)	5 (5%)	5 (10%)	2 (1%)	2 (3%)	8 (8%)			6 (6%)
		No	625 (80%)	8 (89%)	6 (50%)	60 (83%)	36 (77%)	73 (75%)	38 (73%)	130 (88%)	57 (88%)	81 (81%)	18 (86%)	32 (94%)	70 (73%)
		Neutral	108 (14%)		1 (8%)	5 (7%)	10 (21%)	19 (20%)	9 (17%)	16 (11%)	6 (9%)	11 (11%)	3 (14%)	2 (6%)	20 (21%)
			*	*	NS	*	*	*	*	*	*	*	*	*	*
	My friends/family	Yes	301 (38%)	3 (33%)	11 (85%)	32 (44%)	21 (45%)	39 (40%)	34 (65%)	19 (13%)	24 (36%)	49 (48%)	8 (38%)	6 (18%)	42 (43%)
	hunt deer	No	387 (49%)	6 (67%)	2 (15%)	34 (47%)	19 (40%)	40 (41%)	9 (17%)	116 (79%)	33 (50%)	42 (41%)	10 (48%)	26 (76%)	40 (41%)
		Neutral	99 (13%)			6 (8%)	7 (15%)	19 (19%)	9 (17%)	12 (8%)	9 (14%)	11 (11%)	3 (14%)	2 (6%)	16 (16%)
			*	NS	*	*	*	*	*	*	*	*	NS	*	*

Table C.4 Responses to questions about approval and methods of deer hunting, asked in a survey of residents of Maine's unbridged, off-shore islands, 2016.

Category	Question	Responses	All Islands	Frenchboro	Cranberry_Isles	Swans	Isle_au_Haut	Islesboro	North_Haven	Peaks	Vinalhaven	Chebeague	Cliff	Great_Diamond	Long
Deer hunting	General	Agree	622 (78%)	9 (90%)	11 (85%)	61 (82%)	35 (78%)	85 (83%)	44 (85%)	94 (63%)	54 (78%)	85 (83%)	15 (71%)	25 (76%)	81 (84%)
approval		Disagree	55 (7%)		1 (8%)	3 (4%)	2 (4%)	4 (4%)	2 (4%)	26 (17%)	6 (9%)	2 (2%)		5 (15%)	3 (3%)
		Neutral	118 (15%)	1 (10%)	1 (8%)	10 (14%)	8 (18%)	13 (13%)	6 (12%)	29 (19%)	9 (13%)	15 (15%)	6 (29%)	3 (9%)	13 (13%)
			*	*	*	*	*	*	*	*	*	*	*	*	*
	On my island	Agree	584 (74%)	9 (90%)	11 (85%)	57 (78%)	33 (73%)	86 (84%)	43 (83%)	73 (49%)	55 (81%)	80 (78%)	15 (71%)	20 (61%)	84 (86%)
		Disagree	102 (13%)		1 (8%)	4 (5%)	5 (11%)	3 (3%)	3 (6%)	50 (34%)	6 (9%)	6 (6%)	2 (10%)	8 (24%)	8 (8%)
		Neutral	108 (14%)	1 (10%)	1 (8%)	12 (16%)	7 (16%)	13 (13%)	6 (12%)	25 (17%)	7 (10%)	17 (17%)	4 (19%)	5 (15%)	6 (6%)
			*	*	*	*	*	*	*	*	*	*	*	*	*
Methods of	doe permits	Agree	306 (62%)	6 (100%)	3 (43%)	31 (72%)	11 (46%)	51 (75%)	29 (88%)	19 (24%)	43 (75%)	44 (72%)	7 (58%)	5 (83%)	48 (61%)
reducing deer		Disagree	69 (14%)		1 (14%)	1 (2%)	5 (21%)	3 (4%)		38 (48%)	4 (7%)	4 (7%)	3 (25%)	1 (17%)	5 (6%)
		Neutral	119 (24%)		3 (43%)	11 (26%)	8 (33%)	14 (21%)	4 (12%)	23 (29%)	10 (18%)	13 (21%)	2 (17%)		26 (33%)
			*	.	NS	*	NS	*	*	*	*	*	NS	NS	*
	expanded archery	Agree	295 (60%)	6 (100%)	5 (71%)	20 (47%)	9 (38%)	54 (79%)	27 (84%)	18 (23%)	33 (57%)	46 (75%)	3 (25%)	4 (67%)	58 (74%)
		Disagree	101 (20%)		2 (29%)	9 (21%)	6 (25%)	6 (9%)		44 (55%)	11 (19%)	6 (10%)	7 (58%)	2 (33%)	6 (8%)
		Neutral	97 (20%)			14 (33%)	9 (38%)	8 (12%)	5 (16%)	18 (23%)	14 (24%)	9 (15%)	2 (17%)		14 (18%)
			*	.	NS	NS	NS	*	*	*	*	*	NS	NS	*
	expanded firearms	Agree	193 (39%)	6 (100%)	3 (43%)	20 (47%)	3 (13%)	38 (56%)	16 (48%)	6 (8%)	22 (40%)	32 (52%)	3 (23%)	5 (83%)	32 (41%)
		Disagree	167 (34%)		3 (43%)	8 (19%)	10 (42%)	14 (21%)	9 (27%)	53 (66%)	21 (38%)	15 (25%)	7 (54%)	1 (17%)	21 (27%)
		Neutral	132 (27%)		1 (14%)	15 (35%)	11 (46%)	16 (24%)	8 (24%)	21 (26%)	12 (22%)	14 (23%)	3 (23%)		25 (32%)
			*	.	NS	NS	NS	*	NS	*	NS	*	NS	NS	NS
	sharpshooter	Agree	312 (63%)	2 (33%)	1 (14%)	26 (60%)	12 (50%)	53 (78%)	14 (42%)	72 (89%)	29 (51%)	37 (61%)	10 (77%)	6 (100%)	41 (53%)
		Disagree	104 (21%)	3 (50%)	6 (86%)	8 (19%)	4 (17%)	13 (19%)	11 (33%)	5 (6%)	15 (26%)	13 (21%)	1 (8%)		21 (27%)
		Neutral	79 (16%)	1 (17%)		9 (21%)	8 (33%)	2 (3%)	8 (24%)	4 (5%)	13 (23%)	11 (18%)	2 (15%)		16 (21%)
			*	NS	NS	*	NS	*	NS	*	*	*	*	.	*
	allow off-islanders	Agree	144 (29%)	3 (50%)	1 (14%)	17 (40%)	4 (17%)	26 (39%)	14 (42%)	5 (6%)	9 (16%)	21 (35%)	2 (17%)		38 (49%)
	if family	Disagree	198 (40%)	3 (50%)	2 (29%)	14 (33%)	13 (54%)	13 (20%)	4 (12%)	65 (80%)	18 (32%)	23 (38%)	9 (75%)	4 (67%)	21 (27%)
		Neutral	147 (30%)		4 (57%)	11 (26%)	7 (29%)	27 (41%)	15 (45%)	11 (14%)	29 (52%)	16 (27%)	1 (8%)	2 (33%)	19 (24%)
			*	NS	NS	NS	NS	NS	*	*	*	NS	*	NS	*
	allow any off-islander	Agree	69 (14%)	2 (33%)		7 (16%)	1 (4%)	23 (34%)	4 (12%)	2 (2%)	13 (23%)	7 (11%)			7 (9%)
		Disagree	315 (64%)	4 (67%)	4 (57%)	25 (58%)	18 (75%)	24 (36%)	18 (55%)	69 (85%)	25 (44%)	40 (66%)	12 (100%)	5 (83%)	57 (74%)
		Neutral	108 (22%)		3 (43%)	11 (26%)	5 (21%)	20 (30%)	11 (33%)	10 (12%)	19 (33%)	14 (23%)		1 (17%)	13 (17%)
			*	NS	NS	*	*	NS	*	*	NS	*	.	NS	*
	how to pay	Any	14 (4%)						3 (17%)	2 (3%)	6 (15%)	3 (8%)			
	sharpshooter	Private funds	28 (9%)			1 (4%)	1 (8%)	15 (28%)		2 (3%)	3 (8%)	1 (3%)	1 (10%)		2 (5%)
		State or federal funds	175 (54%)	2 (100%)	1 (50%)	17 (63%)	5 (42%)	18 (34%)	11 (61%)	45 (65%)	22 (56%)	22 (59%)	4 (40%)	3 (50%)	20 (49%)
		Town budget	108 (33%)		1 (50%)	9 (33%)	6 (50%)	20 (38%)	4 (22%)	20 (29%)	8 (21%)	11 (30%)	5 (50%)	3 (50%)	19 (46%)
			*	.	NS	*	NS	NS	*	*	*	*	NS	NS	*

Table C.5. Responses to questions about who should be responsible for tick control, asked in a survey of residents of Maine's unbridged, off-shore islands, 2016.

Category	Question	Responses	All Islands	Frenchboro	Cranberry_Isles	Swans	Isle_au_Haut	Islesboro	North_Haven	Peaks	Vinalhaven	Chebeague	Cliff	Great_Diamond	Long
Responsibility	U.S. government	Agree	308 (40%)	2 (20%)	2 (15%)	26 (37%)	19 (42%)	37 (38%)	16 (33%)	59 (42%)	43 (65%)	45 (44%)	8 (38%)	8 (24%)	31 (32%)
		Disagree	253 (33%)	5 (50%)	11 (85%)	25 (36%)	12 (27%)	42 (43%)	10 (21%)	46 (33%)	9 (14%)	24 (23%)	6 (29%)	20 (61%)	37 (39%)
		Neutral	210 (27%)	3 (30%)		19 (27%)	14 (31%)	19 (19%)	22 (46%)	35 (25%)	14 (21%)	34 (33%)	7 (33%)	5 (15%)	28 (29%)
			*	NS	*	NS	NS	*	NS	*	*	*	NS	*	NS
	State government	Agree	553 (71%)	4 (40%)	3 (23%)	47 (67%)	30 (67%)	64 (63%)	33 (67%)	108 (74%)	60 (90%)	83 (80%)	15 (71%)	17 (52%)	67 (70%)
		Disagree	114 (15%)	3 (30%)	9 (69%)	11 (16%)	7 (16%)	23 (23%)	5 (10%)	19 (13%)	1 (1%)	9 (9%)	2 (10%)	13 (39%)	11 (11%)
		Neutral	115 (15%)	3 (30%)	1 (8%)	12 (17%)	8 (18%)	14 (14%)	11 (22%)	18 (12%)	6 (9%)	12 (12%)	4 (19%)	3 (9%)	18 (19%)
			*	NS	*	*	*	*	*	*	*	*	*	*	*
	Town	Agree	615 (79%)	3 (30%)	7 (54%)	61 (86%)	35 (78%)	85 (84%)	35 (69%)	104 (74%)	58 (85%)	86 (83%)	16 (76%)	24 (73%)	80 (84%)
		Disagree	68 (9%)	1 (10%)	6 (46%)	4 (6%)	6 (13%)	5 (5%)	2 (4%)	21 (15%)	3 (4%)	8 (8%)	1 (5%)	5 (15%)	5 (5%)
		Neutral	97 (12%)	6 (60%)		6 (8%)	4 (9%)	11 (11%)	14 (27%)	16 (11%)	7 (10%)	9 (9%)	4 (19%)	4 (12%)	10 (11%)
			*	NS	NS	*	*	*	*	*	*	*	*	*	*
	Non-governmental organization	Agree	267 (35%)	1 (10%)	3 (25%)	20 (29%)	20 (45%)	41 (41%)	15 (31%)	35 (25%)	33 (51%)	41 (41%)	10 (48%)	9 (27%)	30 (32%)
		Disagree	210 (27%)	3 (30%)	6 (50%)	18 (26%)	11 (25%)	19 (19%)	12 (25%)	48 (34%)	14 (22%)	24 (24%)	5 (24%)	14 (42%)	30 (32%)
		Neutral	288 (38%)	6 (60%)	3 (25%)	30 (44%)	13 (30%)	40 (40%)	21 (44%)	57 (41%)	18 (28%)	36 (36%)	6 (29%)	10 (30%)	35 (37%)
			*	NS	NS	NS	NS	*	NS	NS	*	NS	NS	NS	NS
	Individuals	Agree	267 (35%)	3 (30%)	5 (38%)	26 (38%)	18 (41%)	41 (41%)	14 (30%)	29 (21%)	22 (33%)	43 (42%)	8 (38%)	14 (42%)	33 (35%)
		Disagree	231 (30%)	1 (10%)	7 (54%)	18 (26%)	11 (25%)	28 (28%)	10 (21%)	63 (45%)	20 (30%)	25 (24%)	8 (38%)	8 (24%)	28 (29%)
		Neutral	270 (35%)	6 (60%)	1 (8%)	25 (36%)	15 (34%)	31 (31%)	23 (49%)	47 (34%)	24 (36%)	35 (34%)	5 (24%)	11 (33%)	34 (36%)
			NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS
	Community	Agree	510 (66%)	5 (56%)	8 (62%)	51 (73%)	28 (64%)	79 (78%)	29 (59%)	76 (54%)	48 (72%)	68 (67%)	17 (81%)	21 (64%)	64 (68%)
		Disagree	98 (13%)		4 (31%)	5 (7%)	5 (11%)	7 (7%)	7 (14%)	34 (24%)	5 (7%)	11 (11%)	1 (5%)	4 (12%)	13 (14%)
		Neutral	163 (21%)	4 (44%)	1 (8%)	14 (20%)	11 (25%)	15 (15%)	13 (27%)	30 (21%)	14 (21%)	23 (23%)	3 (14%)	8 (24%)	17 (18%)
			*	NS	NS	*	*	*	*	*	*	*	*	*	*
Pesticide	Apply pesticide if not harmful	Agree	475 (59%)	4 (40%)	4 (31%)	47 (64%)	28 (60%)	57 (56%)	30 (57%)	90 (60%)	36 (53%)	66 (63%)	11 (52%)	23 (68%)	64 (65%)
		Disagree	172 (21%)	3 (30%)	7 (54%)	13 (18%)	8 (17%)	23 (23%)	13 (25%)	34 (23%)	15 (22%)	19 (18%)	5 (24%)	8 (24%)	17 (17%)
		Neutral	157 (20%)	3 (30%)	2 (15%)	14 (19%)	11 (23%)	22 (22%)	10 (19%)	27 (18%)	17 (25%)	19 (18%)	5 (24%)	3 (9%)	18 (18%)
			*	NS	NS	*	*	*	*	*	*	*	NS	*	*

Table C.6. Responses to questions about interest in more about the ecology of Lyme disease and level of trust in scientiests and government, asked in a survey of residents of Maine's unbridged, off-shore islands, 2016.

Category	Question	Responses	All Islands	Frenchboro	Cranberry_Isles	Swans	Isle_au_Haut	Islesboro	North_Haven	Peaks	Vinalhaven	Chebeague	Cliff	Great_Diamond	Long
Information-seeking	My knowledge about tick bite prevention	A lot	403 (50%)	4 (40%)	6 (46%)	33 (45%)	31 (65%)	72 (69%)	20 (38%)	51 (34%)	35 (51%)	59 (56%)	9 (43%)	9 (26%)	61 (62%)
		None	12 (1%)			3 (4%)		1 (1%)	2 (4%)	2 (1%)		2 (2%)		1 (3%)	
		Some	394 (49%)	6 (60%)	7 (54%)	38 (51%)	17 (35%)	31 (30%)	31 (58%)	98 (65%)	34 (49%)	44 (42%)	12 (57%)	24 (71%)	38 (38%)
			*	NS	NS	*	*	*	*	*	NS	*	NS	*	*
	Want to learn more about tick bite prevention	Agree	388 (48%)	3 (30%)	5 (42%)	32 (43%)	19 (40%)	34 (33%)	28 (53%)	86 (57%)	36 (52%)	57 (54%)	12 (57%)	18 (53%)	42 (42%)
		Disagree	143 (18%)	1 (10%)	3 (25%)	15 (20%)	15 (31%)	30 (29%)	9 (17%)	17 (11%)	11 (16%)	12 (11%)	1 (5%)	6 (18%)	19 (19%)
		Neutral	277 (34%)	6 (60%)	4 (33%)	27 (36%)	14 (29%)	40 (38%)	16 (30%)	48 (32%)	22 (32%)	36 (34%)	8 (38%)	10 (29%)	38 (38%)
			*	NS	NS	*	NS	NS	*	*	*	*	*	*	*
Trust	Scientists	Agree	598 (76%)	7 (70%)	8 (62%)	50 (69%)	35 (78%)	74 (73%)	38 (76%)	116 (81%)	52 (76%)	75 (74%)	21 (100%)	29 (88%)	74 (77%)
		Disagree	35 (4%)		2 (15%)	4 (6%)	3 (7%)	6 (6%)	2 (4%)	5 (3%)	4 (6%)	6 (6%)			2 (2%)
		Neutral	150 (19%)	3 (30%)	3 (23%)	18 (25%)	7 (16%)	22 (22%)	10 (20%)	22 (15%)	12 (18%)	21 (21%)		4 (12%)	20 (21%)
			*	NS	NS	*	*	*	*	*	*	*	.	*	*
	Town government	Agree	449 (57%)	4 (40%)	4 (31%)	34 (47%)	23 (51%)	57 (56%)	29 (58%)	80 (56%)	38 (56%)	59 (58%)	13 (62%)	24 (73%)	70 (74%)
		Disagree	83 (11%)		5 (38%)	14 (19%)	7 (16%)	17 (17%)	2 (4%)	15 (11%)	3 (4%)	6 (6%)	1 (5%)	1 (3%)	8 (8%)
		Neutral	249 (32%)	6 (60%)	4 (31%)	24 (33%)	15 (33%)	28 (27%)	19 (38%)	47 (33%)	27 (40%)	37 (36%)	7 (33%)	8 (24%)	17 (18%)
			*	NS	NS	*	*	*	*	*	*	*	*	*	*

Table C.7. Responses to questions about what are thought to be causes of increased deer tick abundance and a question about pesticide use, asked in a survey of residents of Maine's unbridged, off-shore islands, 2016.

Category	Question	Responses	All Islands	Frenchboro	Cranberry_Isles	Swans	Isle_au_Haut	Islesboro	North_Haven	Peaks	Vinalhaven	Chebeague	Cliff	Great_Diamond	Long
Causes of the Tick Problem	climate change	Agree	368 (48%)	3 (33%)	4 (36%)	27 (37%)	17 (38%)	34 (35%)	25 (47%)	78 (54%)	37 (59%)	54 (53%)	16 (76%)	17 (53%)	42 (44%)
		Disagree	77 (10%)		1 (9%)	12 (16%)	3 (7%)	15 (15%)	7 (13%)	10 (7%)	6 (10%)	8 (8%)			12 (13%)
		Neutral	329 (43%)	6 (67%)	6 (55%)	34 (47%)	25 (56%)	48 (49%)	21 (40%)	57 (39%)	20 (32%)	39 (39%)	5 (24%)	15 (47%)	42 (44%)
			*	NS	NS	*	*	*	*	*	*	*	*	NS	*
	deer	Agree	622 (79%)	5 (56%)	7 (58%)	60 (81%)	38 (81%)	72 (72%)	44 (83%)	108 (73%)	59 (89%)	84 (82%)	19 (90%)	17 (52%)	87 (88%)
		Disagree	44 (6%)		3 (25%)	5 (7%)		9 (9%)	3 (6%)	13 (9%)	1 (2%)	3 (3%)		3 (9%)	2 (2%)
		Neutral	125 (16%)	4 (44%)	2 (17%)	9 (12%)	9 (19%)	19 (19%)	6 (11%)	26 (18%)	6 (9%)	15 (15%)	2 (10%)	13 (39%)	10 (10%)
			*	NS	NS	*	*	*	*	*	*	*	*	*	*
	invasive plants	Agree	206 (27%)		6 (60%)	8 (11%)	7 (16%)	40 (41%)	9 (17%)	44 (31%)	12 (20%)	34 (34%)	5 (24%)	7 (21%)	27 (28%)
		Disagree	146 (19%)		2 (20%)	23 (32%)	14 (31%)	13 (13%)	11 (21%)	23 (16%)	18 (31%)	10 (10%)	1 (5%)	4 (12%)	22 (23%)
		Neutral	414 (54%)	9 (100%)	2 (20%)	41 (57%)	24 (53%)	44 (45%)	32 (62%)	77 (53%)	29 (49%)	55 (56%)	15 (71%)	22 (67%)	48 (49%)
			*	.	NS	*	*	*	*	*	*	*	*	*	*
	rodents	Agree	483 (62%)	3 (33%)	6 (50%)	46 (63%)	36 (77%)	72 (72%)	32 (62%)	66 (46%)	30 (49%)	73 (73%)	11 (52%)	20 (59%)	75 (76%)
		Disagree	41 (5%)		1 (8%)	6 (8%)	2 (4%)	5 (5%)	2 (4%)	10 (7%)	1 (2%)	2 (2%)	1 (5%)	2 (6%)	8 (8%)
		Neutral	255 (33%)	6 (67%)	5 (42%)	21 (29%)	9 (19%)	23 (23%)	18 (35%)	67 (47%)	30 (49%)	25 (25%)	9 (43%)	12 (35%)	16 (16%)
			*	NS	NS	*	*	*	*	*	*	*	*	*	*

BIOGRAPHY OF THE AUTHOR

Susan Elias was born in 1962 in Lafayette, Indiana, raised in various US east-coast states, and graduated from Maranacook Community School, Readfield, Maine, in 1980. She graduated from the University of Maine in 1984 with a Bachelor of Science in Wildlife Science and from Virginia Tech in 1994 with a Master of Science in Wildlife Science. She was a research associate at the Holt Research Forest in Arrowsic, Maine, 1998-2007, and has been a research associate at the Vector-borne Disease Laboratory of the Maine Medical Center Research Institute in Scarborough, Maine, 2000 through present. After receiving her PhD degree, Susan will continue at the Vector-borne Disease Laboratory and pursue an interest in teaching college-level biostatistics and vector-borne disease ecology. Susan is a candidate for the Doctor of Philosophy degree in Earth and Climate Sciences from the University of Maine in May 2019.