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MOOSE DENSITY, HABITAT, AND WINTER TICK EPIZOOTICS IN A CHANGING CLIMATE

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MOOSE DENSITY, HABITAT, AND WINTER TICK EPIZOOTICS
IN A CHANGING CLIMATE

BY

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B.S., University of New Hampshire, 2009

THESIS

Submitted to the University of New Hampshire

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in

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This thesis has been examined and approved in partial fulfillment of the requirements for the degree of Master of Science in Natural Resources: Wildlife and Conservation Biology by:

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On March 9th, 2017

Original approval signatures are on file with the University of New Hampshire Graduate School.

DEDICATION

In dedication to my Papa, Robert J. Dunfey Sr. (1928-2016), a businessman, a peacemaker, a loving grandfather, and inspiring proof that a poor Irish family can rise through the shackles of poverty in “the acre”, live among giants, and shake the world.

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ABSTRACT

MOOSE DENSITY, HABITAT, AND WINTER TICK EPIZOOTICS IN A CHANGING CLIMATE

by

Kyle Robert Dunfey-Ball

University of New Hampshire, May, 2017

Unregulated hunting and habitat loss led to a near extirpation of moose (*Alces alces*) in New Hampshire in the 1800s. After state protection in 1901, the estimated population increased slowly to ~500 moose in 1977, then increased rapidly in the next 2 decades to ~7500 following an increase in browse habitat created by spruce budworm (*Choristoneura fumiferana*) and related timber salvage operations, and then halved from 1998-2016 despite highly available optimal habitat. The declining population was partially related to the specific management objective to reduce moose-vehicle collisions, and a possible change in deer hunter and moose behavior that influence population estimates. But given the substantial decline in productivity and condition of cows, and frequent episodes of high calf mortality in April, the primary cause of decline was presumed to be is an increase in winter tick abundance.

This study examined the relationships among moose density, optimal habitat, weather/ground conditions, winter tick abundance, and natal dispersal in northern New England. Comparing movement data from the previous (2002-2006) and current (2014-2016) productivity studies in New Hampshire and Maine, the distance of natal dispersal, home and core range size, and home and core range overlap did not significantly ($P > 0.05$) change despite an increase in optimal habitat and a decrease in moose density.

Geographic changes in tick abundance were related to an interaction between moose density, and the onset and length of winter. Annual changes in tick abundance in northern New Hampshire are driven by desiccating late summer conditions, as well as the length of the fall questing season. Lower precipitation (6.4 cm) and higher minimum temperatures (9.8 °C) specifically concentrated during larval quiescence from mid-August through mid-September reduces winter tick abundance and the likelihood of an epizootic event. The onset of winter, defined by the first snowfall event (> 2.54 cm), influenced the length of the questing season relative to the date of long-term first snowfall event (14 November). In the epizootic region, average winter tick abundance on moose harvested in mid-October indicated a threshold of 36.9 ticks, above which an epizootic is like to occur unless an early snowfall event shortened the fall questing season. Optimal habitat created by forest harvesting was produced at an annual rate of 1.3% (1999-2011) and is not considered limiting in northern New Hampshire, but likely concentrates moose density locally (~4 moose/km^2) facilitating the exchange of winter ticks. In northern New Hampshire, snow cover late into April did not reduce tick abundance in the following year and cold temperatures (< 17 °C) that induced replete adult female mortality are extremely rare in April.

Given a continuation of warming climate and conservative moose harvest weather conditions and high local moose densities will continue to favor the life cycle of winter ticks, increasing the frequency of winter tick epizootics and shift the epizootic region slowly northward. Conversely, temporary reduction of moose density may substantially reduce parasite abundance and support a healthier and more productive moose population.

BACKGROUND INFORMATION

Historical context

In the late 1800s moose were nearly extirpated from northern New England due to unregulated hunting and habitat loss. With subsequent legal protection in all 3 states, the population slowly rebounded. Moose density was considered low throughout northern New England through the 1960s, rare in western and northern parts of Maine, and rare-common in central and eastern parts of Maine (MDIFW unpublished data b). The population was estimated at 500 in New Hampshire in 1977 (Bontaites and Gustafson 1993), and 200 in Vermont in 1980 (Alexander 1993).

In conjunction with forest harvest patterns and the maturation of large area, even-aged balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) stands, the spruce budworm (*Choristoneura fumiferana*) breaks out in high abundance periodically (~60 years) in northeastern North America (UVM 1989, James W. Sewall 1993). In the late 1970s and early 1980s, an outbreak occurred from the White Mountains of New Hampshire to ~51° latitude in Québec, and from eastern Ontario through New Brunswick causing severe defoliation and high natural mortality of spruce-fir stands. During and subsequent to the outbreak, large area timber salvage operations occurred throughout northern Maine and New Hampshire. Interestingly, northeastern Vermont was lightly affected by the budworm from 1975-1984 and salvage operations did not occur in Vermont with the intensity in New Hampshire and Maine (UVM 1989, Pers. comm. C. Alexander VTFW).

The shift from late successional to early successional forest structure and changes in species forest composition caused rapid growth in the regional moose population, from rare-common to highly abundant in 25 years (Fig. 1) due to increased forage resources (forests < 20 years old; Bontaites and Gustafson 1993, Alexander 1993). With moose now abundant, regulated hunting was instituted in Maine, New Hampshire, and Vermont in 1980, 1988, and 1993, respectively.

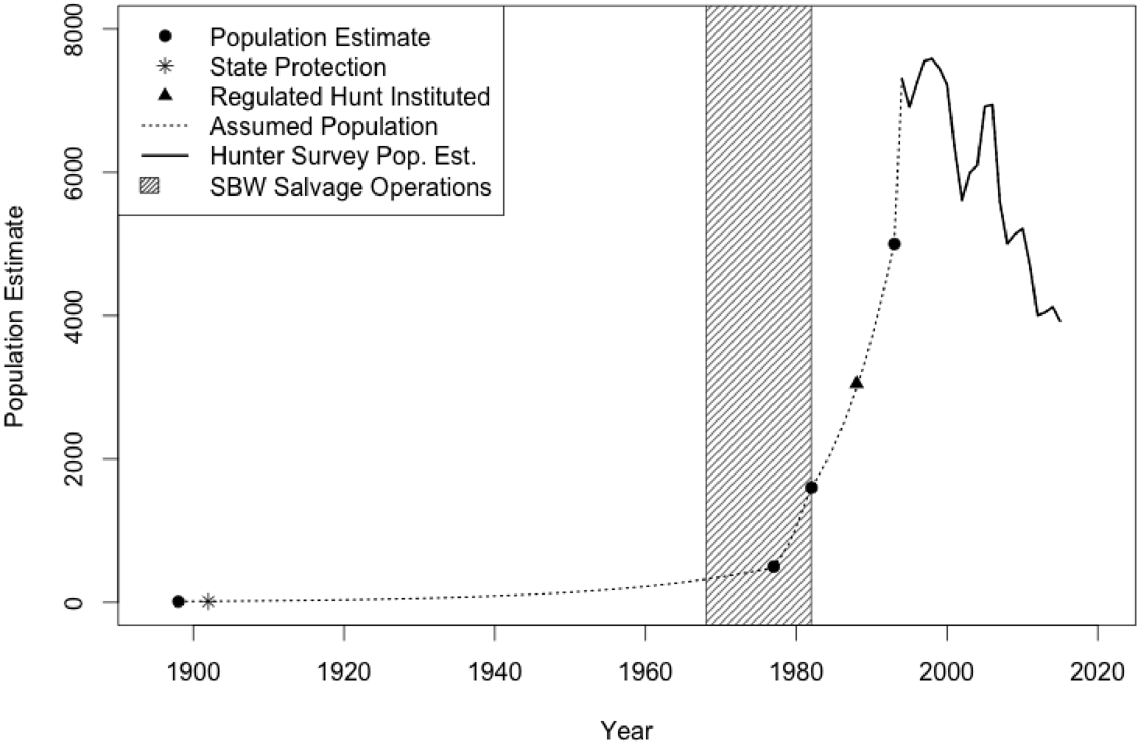


Figure 1: Moose population growth in New Hampshire resulting from state protection, spruce budworm defoliation (1970-1986), and the associated timber salvage operations. Adapted from Bontaites and Gustafson (1993) and NHFG population estimates (Unpublished data 2015).

Consequences of a successful moose population

Winter tick abundance and distribution is correlated with moose density (Blyth 1995, Pybus 1999, Samuel 2004, 2007), and given decades of low density in northern New England, epizootic events were presumably non-existent until at least the 1990s. The earliest anecdotal evidence of winter tick-related mortality was in 1992 (Vermont and Maine), 1995 (Maine), 1997 (Moosehead Lake Region, Maine), 1999 (Maine), and 2001 (Maine); well-documented epizootic events occurred in 2002, 2011, 2014, 2015, and 2016 (Maine Department of Inland Fish and Wildlife (MDIFW) 1998, 1999, 2000, 2001, Samuel 2004, Musante et al. 2010, Bergeron 2011, Jones 2016)

Annual estimates in New Hampshire indicate that the moose population peaked around 1998 and has been in slow decline since (Fig. 1; New Hampshire Fish and Game (NHFG) unpublished data). Northeastern Vermont and central Maine had parallel peaks and declines, as did southern Québec and southern New Brunswick. Conversely, northern Maine, Québec, and New Brunswick had steady, or increasing populations (Vermont Fish and Game unpublished data b, MDIFW unpublished data c, QMFFP unpublished data, NBFW unpublished data). Although certain declines were intentional and rooted in managerial decisions to reduce local populations (e.g., Region E Vermont, CT Lakes Region New Hampshire, NHFG 1998, 2005, Pers. Comm. C. Alexander VTFW), the overall trend indicates a declining population in the southern, and steady or increasing population in the northern sections of the region. This latitudinal decline could relate to the relative abundance of winter ticks that is highly influenced by winter length and ground conditions (DelGiudice et al. 1997, Samuel 2004).

It is also possible that the eventual maturation of forests affected by the spruce budworm reflects a concurrent decline in optimal foraging habitat (4-16 year old forest age class) since the extensive salvage operations. However, habitat quality in northern New Hampshire was considered good in the mid-2000s (Scarpitti 2006).

Further, body weight and productivity in New Hampshire continue to decline, as do ovulation and twinning rates of adults in New Hampshire and Vermont (Bergeron et al. 2013, Jones 2016). Assuming habitat is adequate and non-limiting, these trends suggest that frequent epizootics and continual, moderate-high winter tick loads are influential in the long-term reduction in fitness and productivity of the regional moose population (Samuel 2007, Musante et al. 2010).

Impacts of the winter tick on the moose population

Winter tick epizootics tend to be geographically widespread and temporary, causing abrupt high mortality and short-term impacts on moose populations, specifically declines in the calf and yearling cohorts (Samuel 2004, 2007). High calf mortality (>50%) and epizootic events have been identified with radio-collared moose in New Hampshire in 2002, 2014, 2015, and 2016 (Musante et al. 2010, Jones 2016); anecdotal evidence was consistent throughout the region in 2011. Yearling cows with high tick loads experience poor overall body condition in late winter which can lead to acute anemia and mortality. Additionally, the average dressed body weight of yearlings has dropped below the threshold required for ovulation in this age class (200 kg; Adams and Pekins 1995). High tick loads on calves, yearlings, and adult cows, in concert with poor quality forage resources at the end of winter, manifests itself in reduced fertility overall and a 1-year delay of maturation in yearling cows, and reduces overall fecundity and productivity in the population (Samuel 2004, Musante et al. 2010, Bergeron et al. 2013, Bergeron and Pekins 2014).

Moose populations typically rebound from epizootic events that tend to be sporadic, usually triggered by abnormal and infrequent weather and ground conditions. However, if the frequency of epizootics increase, a continuous deleterious effect may be realized in the population, causing long-term reduction in fitness and productivity (Musante et al. 2010, Bergeron et al. 2013). Given that the increased threat of shorter winters from global climate change favors tick survival, abundance, and attachment rate, a semi-permanent population reduction and contraction of the moose range pose legitimate management concerns.

Impacts of the winter tick on individual moose

Parasites are more likely to be pathogenic when exposed to a host without adaptation to that parasite (Holmes 1996). It is believed that moose lack a natural programmatic grooming response to winter ticks because they did not interact with ticks prior to crossing the Bering land bridge 10,000- 24,000 years ago (Bubenik 1997, Mooring and Samuel 1999). Moose are considered stimulus groomers, and do not groom until responding to the discomfort associated with feeding nymphal and adult ticks (Mooring and Samuel 1998).

Moose respond to winter ticks by avoiding infested vegetation, tolerating corvids feeding on winter ticks, and grooming. The primary response to the itch stimulus is to groom, which includes licking, biting, scratching, and shaking, although grooming is relatively ineffective at removing ticks (Samuel 1991). Increased grooming has negative effects including alopecia (loss of hair), reduced time spent feeding, use of fat stores, restlessness, anemia, and in severe cases, mortality (Samuel 2004), although high associated tick loads produce many of these symptoms. Moose experimentally infested with winter ticks had less fat and lower average weight gain than uninfested moose (McLaughlin and Addison 1986). High tick loads typically lead to excessive grooming and measurable hair loss; hair-loss is rarely severe before March when temperatures usually begin to moderate, and hypothermia is probably rare (Welch et al. 1990). McLaughlin and Addison (1986) estimated that the daily energy requirements of a yearling moose would double if it lost 30% of its hair and temperatures were -20 °C.

High calf mortality was observed in northwestern Minnesota when calves with heavy tick loads and severe hair-loss died after 2 days of -30 °C temperatures and 130 km/h winds (Berg 1975). The amount of hair loss usually corresponds to time spent grooming; hair-loss is observed about 1 month following the start of grooming (Mooring and Samuel 1999).

Samuel and Welch (1991) found an average of 32,500 winter ticks on moose, but tick loads in the New Hampshire study area were 44% higher on average during epizootic years (2014-2015; Jones 2016). Depending on severity of the infestation, engorged adult females are predicted to extract 27-112% of the total blood volume of a calf moose over the course of 3 weeks; this high blood loss causes severe protein deficiency leading to acute anemia (Musante et al. 2007).

Winter tick ecology

Winter ticks occur south of 60 °N latitude excluding Alaska and Newfoundland. They are found on elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer, and the American bison (*Bison bison*), but most severely affect moose (Lankester and Samuel 2007). The winter tick has 3 on-host life stages (Fig. 2), each requiring a blood meal from its single host to develop into the next life stage. Eggs hatch in July-August, and larvae enter a quiescent stage (aka: resting, pre-activity) where they “rest” under leaf litter, and then ascend nearby vegetation to quest for a host in September-October until low temperatures (0 °C) or snow cover prevents activity (Wilkinson 1967, Drew 1984).

Larvae take a blood meal in October-November and molt into nymphs 10-22 days after attachment (Addison and McLaughlin 1988). Nymphs are inactive in December and early January, and take a blood meal and molt into adults in late January-March. Adult ticks take a blood meal and mate on the host in February-May; the engorged adult female drops to the ground, and stays dormant in the leaf litter until June laying 6,000-8,000 eggs and dying thereafter (Addison et al. 1998a, Samuel 2004). In Alberta, peak female engorgement occurs in early April and disengagement occurs over a 9-10 week period from late February to mid-May (Drew and Samuel 1989).

Seasonal temperatures and photoperiod control the life cycle of the winter tick (Addison and McLaughlin 1988, Addison et al. 1998a, Samuel 2004, Addison et al. 2016). Photoperiod likely stimulates initiation of egg laying and oviposition given the substantial variation in spring temperature (Drew and Samuel 1986). Diapause in the nymphal and adult stages allow larvae that attach at different times to mature and oviposit synchronously (Drew and Samuel 1986, Addison and McLaughlin 1988).

Winter ticks use sensory receptors to find and attach to large mammals. The sensory organs enable the tick to detect respiratory carbon dioxide from an animal 20 m distant, shade, and vibration from a nearby host (Samuel 2004). Larvae actively quest at temperatures >10 ^{o}C, but at 0 ^{o}C respond to skin contact only after 2 minutes (Samuel and Welch 1991, Samuel 2004). Larval ticks ascend vegetation to quest and form clumps that range from 10-1,000 at the tips of vegetation at an average height of 1 meter. Larvae may persist on vegetation well into November and December, but transmission is mostly complete when temperatures are < 0 ^{o}C in late October and November (Samuel 1991). Increased bull moose activity during the rut increases the likelihood of larval attachment (Bubenik 1997, Samuel et al. 2000), and is especially true for adult bulls that actively search for receptive cows. Because calves forage more than adults, the average tick load on bulls and calves can be substantially higher than on cows (Drew and Samuel 1985). In New Hampshire, Bergeron et al. (2013) found that the relative tick abundance on calves was consistently higher than on adults. Fall weather is important, as Aalangdong (1994) found that a heavy snowfall in mid-October nearly ceased larval transmission, presumably reducing the winter abundance on moose (Samuel 2007).

Climate change

Biologists have identified declining populations across the southern range of moose in the last decade, including Minnesota, Manitoba, Nova Scotia, Vermont, New York, and New Hampshire (Murray 2006, Broders et al. 2012). Although varied regional differences exist, climate change/warming temperatures are believed to have a negative impact on these southern populations, including increased prominence of disease and parasites (Samuel 2004, Murray 2006, Lankester 2010).

In addition, warmer temperatures associated with climate change were hypothesized by Lenarz et al. (2009) to have direct (negative) thermoregulatory influence on moose resulting in reduced productivity and fitness, higher mortality, and population decline. Heat is the most critical factor limiting the southern distribution of moose, specifically during late winter when moose have thick winter pelage (Karns 2007, Renecker and Schwartz 2007). If moose maintained a consistent temporal foraging pattern, heat stress would increase energy expenditure, reduce activity, and consequently reduce food intake (Renecker and Hudson 1986). However, moose employ thermoregulatory behavior such as increasing nocturnal foraging and seeking out thermal refugia such as conifer forests and wetlands in high ambient temperatures (Dussault et al.

2004, Lowe et al. 2010, Broders et al. 2012, Street et al. 2015), and no direct evidence exists to support the hypothesis.

Weather, ground conditions and the winter tick

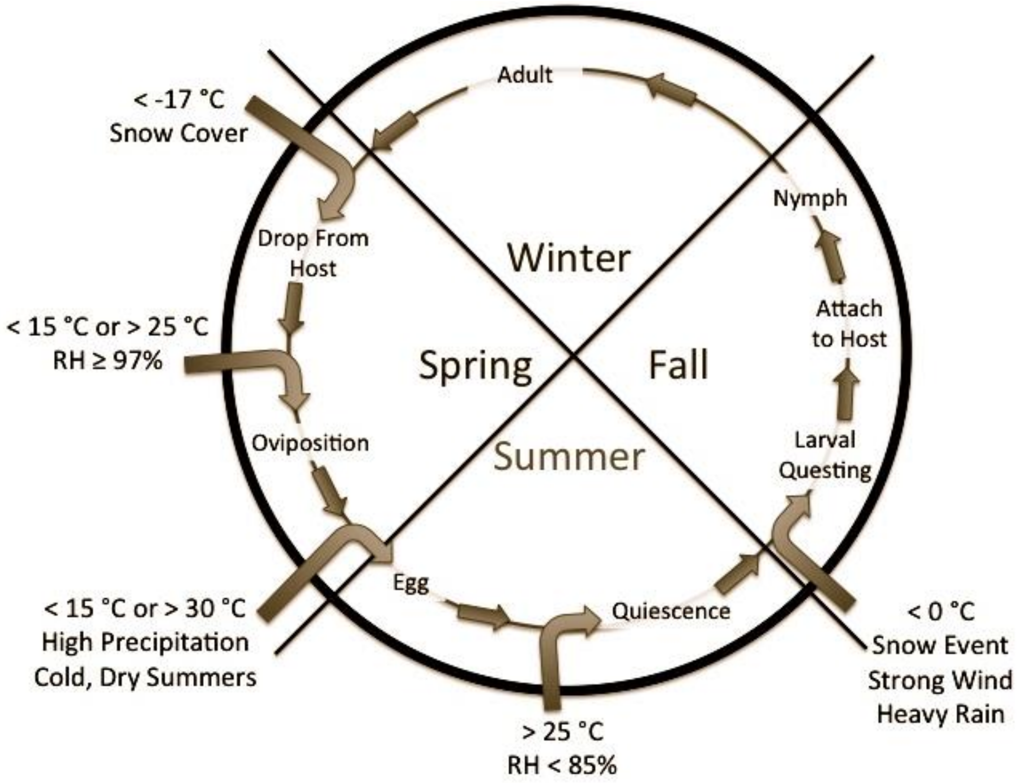


Figure 2: Weather conditions that negatively affect the off-host winter tick life stages; conditions decrease abundance and/or decrease larval attachment to host.

i. Late winter/spring

Winter tick distribution and abundance are largely influenced by weather and ground conditions (Fig. 2; DelGiudice et al. 1997, Samuel 2004). In northern New England, shorter winters, earlier springs, and longer autumns provide better conditions for tick survival, productivity, and questing. Snow cover in late winter/early spring adversely affects the survival of adult female ticks, and consequently egg production (Drew and Samuel 1986). Wilton and Garner (1993) found that major die-offs and hair loss severity were directly related to the mean annual temperature in the prior April. In field trials only 11% of replete adult female ticks survived in snow from mid-March to mid-May with prolonged exposure to temperatures <-17 °C. Conversely, engorged female ticks placed in cages on leaf litter had survival rates of 73% and 55% after snowmelt (Drew and Samuel 1986, Timmerman and Whitlaw 1992).

ii. Early/late summer

In early summer (June-July), cold temperatures and dry conditions reduce egg survival (Aalangdong 1994, Samuel 2004). Lower and upper critical temperature thresholds for successful egg production are 15 and 30 °C, and high ambient temperatures and dry conditions increase larval desiccation in *Dermacentor* and other tick species (Knülle 1966, Yoder et al. 2015).

In late summer, severe drought (dry) conditions and high ambient temperature adversely affect survival of many tick species (Table 1; Knülle 1966). Ticks are irregularly distributed according to how their host utilizes the landscape (Daniel et al. 1977) and the horizontal dispersal of replete adult females is minimal providing little opportunity to select sites for oviposition (Patrick and Hair 1979, Drew 1984). Microclimate in fields, clearcuts, and at forest edges differ in ambient temperature, vapor pressure deficit, and humidity, but conditions in clearcut forest and “open” habitats are more variable and influential in the survival of tick larvae than mature forest (Sonenshine and Tigner 1969, Patrick and Hair 1975, 1979, Koch 1984, Aalangdong 1994, Bertrand and Wilson 1996, Hashimoto and Suzuki 2004, Addison 2016).

Bertrand and Wilson (1996) found greater larval desiccation of the black-legged tick (*Ixodes scapularis*) in field habitats in comparison to the forest or forest edge habitats due to higher air and soil temperature, as well as lower relative humidity and higher vapor pressure deficit. Similarly, Patrick and Hair (1975, 1979) observed a higher desiccation rate of winter and lone star ticks in a meadow habitat than an oak-hickory forest. They concluded that the meadow experienced higher temperature (+2-3 °C in spring, +3-4 °C in summer) relative to the forest in early spring, leading to earlier pre-oviposition in replete females that appeared to stimulate a more rapid vitellogenesis, an earlier oviposition and hatch, increased larval pre-activity, and reduced larval longevity. The inverse also occurred— lower temperatures, higher humidity, and higher precipitation increased larval survival (Patrick and Hair 1979). Koch (1984) measured 50% reduction in larvae of the lone star tick when high temperatures, low humidity, and low rainfall caused severe drying (<65% RH) in July and August; desiccation in dry upland habitats was higher than in moist lowland habitats. Per gram of engorged female winter tick, Addison et al. (2016) measured >2X as many larvae in open deciduous forest habitats during cool, wet summers than in open forest habitats during hot and dry years or closed deciduous forest habitats. Further, larval hatching and questing in open deciduous habitat occurred 2 weeks earlier.

Water balance influences the level of desiccation affecting winter tick larvae in summer and early fall, and is fundamental to the longevity of ticks (Knülle 1966, Yoder et al. 2015). Field measurements of air and soil temperature, relative humidity, and vapor pressure deficit, every 2 h indicated that field habitats were more severe, with maximum air temperatures 3-10 °C higher than at the forest edge or interior forest (Bertrand and Wilson 1996). Hashimoto and Suzuki (2004) found that maximum soil temperatures within 0.5 m of the surface were 3.2 °C higher in clearcut Douglas fir (*Psuedotsuga* *menziesii*) forests. Because high heat and low relative humidity at mid-day are the conditions most severe for ticks, moisture deficits that create critical desiccating conditions limit hatching of eggs to < 50% for 7-13 h/day in grassy and low deciduous environments (Sonenshine and Tigner 1969); however, some eggs are more resistant to desiccation than others (Rechav and Von Maltzahn 1977).

Clearly, extremes (particularly mid-day) in temperature and moisture deficit significantly and negatively affect the equilibrium humidity of larvae, but ticks have the ability to absorb water vapor from air and retain water above a certain relative humidity (Lees 1946, 1947, 1948, Browning 1954, Belozerov and Seravin 1960); e.g. dew formation in dry habitats can be used to equilibrate and recharge from daytime extremes (Wilkinson 1953, Wilkinson and Wilson 1959). A tick can tolerate acute mid-day extremes and recover, but persistent hot and dry conditions can have deleterious effects. For example, Knülle (1966) found that the moisture equilibrium breaks down in *Dermacentor varabilis* after 72 h at relative humidity of 53-60%, and mortality occurs in 5 days. If mid-day conditions create deleterious effects, but ticks are able to equilibrate at night, then presumably, high daily minimum temperatures may be more influential in maintaining persistent desiccating conditions. Yoder et al. (2015) inferred from laboratory experiments that water loss rate of winter tick larvae is related to the maternal water balance at the time of egg production as well as photoperiod. Physiologically, larvae in long-day photoperiods (quiescence) in the summer reduce and conserve moisture loss and short-day photoperiods increase moisture loss.

Table 1: Effect of temperature and moisture on various tick species. Adapted from Knülle (1966).

Species	Stage	Relative Humidity (%)	Temp (° C)	Effect of Treatment	Reference
Dermacentor albipictus	oviposition	97	25	Lavae produce by overhydrated mothers have a greater Critical Equilibrium Humidity (RH: 93-97%)	Yoder et al. 2015
Dermacentor albipictus	oviposition	NA	15 < X ≤ 25	oviposition normal	Wilkinson 1967
Dermacentor albipictus	oviposition	NA	10 < X ≤ 15	oviposition slow	Wilkinson 1967
Dermacentor albipictus	oviposition	NA	≤ 10	oviposition not observed	Wilkinson 1967
Dermacentor albipictus, Amblyomma americanum	oviposition	NA	"high"	Increased larval preactivity	Patrick and Hair 1975,1979
Dermacentor albipictus	larval	"wet"	"cool"	2X larvae survival per gram of engroged female than in hot and dry years in open forest habitat	Addison et al 2016
Dermacentor albipictus	larval	85	25	longevity = several weeks	Yoder et al. 2015
Dermacentor albipictus	larval	NA	≤ 0	Questing attachment slow/stopped	Drew et al. 1984
Dermacentor andersoni	larval	43	25	48 hr: 18.8% weight gain	Knülle 1966
Dermacentor andersoni	larval	43 for 48 hr then 40	25	40% RH: 24, 48 hr 0% weight gain	Knülle 1966
Dermacentor andersoni	larval	43 for 48 hr then 60	25	60% RH: 24 hr: +1%; 48 hr: 0% weight gain	Knülle 1966
Dermacentor andersoni	larval	43 for 48 hr then 80	25	80% RH: 24 hr: +2.9%; 48 hr: cont. weight gain	Knülle 1966
Dermacentor andersoni	larval	43 for 48 hr then 93	25	93% RH: 24 hr: +8.9%; 48 hr: cont. weight gain	Knülle 1966
Dermacentor varabilis	larval	53	25	Equilibrium weight breaks down at 72 hr, die in 5 days	Knülle 1966
Dermacentor varabilis	larval	60	25	Equilibrium weight breaks down at 72 hr, die in 5 days	Knülle 1966
Dermacentor varabilis	larval	73	25	Longevity = 9 days	Knülle 1966
Dermacentor varabilis	larval	85	25	Longevity = 64 days	Knülle 1966
Dermacentor varabilis	larval	90	25	Longevity = 90+ days	Knülle 1966
Dermacentor cajennens	larval	53	25	Longevity = 6 days	Knülle 1966
Dermacentor cajennens	larval	60	25	Longevity = 7 days	Knülle 1966
Dermacentor cajennens	larval	73	25	Longevity = 21 days	Knülle 1966
Amblyomma americanum	egg	NA	≥ 50	lethal high temperatures to eggs	Patrick and Hair 1979
Amblyomma americanum	larval	69	NA	longevity = 3 days	Lancaster and McMillan 1955
Amblyomma americanum	larval	≤ 65	NA	2 months resulted 50% reduction in survival	Koch 1984
Boophilus microplus	larval	90	22.2	longevity = 240 days	Hitchcock 1955
Boophilus microplus	larval	70	22.2	longevity = 12 days	Hitchcock 1955
Amlyomma compressum	larval	80	NA	Unfavorable	Referenced in Knülle 1966
Amlyomma compressum	larval	73	NA	decreased longevity	Referenced in Knülle 1966
Ixodes hexagonus	larval	saturation	NA	longevity = 15 months	Arthur 1951
Ixodes hexagonus	larval	"dry conditions"	NA	"soon killed"	Arthur 1951
Ixodes ricinus	adult female	95	25	longevity = 3 months	Lees 1946
Ixodes ricinus	adult female	70	25	longevity = 4-8 days	Lees 1946
Hard tick group	larval	70	NA	Unfavorable	Aeschlimann 1963

iii. Fall

Fall temperatures < 10 °C and frost/snow cover reduce the larval questing period of winter ticks (Aalangdong 1994, Samuel 2004, 2007) and Musante (2006) attributed the 2002 epizootic in New Hampshire to a snow free fall which allowed for a prolonged questing period. Koch (1984) observed that clusters of lone star tick (*Amblyomma americanum*) larvae remain above ground on vegetation well into November before clusters gradually diminish in size after each frost, although Wilkinson (1967) suggested that winter ticks survive into January, but are inactive. Winter ticks are poikilothermic, meaning they have a reduced metabolic rate at lower temperatures that slows movement at <10 °C, and stops movement below 0 °C. Drew (1984) and Addison et al. (2016) observed peak attachment in October, and gradually declining availability on the landscape through the fall, with an abrupt decline at 0 °C. Larval aggregations can be blown off naturally vegetated plots by frequent and high wind speeds (18-33 km/hr; Welch et al. 1991) or cause them to drop to prevent desiccation (pers. comm. A. Eaton UNH).

Influence of habitat and local density on abundance

The relationship between moose population density and habitat quality and quantity determines carrying capacity (Cowan et al. 1950), and has direct implications for winter tick abundance (Blyth 1995, Pybus 1999, Samuel 2004, 2007), and the nutritional state and productivity of moose (Oldemeyer et al. 1977, Adams and Pekins 1995). Studies indicate that changes in moose density correspond to the proportion of disturbed forestland (Peek et al. 1976, Schwartz and Franzmann 1989).

Large natural forest disturbance in northern New England is generally limited to catastrophic fire and windthrow events. These are rare, occurring once every ~800 and 1,150 years, respectively (Lorimer 1977); smaller localized disturbances are more frequent (15-150 years) and can be severe (DeGraff et al. 2007). However, large area forest disturbance in northern New England is essentially a function of consistent forest harvest activity, such as that associated with large area salvage harvesting associated with the spruce budworm that allowed an expansion of moose in northern New England (Bontaites and Gustafson 1993).

Schwartz and Franzmann (1989) provided a conceptual relationship between forest disturbance (fire) and the density of moose suggesting that density in forest age classes 0-5 and >40 years is low with peak density occurring ~15 years after the disturbance event. Similarly, they infer that areas without predation realize a higher absolute peak density compared to areas with predation. Peek et al. (1976) found moose density to be ~2.5 times higher in recently logged areas relative to surrounding older forests.

Daniel et al. (1977) suggested that tick distribution is irregular even in conditions that are favorable, and is connected with host activity. If a large forest harvest increases local moose density, it could also concentrate where replete adult female ticks drop, and facilitate the subsequent attachment of larvae in fall (Blyth 1995, Pybus 1999). Similarly, if an area lacks optimal browse habitat, it should have relatively low density of moose, and presumably, low winter tick abundance.

Chapter One:

Yearling Dispersal in Northern New England's Declining Moose Population

INTRODUCTION

Dispersal affects density, spatial distribution, colonization, and gene flow of populations (Baker 1978, Greenwood 1980, 1983, Shields 1983, 1987). Greenwood (1980) defined 4 distinct types of dispersal: 1) natal dispersal is the movement of an individual from its natal home range to where it will potentially breed, 2) breeding dispersal is the movement of an individual between successive breeding sites, 3) gross dispersal is the permanent movement of animals away from their natal home range, and 4) effective dispersal indicates gross dispersers that breed in their new range. Numerous studies indicate that the distance of dispersal from the natal home range reflects the relative population density of moose (Howard 1960, Houston 1968, Gasaway et al. 1980, 1985, Cederlund et al. 1987, Ballard et al. 1991); i.e., longer natal dispersal distances are associated with population density near or above carrying capacity. Dispersal distance is also influenced by habitat quality as yearlings move farther to establish new home ranges with better habitat quality (Howard 1960, Gasaway et al. 1980, 1985).

Natal dispersal generally occurs at 9-16 months of age when the cow disassociates with the calf through aggressive behavior associated with parturition. In general, dispersal distance is relatively short, ~2-5 km (Gassaway et al. 1985, Cederlund et al. 1987, Ballard et al. 1991), although home range fidelity may not occur until 2 years of age, inferring that the yearling home range may not be permanent (Houston 1974). Similarly, Cederlund and Sand (1992) observed exploratory movements for 1.5 years, on average, before moose established a home range. These studies support the idea that dispersing yearlings initially occupy marginal, low density and/or low quality habitat until they reach an age where they can compete for high quality habitat (Houston 1968).

At high population density there is increased aggressive and dominant adult behavior causing increased movement and marginalization of yearlings. Such behavior toward yearlings primarily occurs during late spring and summer; yearling males avoid adults following such interactions, with a direct relationship between aggression and dispersal. Further, yearlings are generally absent in areas with a high density of resident adults in late summer, and marginalized to areas of lower quality habitat (Houston 1974).

Home (and core) range size and juxtaposition (overlap) are used to assess relative habitat quality and behavioral relationships and interactions within a population. Both are related to population density and are used as spatial measurements to assess resource competition and natal dispersal. For example, in 2 high-density Alaskan populations (0.6-0.8 moose/km^2) the majority of offspring home ranges (10 of 15) overlapped with the parental home range (Ballard et al. 1991), whereas in a moderate density population (0.2-0.6 moose/km^2) only 1 in 36 overlapped (Gassaway et al. 1985). Additionally, males dispersed farther and had less overlap with their mothers than females (Ballard et al. 1991), an evolutionary strategy that balances the benefit of avoiding inbreeding depression with the cost of dispersal (Auld and Rubio de Casa 2013).

It is assumed that a low density population in good habitat has fewer aggressive or dominant adult-yearling interactions, and consequently, dispersal distance and home and core range size should be smaller, and there should be increased home and core range overlap with maternal ranges, relative to a high density population. The influence of habitat quality can also affect dispersal, hence, its assessment is important to understand and predict dispersal behavior. Temporal change in availability and quality of optimal foraging habitat (i.e., regenerating forest 4-16 years old) is directly associated with timber harvesting activity in the northeastern United States. For yearling moose, dispersal distance, home range, core area, and % overlap with the maternal range should reflect population density. Dispersal distance and home and core range size should decline, and overlap with the maternal range should increase at lower population density, particularly if habitat quality is adequate/increasing; the opposite would presumably occur if habitat quality is poor/declining.

The moose population in New Hampshire has declined measurably from ~6,000 to ~4,000 animals from 2003-2015 (NHFG unpublished data). In a declining population influenced by density dependent mechanisms, individuals should eventually realize reduced resource competition and increased fitness and productivity, assuming resource (food) availability was limited at peak density. However, body weight and productivity continue to decline (Bergeron et al. 2013) despite the assumption that habitat quality in northern New Hampshire is considered good (Scarpitti 2006) and presumably unchanged given the preponderance of commercial forest. Conversely, it is possible that the proportion of optimal foraging habitat has declined measurably since the high timber harvest rates in the 1980s that were associated with both the spruce budworm (*Choristoneura fumiferana*) epidemic and the rapid growth and expansion of the moose population in New Hampshire (Bontaites and Gustafson 1993).

A declining population density presumably results in fewer aggressive or dominant adult interactions with yearlings. Consequently, dispersal distance and home and core range size should decrease at lower density, and home and core range overlap with maternal ranges should increase. To best test this assumption, it is also important to conduct a temporal assessment of relative habitat quality because the relative availability of optimal moose habitat can also influence dispersal.

The overall objective of this study was to measure current dispersal characteristics of radio-marked yearling moose in New Hampshire and Maine to determine whether they reflect changes in population density and/or habitat quality. Specific objectives were to:

1) measure and test for sex-bias in home and core range size, % home and core range overlap with the natal range, and dispersal distance of yearling moose in 2003-2015,
2) measure home and core range size, % home and core range overlap with natal ranges, and dispersal distance for yearling moose in 2014-2015 and compare with similar data measured in New Hampshire in 2003-2005,
3) estimate the percent optimal habitat (4-16 year-old regenerating forest) in the New Hampshire and Maine study areas from 2001-2015, and
4) evaluate the dispersal measurements relative to temporal changes in population density and habitat quality.

METHODS

Study area

The New Hampshire study area is generally the same as used in a previous study (2002-2005) with radio-collared moose (Musante et al. 2010). It is located in eastern Coos County in the towns of Berlin, Stark, Odell, Randolph, Gorham, Erving's Location, Success, Milan, Dummer, Cambridge, Millsfied, Second College Grant, Dix's Location, Errol, Dixville, Wentworth's Location, and Shelburne covering ~2,050 km^2 of primarily mountainous terrain (Fig. 3). This area includes portions of the White Mountain, North, and Connecticut Lakes Moose Management Regions and is primarily located in the Androscoggin and Connecticut River watersheds. The majority of land is privately owned and operated for commercial timber production, and is considered the core moose range with the highest moose density in New Hampshire. Moose density in the North Region has declined ~20% to ~0.55 moose/km^2 from 2002 to 2015 (NHFG unpublished data).

The Maine study area is ~80 km to the northeast allowing for direct biogeographical comparison and is located in Somerset County between the Canadian border and Moosehead Lake, covering ~3,300 km^2 of lowlands and rolling terrain (Fig. 3). It includes Chase Stream Township (Twp), Taunton & Raynham Academy Grant, West Middlesex Canal Grant Twp, Tomhegan Twp, Soldiertown Twp T2 R3 NBKP, Pittston Academy Grant, Thorndike Twp, Long Pond Twp, Shirley, Big Moose Twp, Indian Stream Twp, Bradstreet Twp, Johnson Mountain Twp, Brassua Twp, West Forks Plt, Plymouth Twp, Rockwood Strip T1 R1 NBKP, East Moxie Twp, Lower Enchanted Twp, Rockwood Strip T2 R1 NBKP, Alder Brook Twp, Moosehead Junction Twp, The Forks Plt, Moxie Gore, Jackman, Misery Gore Twp, Bald Mountain Twp T4 R3,Misery

Twp, Squaretown Twp, Sapling Twp, Bowtown Twp, Moose River, Greenville, Upper Enchanted Twp, Pierce Pond Twp, Sandwich Academy Grant Twp, and Parlin Pond Twp. The majority of land is privately owned and operated for commercial timber production. Density in the study area (District 8) was estimated to be 1.35 moose/km^2 in 2015 (MDIFW unpublished data).

In both areas the dominant forest types are northern hardwoods consisting of American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and paper birch (*Betula papyrifera*) in the lower elevations, and boreal forests dominated by red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) at higher elevations, with white cedar (*Thuja occidentalis*) and black spruce (*Picea mariana*) common in lowland swamps.

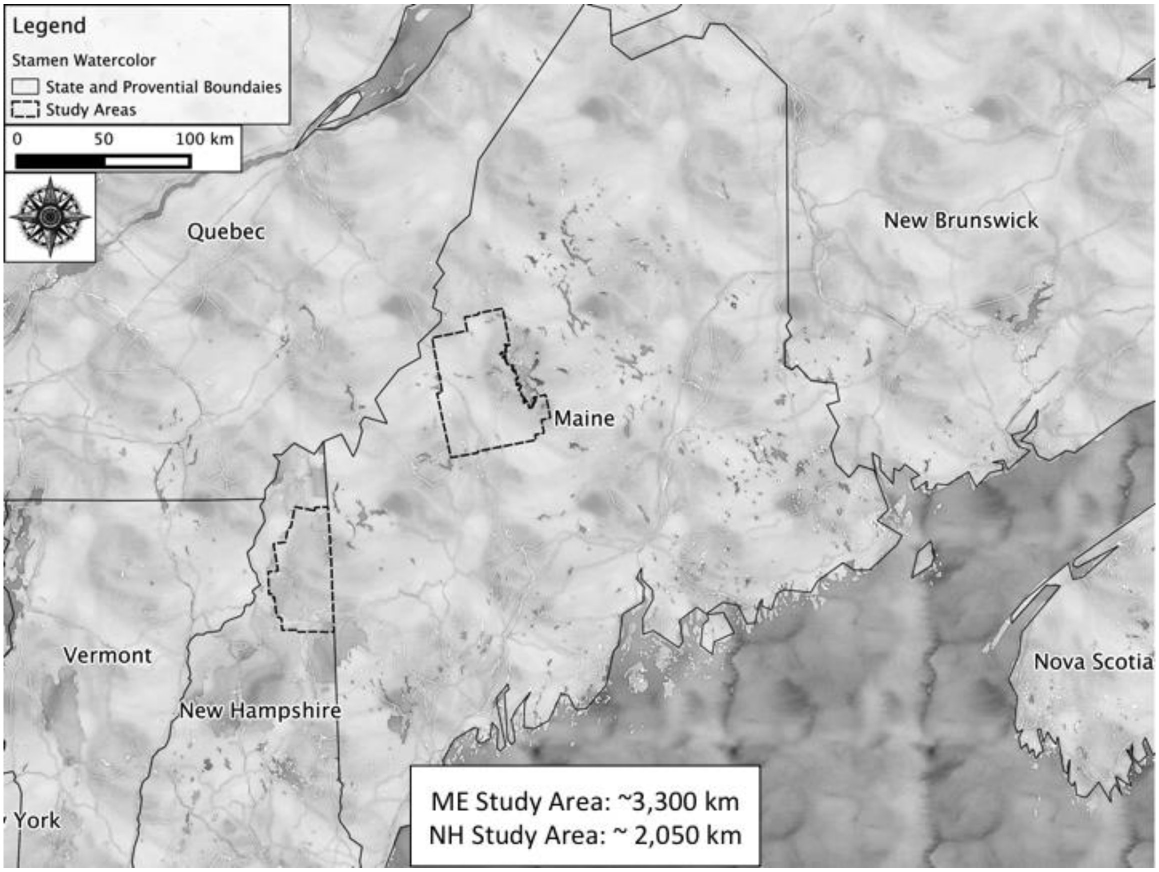


Figure 3: Location of Maine and New Hampshire study areas.

Study animals

The analysis only included yearlings surviving to 1.5 years (past 15 December). Because of the high sampling regime (~1-2 week) implemented in the previous study (2002-2006; Scarpitti 2006), movement data of VHF-collared calves were used to compare with GPS-collared calves in the current studies (Table 2). Direct observations, triangulation, and aerial telemetry were used to identify moose locations. Only GPS-collared calves in the current studies were used in the dispersal analysis, with daily locations acquired at 1200 and 2400 hr in New Hampshire and 0400 and 1600 hr in Maine.

Table 2: Study location and time period, capture year, ear tag number, sex, # of locations measuring natal home range (n NHR), and post-dispersal home range (n PDHR) in New Hampshire (NH) and Maine (ME).

NH Study (2003-2005)					ME Study (2014-2015)					NH Study (2014-2015)				
Year	Tag #	Sex	n NHR	n PDHR	Year	Tag #	Sex	n NHR	n PDHR	Year	Tag #	Sex	n NHR	n PDHR
2002	120	M	43	113	2014	15	M	239	695	2014	29	F	192	133
2002	126	F	84	30	2014	29	F	182	814	2014	37	F	81	329
2002	129	M	52	127	2014	35	F	151	671	2015	79	M	219	280
2002	132	F	43	186	2014	55	F	204	1009	2015	85	M	269	255
2002	139	M	44	54	2014	57	M	353	353	2015	93	F	79	394
2002	141	F	49	177	2014	58	F	205	895					
2002	142	M	42	47	2014	60	M	200	1014					
2002	144	F	45	91	2015	65	F	180	362					
2002	149	M	44	50	2015	68	M	125	258					
2003	118	M	25	77	2015	85	F	162	328					
2003	127	M	15	28	2015	86	M	134	440					
2003	153	M	54	20	2015	91	F	201	321					
2003	154	F	21	99	2015	93	F	149	402					
2003	155	F	26	92	2015	95	F	196	333					
2003	161	F	26	86	2015	96	F	205	353					
2003	162	F	23	88	2015	99	F	177	291					
2003	164	F	22	101	2015	100	F	211	329					
2003	167	F	19	87	2015	101	F	209	363					
2003	168	F	21	47	2015	102	F	200	376					
2003	169	F	19	98	2015	103	F	186	283					
2003	172	M	20	69	2015	104	F	196	342					

<u>Dispersal</u>

Dispersal distance, home and core range areas, and percent home and core range overlap were calculated for 21 yearlings in 2003-2005 (New Hampshire), and 26 yearlings in 2014-2015 (New Hampshire = 5, Maine = 21; Table 2). The date of natal dispersal was defined by a permanent movement (range > 0.2 km) away from the natal home. For those yearlings displaying high fidelity (i.e. movement < 0.2 km), the median calving date (19 May) was assumed as the dispersal date (Musante et al. 2010; Fig. 4).

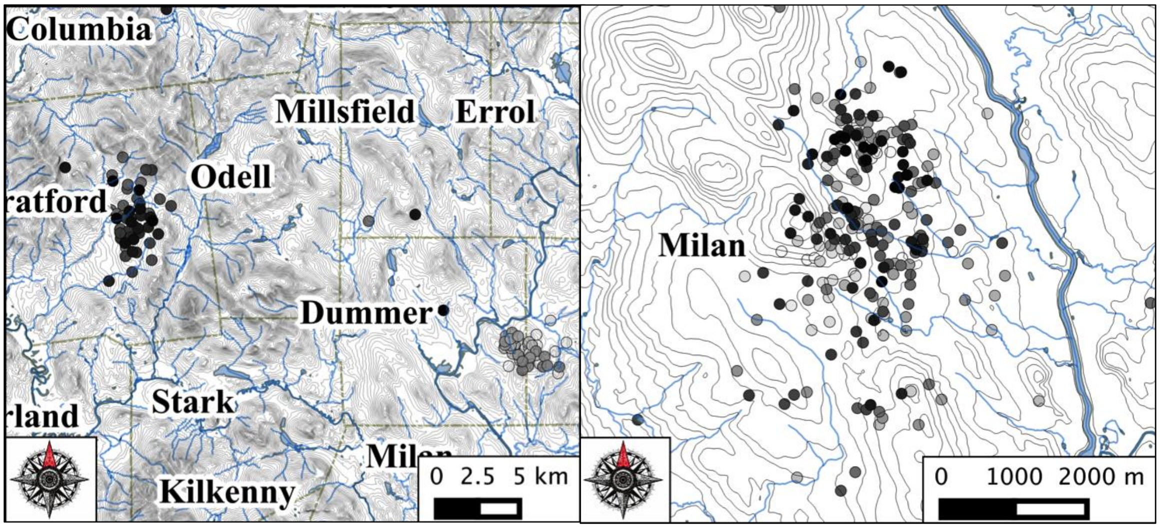


Figure 4: Color stretch by time from white to black. Left: Natal dispersal for yearling 139 was > 0.2 km. Right: Yearling 133 showed high natal home range fidelity and dispersed < 0.2 km.

Prior to dispersal, I assumed that calf movements reflected those of its dam (Ballard et al. 1991). Therefore, natal home and core ranges were estimated from locations between the capture date (~17 January) and natal dispersal (~19 May). Presumably, this timeframe represents a seasonal range and can be expanded in area to reflect the annual home range of the dam. I used the number of days within each season (Scarpitti et al. 2006) as a weighted average to expand the seasonal home and core ranges to annual home and core ranges by factors of 1.82 and 1.51, respectively. Home and core ranges were measured using a bivariate normal kernel density in the R home range statistical package “adehabitatHR”, which produces a probability density that an animal is found in an area relative to historic movements (Worton 1995). Home range was defined as the 90% probability density and core range as the 50% probability density (Börger et al. 2006). The kernel estimator more accurately depicts home range compared to more traditional estimation methods including minimum convex polygon and harmonic mean estimators (Worton 1995, Seaman and Powell 1998).

Post-dispersal home and core ranges were measured if the individual survived through 15 December (last day of the fall season; Scarpitti 2006) and represented all locations after dispersal (Ballard et al. 1991). I assumed that the timeframe between 19 May and 15 December represented the greatest range of movement, was comparable to the annual home range in the study area found by Scarpitti (2006), and seasonally represented the post-dispersal home range.

Dispersal distance was defined as the distance between centroid coordinates of the natal and post-dispersal core ranges, also known as the linear distance between centers of activity. Percent home range overlap was defined as the proportion (%) of intersecting area of the natal and post-dispersal home ranges, and similarly, percent core range overlap was the proportion of intersecting area of the natal and post-dispersal core ranges (Hayne 1949, Dice and Clark 1953, Scarpitti 2006).

Testing for sex-bias dispersal

Data from all studies were combined to measure sex-biased dispersal of 18 males and 29 females (Table 2). The Student’s *t*-test was applied to measure statistical differences between male and female dispersal characteristics: home range area, percent home range overlap, core range area, percent core range overlap, and dispersal distance.

Temporal comparison

With known differences in dispersal behavior between male and female moose (Ballard et al. 1991), sex-biased dispersal was assumed, and only females were used to compare temporal changes in dispersal given their larger sample size (n = 12 and 19; Table 2), reduced dispersal variability, and more predictable behavior. A *t*-test was used to determine if there was a difference between time periods (2003-2005 and 2014-2015) relative to home and core range size, home range and core range overlap, and dispersal distance.

Assessment of optimal habitat

A remote sensing-based Vegetation Change Tracker (VCT) was used to measure the proportion (%) of forest disturbance in the Maine and New Hampshire study areas from 1985-2011. The VCT is a Landsat time series stack (LTSS) of historic (1984-2011) satellite imagery with 30 m spatial resolution that was originally produced to detect the year and magnitude of forest disturbances (Huang et al. 2009). It has been used to map forest fragmentation through time, better account for modeling forest carbon budgets, and map annual forest disturbance types (Li et al. 2009, Masek et al. 2013, Zhao 2015). Landsat scene selection and VCT processing is described by Huang et al. (2009).

The VCT identifies forest disturbances ≥ 0.09 ha that have been detected for ≥ 2 consecutive years. Overall accuracy is 77-86% with a forest change user's accuracy of 64-88% for a disturbance within 1 year of reference data. Stand-clearing disturbances including clearcuts, severe fires, and major storm events have a 75-85% detection rate; given a relaxed temporal window of ±1 year, non-stand clearing disturbances have an accuracy of 60%. In general, omission errors are greater than commission errors and the

VCT underestimates forest disturbance by an average of 24% (Thomas et al. 2011, Masek et al. 2013). VCT data were obtained for the following Landsat path/rows: 13/29, 12/30, 12/29, and 12/28 that cover western Maine and northern New Hampshire.

Peek et al. (1976) indicated that habitat quality (browse) is greatest during the 20 years following a stand-clearing event, and I defined optimal foraging habitat as the 4-16 year age class. The proportion (%) of annual land conversion was defined as the difference in area between the VCT persisting non-forest class (value = 1) and the 2011 National Land Cover Dataset non-forest classes (values = 21, 22, 23, 24, 31, 81, 82) by year. The adjusted annual forest disturbance is the difference between annual land conversion and the proportion (%) of annual forest disturbance. Optimal habitat from 2001-2015 is a 13-year moving sum of the adjusted annual forest disturbances 4-16 years old.

RESULTS

Sex-biased dispersal

Males dispersed ~4X farther than females (2.3 km; $P = 0.0066$). Home and core ranges of males were 2.8X and 2.3X larger than those of females, respectively, but were not significantly different ($P = 0.06$; Table 3). Overall, the majority of post-dispersal home (94% females, 86% males) and core (78% females and 76% males) ranges overlapped with natal home and core ranges, although overlap was < 40% for both. Females had ~2.3X larger overlap in home range ($P = 0.0004$), and ~10X larger overlap in core range than males ($P = 1.4$ e-7).

Table 3: Dispersal distance, home range area, core range area, home range overlap, and core range overlap of male and female yearling moose in northern New England (2003-2015).

		Male				Female				
Variable	unit	mean	se	lower range	upper range	mean	se	lower range	upper range	ρ-value
Dispersal Distance	km	9.3	3.1	1.1	25.4	2.3	0.4	0.1	8.4	0.0066
Home Range	km^2	136.5	69.0	11.1	700.3	48.6	9.0	8.4	256.5	0.0604
Core Range	km^2	31.3	12.6	3.2	130.9	13.1	2.6	2.4	77.6	0.0621
HR Overlap	km^2	16.7	5.8	0.0	43.4	21.0	3.4	0.0	99.3	0.3840
HR Overlap	%	16.9	3.4	0.0	56.4	37.6	3.7	0.0	70.2	0.0004
CR Overlap	km^2	0.6	0.6	0.0	3.9	3.3	0.6	0.0	16.2	0.0004
CR Overlap	%	2.4	2.7	0.0	23.6	24.5	3.1	0.0	61.4	0.0000

Temporal comparison of yearling females

The average date of natal dispersal in both time periods was 26 May. Natal dispersal characteristics between the time periods were not statistically different (Table 4), but absolute differences were measurable. Females in the current studies dispersed ~30% farther than in the previous study (Table 3), although home and core ranges were ~20% larger in that study (53.8 and 14.6 km^2). Percent home range overlap was nearly identical between the studies (~37.6%), although overlap in core range was 33% larger in 2003-2005.

Table 4: Dispersal distance, home range area, core range area, percent home range overlap, and percent core range overlap of females in the previous (2003-2005) and current study periods (2014-2015). No difference were found between the two studies.

		2003-2005				2014-2015				
Variable	unit	mean	se	lower range	upper range	mean	se	lower range	upper range	ρ-value
Dispersal Distance	km	1.9	0.7	0.1	7.0	2.6	0.5	0.4	8.4	0.43
Home Range	km^2	53.8	20.1	12.0	256.5	45.3	7.8	8.4	142.9	0.70
Core Range	km^2	14.6	6.1	2.6	77.6	12.1	2.1	2.4	40.5	0.70
HR Overlap	km^2	18.9	4.1	0.0	49.7	22.4	4.9	6.0	99.3	0.58
HR Overlap	%	37.7	6.3	0.0	70.2	37.6	4.6	5.4	69.4	0.99
CR Overlap	km^2	3.4	0.6	0.0	8.3	3.3	0.9	0.0	16.2	0.93
CR Overlap	%	28.9	5.3	0.0	61.4	21.7	3.8	0.0	44.9	0.28

Assessment of optimal habitat

The mean rate of annual forest disturbance from 1985-2011 was 1.0% and 1.5% in the New Hampshire and Maine study areas, respectively. In New Hampshire, a net increase of 19.0 km^2 (~0.9%) land conversion was realized from 1984-2011; there was no measurable change in the Maine study area. Optimal habitat increased 2.5X in New Hampshire from 2001 (7.0%) to 2015 (17.5%). Concurrently, optimal habitat in the Maine study area declined from 21.5% to 17.8%, and the proportion of quality habitat is now similar in the 2 study areas (Fig. 5).

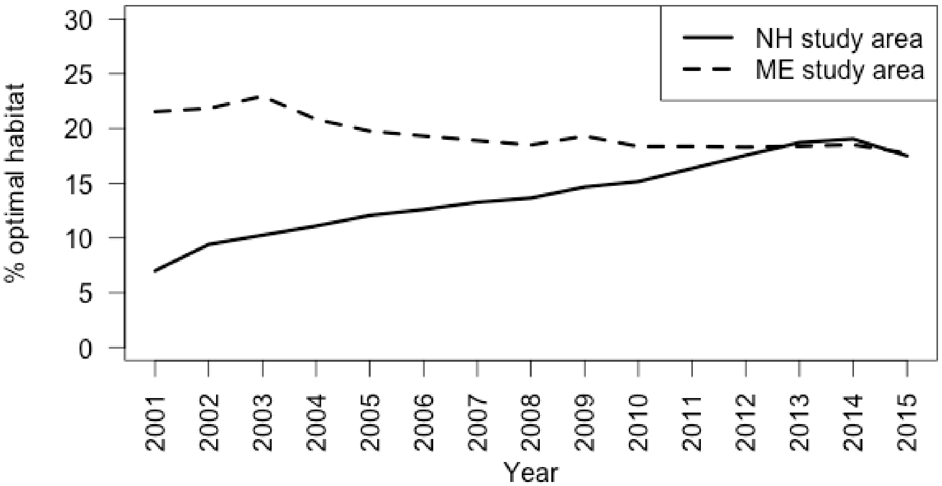


Figure 5: Percent optimal habitat (4-16 year forest age class) in the Maine and New Hampshire study areas measured using a Vegetation Change Tracker.

DISCUSSION

Longer (4X) dispersal by yearling males than females was consistent with previous studies and not unexpected. The average dispersal distance of males (9.26 km) was 2-4X longer than reported in Wyoming, Alaska, and Sweden; dispersal distance of females (2.34 km) was also 1-2X longer (Houston 1968, Gassaway et al. 1985, Cederlund et al. 1987, Ballard et al. 1991, Cederlund and Sand 1992).

Post-dispersal home and core ranges of males were ~2.5X larger than female ranges and tended to have less overlap with the natal home range (Table 3). In comparison to south-central Alaska (Ballard et al. 1991), the home ranges were 37% smaller for females and 50% larger for males; 91% (43 of 47) had overlap with the natal home range, far exceeding the 3% (1 of 36; Gassaway et al. 1985) and 66% (10 of 15; Ballard et al. 1991) measured in Alaska. The proportion of natal home range overlap for males was similar to that in Sweden (10-40%), although the average home range overlap for females was less than the minimum in Sweden (40%; Cederlund and Sand 1992).

The yearling female post-dispersal home ranges were larger than annual adult cow home ranges measured previously in New Hampshire (24.6 km^2; Scarpitti 2006) and Maine (28.0 km^2; Thompson et al. 1995), but 50% smaller than measured in Alaska (Ballard et al. 1991). The difference in home range size between yearling and adult cows supports Houston's (1968) idea that dispersing yearlings exhibit exploratory behavior and may initially occupy marginal, low density and/or low quality habitat assuming it exists and saturation occurs. Given that home range fidelity does not typically occur until 2 years of age (Houston 1974, Cederlund and Sand 1992) and that food resources have presumably increased 2.5X since 2001 (Fig. 5), it seems reasonable that the larger home range size primarily reflects exploratory behavior rather than access to quality resources in a saturated social structure relative to adult cows. Home and core ranges were 20% larger in 2003-2005 suggesting that habitat quality has increased and/or population density has declined. Conversely, it is possible that these larger home ranges reflected use of VHF-radios that yielded locations with less precision, although the home ranges were based on >50 locations and should be comparable with GPS-derived home ranges (Scarpitti 2006).

Longer natal dispersal distances, dispersal into areas of high hunting pressure, and/or low density (bulls in particular) tends to be associated with higher moose densities (Ballard et al. 1991). Despite high density (1.3 moose/km^2) in Sweden in 1982, dispersal distance was short (~2 km) and sex-biased dispersal was not evident, presumably because of high harvest (30%) of the winter population (Cederlund et al. 1987). I found that females in New England dispersed ~30% farther and their average home range overlap was less than the minimum for females in Sweden (40%; Cederlund and Sand 1992), suggesting that moose density has increased, which contradicts the smaller home and core range measurements suggesting that moose density has decreased.

Optimal habitat more than doubled (2.5X) in the New Hampshire study area from 2001 to 2015 and currently represents 17.5% of the landscape as in Maine (Fig. 5). For comparison, the Minnesota moose population peaked with 21% of the landscape in the 0-20 year age class (Peek et al. 1976). Because the VCT underestimates forest disturbance proportions by up to 24%, the availability of optimal habitat is probably >17.5%. Further, VCT accurately detects 75-85% stand-clearing forest disturbance and it is likely that non-stand clearing forest disturbances were also underestimated. Arguably, this analysis underestimates forest disturbance in both states, particularly in Maine where partial harvesting is less detectable and has largely replaced clear-cutting.

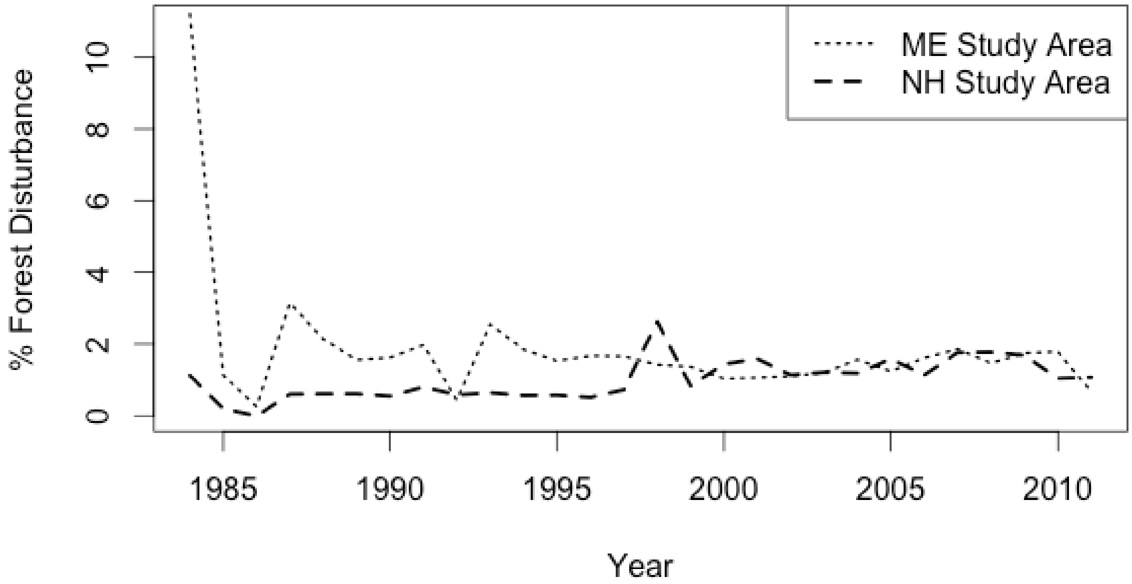


Figure 6: Annual percent forest disturbance from 1984-2011 in the Maine and New Hampshire study measured using a Vegetation Change Tracker.

Although forest disturbance in the early 1980s is roughly identified by VCT in the year 1984, it represents multiple years of forest disturbance and was not used to calculate disturbance rates. However, it does provide insight into how much relative area was disturbed in the early 1980s. For example, large clearcuts (~11% forest disturbance) were evident in the Maine study area, whereas clearcuts (~1% forest disturbance) were less common in New Hampshire. Annual rates of forest disturbance in the New Hampshire study area were ~50% less than in the Maine study area from 1985-1997 and similar to Maine from 1998-2011 (Fig. 6).

Optimal habitat increased 2.5X and moose density decreased ~20% in the North Region of New Hampshire From 2001 to 2015. Therefore, fewer aggressive or dominant adult interactions with yearlings should occur, natal dispersal distance and home and core range size should decrease, and overlap should increase. In concurrence with this prediction, this study showed that home and core range size decreased by ~20%. Conversely, the distance of female yearling dispersal increased by ~30% and core range overlap decreased by 33%, yet home range overlap remained constant, suggesting that density is currently equivalent to or even higher than in 2001 given that optimal habitat is more available.

If natal dispersal has increased, consequently reducing core range overlap, it would conflict with the declining population density estimates in New Hampshire. In 2015, the density estimate in the Maine study area was ~2X higher than in New Hampshire in 2003-2005 (0.7 moose/km^2; NHFG unpublished data) and presumably influenced the 30% higher dispersal distance in the current period, given that 89% of the yearlings measured in the current time period were in Maine District 8. The differences between the time periods are inconsistent and insignificant ($P > 0.05$), and highly variable given the small sample size. The conflicting results could simply reflect minimal or no change in dispersal behavior given that all movement is within the range of natal dispersal measured previously (2-5 km; Ballard et al. 1991), population density was moderate-high in both study periods, and optimal habitat increased between time periods and is considered excellent from a proportional perspective (1.3% annual optimal habitat creation; Peek 1976). The use of dispersal distance to identify change in moose population density is probably limited to circumstances where the change in density is larger than occurred in the study area and where habitat quality is less optimal or geographically variable.

Future Research

Using the vegetation change tracker (VCT) was an effective method to temporally quantify and compare the availability and production of optimal moose habitat. Effectively measuring annual land conversion could be improved. This study estimated the total change from the beginning and end of the observation period and converted it to an average annual rate. Because the study area had a relatively minimal land conversion (~1% 1985-2011) this approach was not considered problematic. In an area where the rate of land conversion is higher it would be prudent to identify more land cover data to best identify its rate and temporal impact. Further, which land cover type was used to compare with the VCT is an important consideration. For example, the National Land Cover Dataset classifies riverbeds differently than the VCT, causing an overestimation of land conversion at the larger town scale. It is interesting to consider that the regional moose population is largely a product of an atypical period of regional scale timber harvesting due to a spruce budworm infestation. Documenting and understanding between such events, production and temporal availability of optimal habitat, and population dynamics of moose is paramount to effective moose management.

CONCLUSIONS

I. Yearling males dispersed 4X farther, had a ~2.5X larger home and core ranges, and 2.3X and 10X less natal home and core range overlap than yearling females in the Maine and New Hampshire study areas (2003-2015). Male and female yearlings generally dispersed farther than reported in previous studies.

II. There were no significant differences in female natal dispersal characteristics between 2003-2005 and 2014-2015. Although distance increased 30% it is likely this reflected the preponderance of Maine data in the analysis where the current moose density was ~2X higher than in New Hampshire in 2003-2005.

III. Home and core range size of female yearling moose were 2X larger than adult cow moose. Larger post-dispersal home ranges likely reflect exploratory behavior more than access to resources in a saturated social structure.

IV. Optimal foraging habitat increased 2.5X in the past 15 years in the New Hampshire study area and is similar to that in the Maine study area (17.8%). In the New Hampshire study area the forest disturbance rate (1.3%) exceeds previous studies and is sufficient to maintain optimal moose habitat.

V. Optimal habitat increased from 2001-2015 as the moose population was in decline, hence it is unlikely that habitat is limiting to moose in New Hampshire.

Chapter Two:

Moose and Winter Tick Epizootics in Northern New England's Changing Climate

INTRODUCTION

Moose populations are in decline along their southern range in the states of Minnesota, central Maine, New Hampshire, Vermont, and New York, as well as the Canadian province of Nova Scotia, and in southern Québec and New Brunswick (Samuel 2004, Murray 2006, Broders 2012, Jones 2016). Although the root cause of these jurisdictional declines differ, the increased prominence of disease and parasites associated with warming temperatures and global climate change presumably have adverse impacts on these populations (Samuel 2004, Murray 2006, Lankester 2010). In northern New Hampshire and central Maine, periodic years of high winter tick (*Dermacentor albipictus*) abundance produce epizootic events causing high calf mortality that affects moose population dynamics. Further, increased frequency of these events is suspected to reduce productivity and overall fitness of yearling and adult cow moose (Musante et al. 2010, Bergeron et al. 2013). It is critical to understand the mechanisms that lead to winter tick epizootics in order to make informed, data-driven moose management decisions.

Winter tick distribution and abundance are primarily controlled by weather, ground conditions, and moose density (Blyth 1995, DelGiudice et al. 1997, Samuel 2004). Snow cover in mid-late April adversely affects adult female tick survival, thereby reducing egg and larval production (Drew and Samuel 1986). Cold temperatures and dry conditions reduce egg survival in early summer (Aalangdong et al. 2001, Samuel 2004, 2007), high temperatures and dry conditions increase larval desiccation during August and September (Knülle 1966, Addison et al. 2016), and cold fall temperatures and frost/snow cover reduce and eventually end the larval questing period (Aalangdong 1994). A warming climate results in shorter and milder winters (i.e., longer falls, earlier springs), higher winter tick abundance, and more frequent reoccurrence of epizootics causing long-term reduction in productivity and overall fitness of moose (Musante et al. 2010, Bergeron et al. 2013, Jones 2016). Musante (2006) attributed the 2002 epizootic in New Hampshire to a prolonged larval questing period the previous fall (2001).

Winter tick abundance tracks changes in moose density (Blyth 1995, Pybus 1999, Samuel 2004, 2007), and Samuel (2004) hypothesized that at higher moose density the probability of larval attachment increases. Research from Elk Island National Park in Ontario suggests that epizootic events occur at densities > 2.9 moose/km^2 (Samuel 2004). Successive epizootics (2014-2016) have occurred at lower moose density (0.43-0.58 km^2; NHFG unpublished data) following 3 moderate-severe winters in northern New Hampshire, suggesting that successive years of favorable weather and ground conditions for winter ticks may allow epizootics to occur at moderate moose densities and that such conditions might eventually reduce the range of moose.

In this study models were developed to investigate the relationship between relative winter tick abundance and weather variables (e.g., min/mean/max monthly/normal temperatures, spring snow persistence, first fall snow), estimated moose density, optimal browse habitat (% town in 4-16 year forest age class), sex, age, date of kill, town of kill, region of kill, and state of kill. Supporting data were from winter tick abundance measured on moose captured in Maine and New Hampshire in January 2014-

2016, and on moose harvested in Québec and New Brunswick. Further, a case study analysis was developed using local weather conditions in Berlin, New Hampshire to compare 5 epizootic with 5 non-epizootic years in 2001-2016.

The specific objectives were to:

1) Measure and compare total relative abundance of winter ticks in regions known to have epizootic events with regions where epizootics are considered more rare, and compare epizootic and non-epizootic years within the respective regions.
2) Measure and compare the relative winter tick abundance on moose harvested in October with moose captured the following January.
3) Examine weather data in Berlin, New Hampshire and compare how weather conditions prior to 5 epizootic years differ from 5 non-epizootic years.
4) Construct a model using weather patterns, ground conditions, habitat availability, and population density that predicts temporal and geographic changes in winter tick abundance in Maine, New Hampshire, and Vermont.

STUDY AREA

The study area used in the regional model included the states of Maine, New Hampshire, and Vermont (Fig. 7); data from the Canadian provinces of Québec and New Brunswick were used descriptively to compliment observed trends in these states. Finally, Berlin, New Hampshire was used as a case study site to investigate weather conditions relative to epizootic and non-epizootic years in northern New Hampshire.

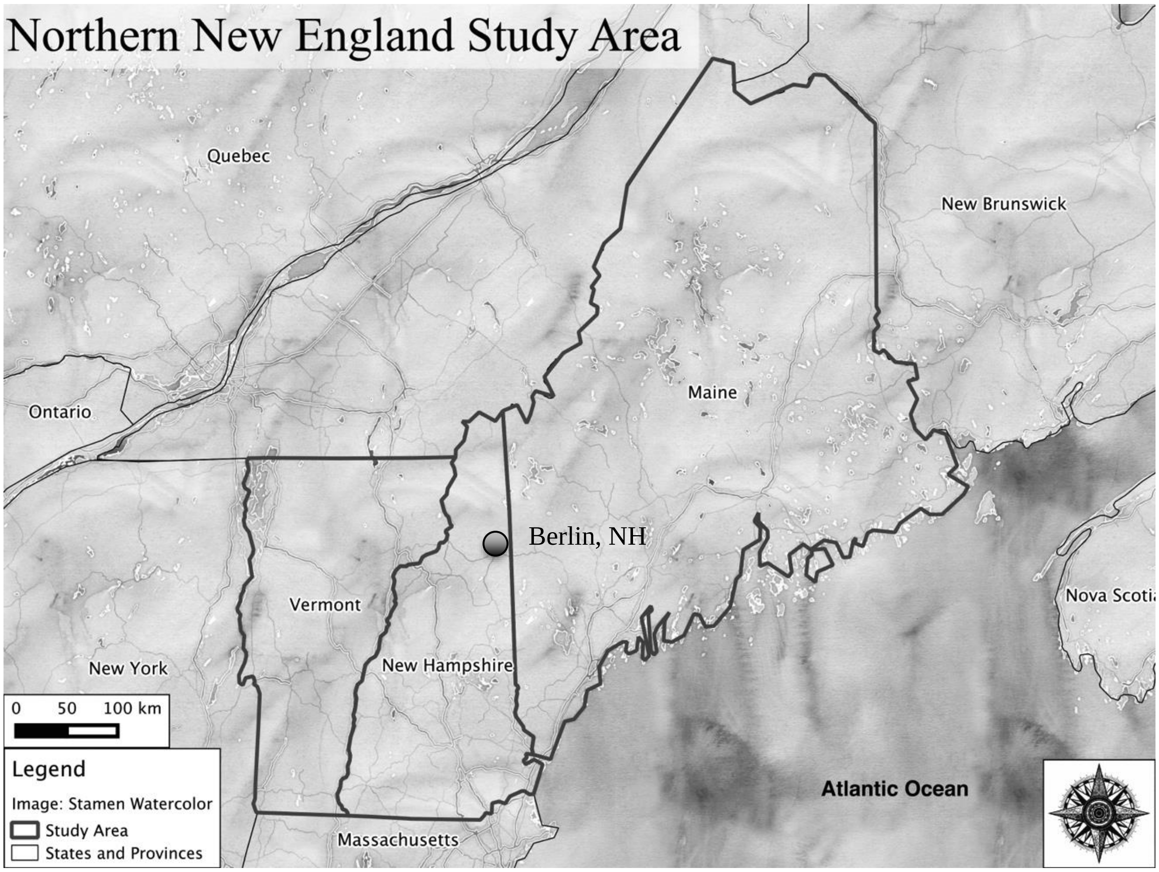


Figure 7: Regional analysis study area includes the states of Maine, New Hampshire, and Vermont. Additional abundance data are described for the provinces of New Brunswick, and Québec. Berlin, New Hampshire is described in depth as a case study of epizootic conditions in the southern portion of the moose’s range.

The majority of land is privately owned and largely forested and managed for commercial timber production; southern and coastal portions of the study area are developed with moose nearly absent along southern coastal areas. Density is estimated as high as 2.5 moose/km^2 in far northern Maine (MDIFW unpublished data).

Dominant forest types are northern hardwoods and boreal forests, consisting of American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and paper birch (*Betula papyrifera*), with red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) at higher elevations and latitudes. White cedar (*Thuja occidentalis*) and black spruce (*Picea mariana*) are found in lowland swamps (DeGraaf et al. 2007).

METHODS

A multifaceted approach was used to evaluate the influence of weather conditions and moose density on winter tick abundance. Ten years of tick abundance data measured on harvested moose were available to construct a regional model, and 20+ years of observational and anecdotal data were available to provide descriptive supporting evidence. It was assumed that high abundance was related to epizootic events, and that high abundance on harvested moose is generally followed by an epizootic event. The primary analysis focused on relationships between relative abundances and weather conditions, and identifying the best predictors of an epizootic.

Descriptive analyses were performed to compliment the regional model to provide wildlife managers with a variety of methods to interpret how weather, time, and density influence winter tick abundance and attachment rate. Additional analyses include: 1) comparison of weather conditions that occurred in epizootic and non-epizootic years in northern New Hampshire, 2) comparison of the relative abundance on moose harvested in September and mid-October with moose captured in January, 3) analysis of fall-winter tick abundance on bull moose in areas with known epizootic years, and 4) comparison of winter tick abundance on moose captured in northern New Hampshire, central Maine, and far northern Maine by location, year, sex, and age. Hereafter, the term abundance exclusively refers to winter ticks while the term density exclusively refers to moose.

Total relative winter tick abundance

The total relative winter tick abundance (hereafter: abundance) on harvested moose was measured along 4- 10 cm transects on the shoulder, rib, neck, and rump by counting all individual larvae/nymphs in the parted hair. Abundance equals the sum count, and is an index used as a comparative metric for identifying temporal and spatial variation in abundance on harvested moose (Sine et al. 2009, Bergeron et al. 2013). Abundance on harvested moose was measured for the past 10, 8, and 3 years at check stations in Maine, New Hampshire, and Vermont, respectively (Table 5). Although the timing of each state hunt differs slightly, the preponderance of sampling occurs in October and state seasons rarely change.

Initially, it was suspected that winter tick larvae leave the host soon after death (Sine et al. 2009). Consequently, a conservative sampling design was implemented in that moose were sampled only if killed within 5 h of being brought to a check station. Anecdotally, there was little evidence to support this sampling design and recent comparisons by both NHFG and VTFW indicate no statistical difference to support this conservative design (Pers. comm., K. Rines NHFG and C. Alexander VTFW). Therefore, all samples were used in this analysis.

Table 5: Sample size for modeling relative winter tick abundance by year, state, age and sex on in Maine (2006-2015), New Hampshire (2008-2015), and Vermont (2013-2015).

	2006				2007				2008				2009				2010			
State	AF	AM	CF	CM	AF	AM	CF	CM	AF	AM	CF	CM	AF	AM	CF	CM	AF	AM	CF	CM
ME	6	58	0	0	8	62	1	0	1	63	0	0	5	86	1	0	8	165	0	0
NH	0	0	0	0	0	0	0	0	46	36	5	0	30	27	2	2	17	23	3	1
VT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
All	6	58	0	0	8	62	1	0	47	99	5	0	35	113	3	2	25	188	3	1
	2011				2012				2013				2014				2015			
State	AF	AM	CF	CM	AF	AM	CF	CM	AF	AM	CF	CM	AF	AM	CF	CM	AF	AM	CF	CM
ME	18	130	0	0	62	78	1	2	27	81	1	2	36	134	0	0	44	163	2	1
NH	21	39	1	3	17	31	3	1	19	28	7	3	11	17	1	0	24	42	1	0
VT	0	0	0	0	0	0	0	0	18	42	2	5	35	81	5	2	13	73	0	2
All	39	169	1	3	79	109	4	3	64	151	10	10	82	232	6	2	81	278	3	3

A = Adult or Yearling, C = Calf, F = Female, M = Male

Density estimates

The state moose biologists in Maine, New Hampshire, and Vermont provided moose density estimates by management unit. Maine’s estimates are derived from aerial surveys (density and composition), tooth age distributions (bull and cow), estimates of adult and juvenile survival, corpora lutea data, and harvest. New Hampshire and Vermont densities are a population index estimated from surveys that measure moose observation rates by deer hunters (Bontaites et al. 2000). Moose density estimates were used at the wildlife management unit scale. For gaps in density estimates, the most recent estimate for that WMU was used, and if bounded by 2 estimates they were averaged. For example, if there was no estimate for a WMU in 2006 but was in 2007, the 2007 estimate was used. Similarly, if there was no estimate for 2009 but there was in 2008 and 2010, the two estimates were averaged.

Snow cover

Spring snow persistence (earliest day of no snow cover) and the first snowfall day (> 1 in) in the fall were identified (2003-2015) using the Snow Data Assimilation System (SNODAS) produced by the National Snow and Ice Data Center. Using estimates from weather stations, as well as satellite and aerial remote sensing platforms, SNODAS is an interpolated surface that was originally produced to provide estimates of snow cover to support hydrologic modeling and analysis (NSIDC 2016). SNODAS has a spatial resolution of 30 arc seconds, temporal resolution of 1 day, and radiometric resolution of 16 bits (NSIDC 2016). With temporal and geographic sensitivity to snow events, this data is effective at determining the relative timing of snow cover between regions and years. To model snow persistence, the following logic was used:

1) If max snow depth in February is zero, then allow "no snow cover" in January.
2) If max snow depth in March is zero, then allow "no snow cover" in February.
3) Select the earliest Julian day with no snow cover by pixel.

The first snowfall day (>1 in) in the fall was the earliest Julian day selection of snowfall for each pixel. Snow cover persistence was extracted and averaged by year using town boundaries. Snow persistence from the 2 most recent springs and the first snowfall day in the previous fall were used as predictor variables to model the influence of snow cover on tick abundance. Snow cover variables were merged with the year and town attribute of abundance for each harvested moose.

Temperature and precipitation

Temperatures for March (mean), April (mean), August (min and max), September (min and max), October (min), November (min) and December (min) monthlys and normals were identified using PRISM Climate data produced by the Prism Climate Group of Oregon State University. PRISM is a model that interpolates weather variables (min, max, mean temperature, and precipitation) between weather stations and was produced in 1991 to emulate and automate professionally, hand drawn state climate maps, and is currently used to produce daily and monthly weather surfaces (PRISM 2013). PRISM is created using traditional and cooperative weather stations in combination with latitudinal and elevational gradients. PRISM has a spatial resolution of 4 km and a temporal resolution of 1 month. Given the 4 km spatial resolution, town centroids were used to extract temperature measurements. PRISM is sensitive to elevational gradients and is helpful in determining the variable's intensity relative to other years.

Optimal habitat

A remote sensing-based Vegetation Change Tracker (VCT) was used to measure forest disturbance from 1985-2011. The VCT is a Landsat time series stack (LTSS) of historic (1984-2011) Landsat satellite imagery with 30 m spatial resolution that was originally produced to detect the year and magnitude of forest disturbances (Huang et al. 2009). It has been used to map forest fragmentation through time, better account for modeling forest carbon budgets, and map annual forest disturbance types (Li et al. 2009, Masek et al. 2013, Zhao 2015). Landsat scene selection and VCT processing is described by Huang et al. (2009).

The VCT identifies forest disturbances ≥ 0.09 ha that have been detected for 2 or more consecutive years. Overall accuracy is 77-86% with a forest change user's accuracy of 64-88% for a disturbance within 1 year of reference data. Stand-clearing disturbances including clearcuts, severe fires, and major storm events have a 75-85% detection rate; given a relaxed temporal window of ±1 year, non-stand clearing disturbances have an accuracy of 60%. In general, omission errors are greater than commission errors, resulting in the average underestimation of forest disturbance by 24% (Thomas et al. 2011, Masek et al. 2013). VCT data were obtained for the following Landsat path/rows: 13/30, 13/29, 12/30, 12/29, 12/28, 12/27, 11/29, 11/28, 11/27, and 10/29 that cover the majority of Maine, New Hampshire, and Vermont.

Peek et al. (1976) indicated that optimal browse habitat is greatest during the 20 years following a stand-clearing event; therefore, I defined optimal habitat quality as the 4-16 year forest age class. Annual forest disturbance was quantified by extracting values within the study area boundaries by year and summing the area of initial and secondary forest disturbance. The rate of yearly land conversion was equal to the difference in area between the persisting non-forest class (Value = 1) and the area of non-forest classes in the 2011 National Land Cover Dataset (Values = 21, 22, 23, 24, 31, 81, 82) divided by the timeframe. The adjusted yearly forest disturbance was the annual forest disturbance after accounting for land conversion. The previous 13 years of adjusted forest disturbances in the town were summed to calculate optimal habitat for a town in a given year.

Annual tick abundance data

Every year from 2002-2016 was assigned as “epizootic” or “non-epizootic” (excluding 2006 which has no quantifiable data) using a combination of analytical, observational, and anecdotal sources that included productivity studies (2002-2006, 2014-2016), relative tick abundance on harvested moose (2006-2015), and communication with state biologists who produce winter mortality reports, tick abundance, and conduct hair loss surveys (New Hampshire only).

Epizootic events were identified in the springs of 2002, 2011, 2014, 2015, and 2016. Years classified as non-epizootic were 2003, 2004, 2005, 2007, 2009, 2010, 2012, and 2013. Anecdotally, the spring of 2008 may have been an epizootic year based on winter mortality reports, however there was not broad regional agreement in the data to support the claim (Maine data, pers. comm., K. Rines NHFG and L. Kantar MDIFW).

Comparison of abundance in epizootic and non-epizootic years

Relative abundance on harvested moose during epizootic and non-epizootic years were compared in management units where epizootics were known to occur (New Hampshire: A1, A2, B, C1, C2, and D1; Maine: 7, 8, 9, 12, 13, and 14). Additionally, these regions and districts were compared with districts of far northern Maine where epizootics were considered uncommon (Districts 1, 2, 3, 4, 5, and 6; Fig. 8). Total relative abundance and relative abundance on the shoulder/rump (Table 6) were log transformed to stabilize the variance; significance was determined using a student's t-test, after which results were exponentiated for descriptive comparison.

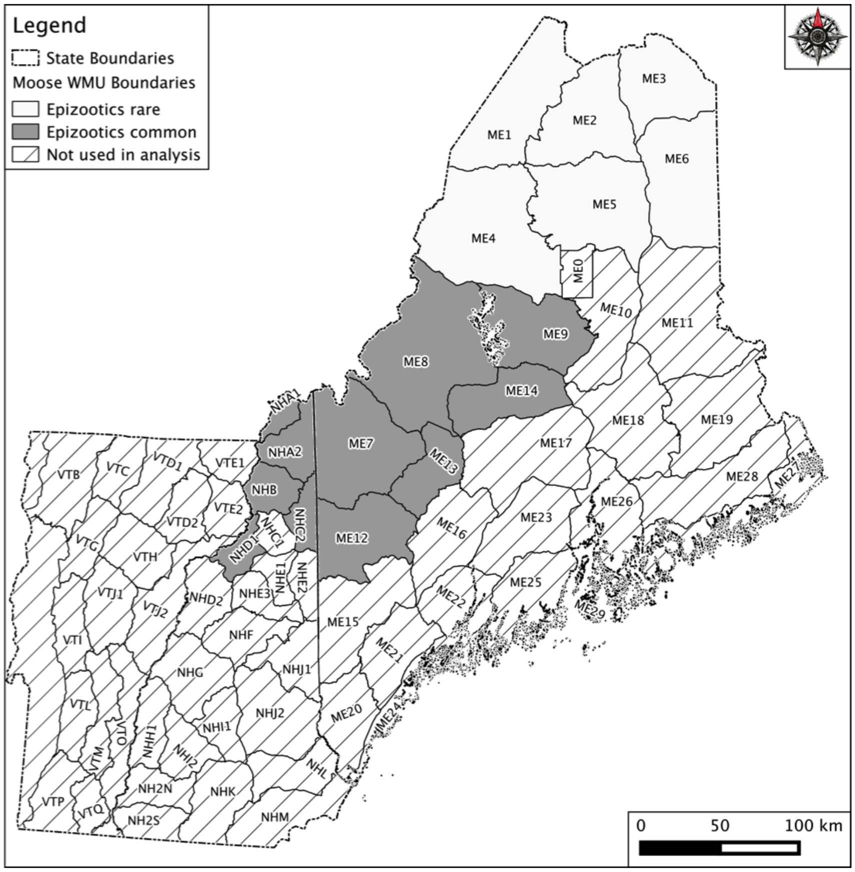


Figure 8: Wildlife management units identified with common or rare epizootic occurrence in Maine and New Hampshire.

Table 6: Sample size for comparing the relative winter tick abundance on harvested moose in northern New Hampshire, and central and northern Maine.

	Central ME/Northern NH		Northern Maine	
Epizootic	n(female)	n(male)	n(female)	n(male)
Yes	61	498	103	107
No	106	498	85	65

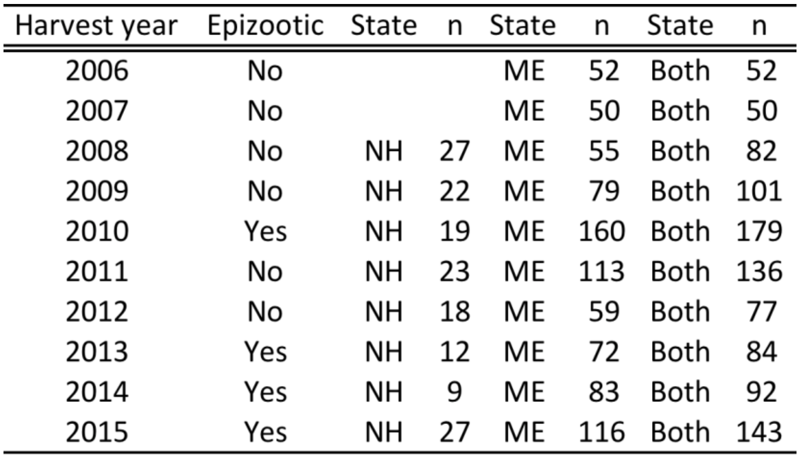
Latitudinal change in shoulder-rump winter tick abundance in Québec, Canada

Shoulder-rump winter tick abundance was measured on harvested bull moose during epizootic years (2014-2016) in Québec, Canada with moderate moose densities (0.4-0.8 moose/km^2) and high density (0.8-3.3 moose/km^2). Tick data were log transformed to stabilize the variance, after which they were exponentiated for descriptive comparison. The data were broken into 3 latitudinal divisions: 1) Southern Québec extending from the US boarder to the same latitude as Moosehead Lake in Maine (45.2°-45.5°), 2) mid-Québec extending from the same latitude as Moosehead lake in Maine to the latitude of the northern tip of Maine (45.5°-47.3°), and 3) northern Québec extending from the latitude of the northern tip of Maine to the Arctic ocean (47.3°-49.5°). Significance was determined using a student's t-test ($P < 0.05$).

Ranking fall abundance by year on bull moose in areas known to have epizootics

Tick abundance measured on harvested bull moose (2006-2015) in New Hampshire (North and CT Lakes Regions) and Maine (Districts 7, 8, 9, 12, 13, and 14) were log transformed to stabilize the variance, after which they were exponentiated for descriptive comparison, and ranked to assess severity by year (Table 7). Further, a logistic regression was used to investigate a fall abundance threshold preceding an epizootic year, although the sample size was small (n = 10). For example, if the mean abundance exceeds this probability threshold (0.5) what is the likelihood of an epizootic occurrence? Additionally, 3 probability thresholds were measured (0.3, 0.5, 0.7) to identify 4 intensities of abundance: light, light-moderate, moderate-severe, and severe.

Table 7: Sample size for comparing and ranking relative winter tick abundance on harvested bulls in northern New Hampshire, and central Maine.



Harvest year	Epizootic	State	n	State	n	State	n
2006	No			ME	52	Both	52
2007	No			ME	50	Both	50
2008	No	NH	27	ME	55	Both	82
2009	No	NH	22	ME	79	Both	101
2010	Yes	NH	19	ME	160	Both	179
2011	No	NH	23	ME	113	Both	136
2012	No	NH	18	ME	59	Both	77
2013	Yes	NH	12	ME	72	Both	84
2014	Yes	NH	9	ME	83	Both	92
2015	Yes	NH	27	ME	116	Both	143

Comparison of abundance on moose harvested in September, mid-October, and moose captured in January

Winter tick abundance measured from the sum of shoulder/rump plots was log transformed to stabilize the variance, and then exponentiated for descriptive comparison. The first comparison was between moose harvested in Fredericton, NB (~23 September 2015), Districts 8, 9, and 14 in Maine (~Mid-October), and captured moose (January 2014-2016) from District 8 in Maine. The second was between harvested moose in the North and CT Lakes Regions in New Hampshire with captured moose in the North Region in January 2014-2016. The analysis assumed that additional larval attachment was insignificant after December, and used 31 December to compare abundances measured at January captures (Table 8).

Table 8: Sample size for temporal comparison of shoulder/rump tick abundance on harvested and captured moose by location and date.

State/Province	Year	Julian day	n
ME	2013	290	36
ME	2013	365	55
NH	2013	293	27
NH	2013	365	46
ME	2014	286	38
ME	2014	365	53
NH	2014	291	14
NH	2014	365	43
NB	2015	266	42
ME	2015	287	78
ME	2015	365	36
NH	2015	290	40
NH	2015	365	48

Fredericton, New Brunswick is similar in climate and latitude to Maine District 8. The estimated moose density in 2015 in Zones 12, 15, 16, 17, 20, and 21 was 0.23-0.47 moose/km^2 (GNB unpublished data), lower than in Maine District 8 (1.4 moose/km^2; MDIFW unpublished data) and the North Region in New Hampshire (0.55 moose/km^2; NHFG unpublished data).

Comparison of winter tick abundance on captured moose

Abundance measured on the shoulder and rump of moose captured in January 2014-2016 in the North Region of New Hampshire and Districts 2 and 8 of Maine were compared to assess if abundance varies by location, year, sex, and age (Table 9). Abundances were log transformed to stabilize the variance, and then exponentiated for descriptive comparison.

Table 9: Sample size for comparing the relative winter tick abundance on captured moose by for in northern New Hampshire, central (District 8) and northern (District 2) Maine. A = adult, C = calf, M = male, F = female.

		2014		2015		2016		
Age	Sex	ME8	NH	ME8	NH	ME8	NH	ME2
A	F	26	21	12	17	0	10	27
C	F	16	13	26	11	20	20	16
C	M	13	12	15	16	16	18	11

Moose density and optimal habitat by town in northern New Hampshire

A linear model was used to evaluate the relationship between the proportion of optimal habitat and local moose density in 26 northern towns. We predicted moose density from the survey data from 2010-2015 in towns within WMU C1 or the North and CT Lakes Regions. Hunter effort by town had to be > 650 h but averaged ~2,400 h. A goodness of fit (R^2) indicated the strength of the relationship.

Weather patterns: epizootics vs. non-epizootics in Berlin, New Hampshire

Weather conditions during off-host stages of the life cycle (replete adult female, egg, larvae) that preceded 5 epizootic and 5 non-epizootic years were compared descriptively to investigate if certain conditions consistently occurred prior to epizootic or non-epizootic years (springs). Known epizootic (2002, 2014, 2015, 2016) and non-epizootic (2003, 2004, 2005) years were identified from the previous (2002-2005) and current (2014-2016) research (7 years). Epizootic year 2011 was supported by high relative abundance on harvested moose in Maine and New Hampshire, and anecdotally, by public and agency reports of high moose mortality in the spring (NHFG and MDIFW, unpublished data). Classifying 2012 and 2013 as non-epizootic years is supported by relatively low winter tick abundance on 2011 and 2012 fall-harvested moose in Maine and New Hampshire, and anecdotally, by minimal reports of moose mortality in spring of 2012 and 2013 (NHFG and MDIFW, unpublished data).

Daily weather measurements including precipitation, snow depth, and ambient temperature (min and max) were available from the weather station in Berlin, New Hampshire (GHCND: USC00270690) from 1938 through February 2016; 1969, 1970, 1973, and 1974 were excluded due to data gaps. In all, 76 variables (Tables 10, 11) were used to evaluate relationships between weather conditions and epizootic events. Some study parameters were based on previous laboratory and field research, while others were exploratory.

Mean, range, and standard error were used to descriptively compare the categorical differences, and student’s t-tests to measure statistical significance ($\alpha = 0.05$). Mean normal conditions were calculated for each variable from 1938-2015, and linear model and goodness of fit (R^2) were calculated to evaluate the trend of each condition within the context of global climate change.

Table 10: Comparing weather variables in epizootic and non-epizootic years in Berlin, New Hampshire.

Season	Stage	Variable	Description
Late Winter/Early Spring	Females off-host, prior to laying eggs	depth.day	The last day of snow cover
		snow	The number of days of snow cover from 1 April through May
		cold	The number of days with min temps < -17° C
		snow.cold	The number of days with snow cover and min temps < -17° C
		avg.min.mar	Average March min temps (° C)
		avg.max.mar	Average March max temps (° C)
		avg.min.apr	Average April min temps (° C)
		avg.max.apr	Average April max temps (° C)
		avg.may.min	Average May min temps (° C)
		avg.may.max	Average May max temps (° C)
early summer	Egg	cool.egg	Number of days min < 15° C
		hot.egg	Number of days max >30° C
		prec.egg	Total amount of precipitation (cm)
Late Summer/Early Fall	Larval Quiescence	hot.l.30	Number of days max >30° C
		avg.max.l	Average max temps August-September (° C)
		prec.l	Total amount of precipitation August-September (cm)
		no.prec	Number of days of no precipitation
		yes.prec	Number of days of precipitation
		days.nr1	Longest drought (days)
		days.nr2	Second longest drought (days)
		days.nr3	Third longest drought (days)
		day.nr1.e	Longest drought ended (Julian day)
		day.nr2.e	Second longest drought ended (Julian day)
		day.nr3.e	Third longest drought ended (Julian day)
		days.3.nr	Total number of days in three longest droughts (days)
		avg.date.allnr	Average date of three longest droughts (Julian day)
		sept.prec	Total precipitation in September (cm)
		sum.nr1.2	Total precipitation between middle and latest droughts (cm)
		sum.nr1.3	Total precipitation between earliest and latest drought (cm)
		temp.nr1.min	Average min temp of longest drought (° C)
		temp.nr2.min	Average min temp of second longest drought (° C)
		temp.nr3.min	Average min temp of third longest drought (° C)
		temp.nr1.max	Average max temp of longest drought (° C)
		temp.nr2.max	Average max temp of second longest drought (° C)
		temp.nr3.max	Average max temp of third longest drought (° C)
		temp.nr.min	Average min temp of three longest droughts (° C)
		temp.nr.max	Average max temp of three longest droughts (° C)
		min.10.l	Average of 10 hottest min temps (° C)
		min.20.l	Average of 20 hottest min temps (° C)
		avg.date.l.min	Average date of 20 hottest min temps (° C)
		max.10.l	Average of 10 hottest max temps (° C)
		max.20.l	Average of 20 hottest max temps (° C)
		avg.date.l.max	Average date of 20 hottest max temps (° C)
		min.10.aug	Average of 10 hottest August min temps (° C)
		max.10.aug	Average of 10 hottest August max temps (° C)
		min.10.sept	Average of 10 hottest September min temps (° C)
		max.10.sept	Average of 10 hottest September max temps (° C)
		avg.aug.min	Average August min temps (° C)
		avg.aug.max	Average August max temps (° C)
		avg.sept.min	Average September min temps (° C)
		avg.sept.min	Average September max temps (° C)

Table 11: Comparing weather variables in epizootic and non-epizootic years in Berlin, New Hampshire.

Season	Stage	Variable	Variable
Fall	Larval Questing	avg.oct.min	Average October min temps (° C)
		avg.oct.max	Average October max temps (° C)
		avg.nov.min	Average November min temps (° C)
		avg.nov.max	Average November max temps (° C)
		avg.dec.min	Average December min temps (° C)
		avg.dec.max	Average December max temps (° C)
		perm.snow.1	First day of permanent snow
		days.b.perm	Number of days with snow cover before permanent snow
		max.snow.b	Max snow depth before permanent snow
		snow.1	First day of snow
		last.b.perm	Last day of snow cover before permanent snow
		avg.temp.snow	Average Julian day of temporary snow
		frost.0.25ft	Julian day of 75 degree day (~1/4 ft of frost)
		frost.0.5ft	Julian day of 150 degree day (~1/2 ft of frost)
		frost.1ft	Julian day of 250 degree day (~1 ft of frost)
		days.max.l.17	The number of days with max temps < -17° C
		max.1.l.17	First day with max temps < -17° C
		fall.hot.20.min	Average of 20 hottest min temps (° C)
		fall.hot.20.date.min	Average date of 20 hottest min temps (° C)
		fall.hot.20.max	Average of 20 hottest max temps (° C)
		fall.hot.20.date.max	Average date of 20 hottest max temps (° C)
		week3.nov.mean.temp	Average mean temp of 3rd quarter of nov
		week4.nov.mean.temp	Average mean temp of 4th quarter of nov
		week1.dec.mean.temp	Average mean temp of 1st quarter of dec
		week2.dec.mean.temp	Average mean temp of 2nd quarter of nov

Regional predictive model

The response variable (abundance) has a poisson distribution that contains overdispersion (variance (1328) > mean (36.6)). With non-parametric response curves evident, generalized additive models (GAM) linked with a negative binomial generalized linear model (gam function; R 3.2.1, R Core Team, 2015) were constructed to test competing hypotheses, and build a predictive model of winter tick abundance in northern New England. Generalized linear models (GLM) and GAMs are successfully applied and well-described in ecological studies (Austin and Cunningham 1981, Nicholls 1989, Austin et al. 1990, Yee and Mitchell 1991, Brown 2011), and GAMs can represent the underlying ecological data better than parametric approaches (Pearce & Ferrier 2000).

Another advantage of GAMs is that the predicted values are rooted in the input data rather than an *a priori* model (Yee and Mitchell 1991).

Table 12: Candidate predictor variables for regional prediction of tick abundance in northern New England.

Covariate	Description	Units
total	Total relative tick abundance on harvested moose	# ticks
region	Wildlife Management Region in NH, and VT, and Districts in ME	Factor
sex	Sex of sampled animal	Factor
density	Population density of Wildlife Management Units	Moose/km^2
habitat	Area of forest in the 4-16 year age class of town	% land area
s1snow.y	Spring snow persistence 2 springs previous of town	Julian day
s2snow.y	Spring snow persistence in the previous spring of town	Julian day
fsnow.y	First day of fall snow depth > 2.54 cm from the previous year of town	Julian day
fall.snow	Normal first day of fall snow depth > 2.54 cm	Julian day
min.aug2	Average minimum August temperature of town	° C
min.sept2	Average minimum September temperature of town	° C
min.nov	Average minimum Novemeber temperature from previous year of town	° C
min.dec	Average minimum Decemeber temperature from previous year of town	° C

Using an information-theoretic approach (Anderson and Burnham 1998), predictor variables were selected based on current scientific understanding of how weather conditions and moose density interact with tick abundance and attachment. Parameters known to have influential relationships with tick abundance and larval attachment were tested for collinearity (R statistical software). Continuous predictor variables with a variable inflation factor (VIF) > 10, or correlation (R function: cor.test) > 0.60 were considered "highly correlated" with covariates. Highly correlated predictor variables were discarded, and predictor variables were determined by using the VIF step function (Table 12). Candidate independent variable were accepted when the relationships between a predictor variable and abundance proved to be consistent with current scientific understanding. Additionally, variables relationships were cross-validated and compared with local weather patterns and trends established in the Berlin, NH weather section

Model hypotheses

Independent and interacting hypotheses were tested to evaluate how sex, weather/ground conditions, and moose density/habitat influence the abundance of winter ticks on harvested moose. This analysis tested 4 categorical hypotheses: late winter/early spring conditions, late summer drought, fall larval questing, and density (Table 13).

Late winter/early spring conditions (April-May) influence reproductive success of an engorged female tick and was modeled with two variables: snow cover and ambient temperature. Successful egg production is reduced when snow cover is present and at extremely low nocturnal temperature; the survival threshold of adult females is estimated as -17° C (Drew 1984). Variables that influence this relationship (directly or indirectly) are snow persistence from the previous spring (s2snow.y; first Julian day that snow depth = 0).

Late summer (August-September) survival of quiescent larvae is modeled with 2 variables: relative humidity and ambient temperature. Prolonged drought (low precipitation) and high ambient temperature reduces egg production and larval survival, and for optimal survival during quiescence and questing, relative humidity needs to be ≥ 85% at 25 °C (Yoder et al. 2015). Variables that measure this relationship (directly or indirectly) are: average minimum temperatures (°C) in August (min.aug2), and average minimum temperatures (°C) in September (min.sept2)

Fall larval questing (October-December) was modeled with 2 variables: ambient temperature and snow cover. Questing of larvae is reduced at temperatures 0-10° C, stops at < 0 °C, or when larvae are snow-covered (Drew and Samuel 1986). Given that sampling occurs during the moose hunt (mid-October), there is one direct and one indirect hypothesis: abundance is a function of the timing of normal fall snow, or abundance is a function of the previous fall's weather conditions. Variables that influence these relationships are: 1) average minimum temperatures (° C) the previous November (min.nov), 2) average minimum temperatures (° C) in the previous December (min.dec), 3) the first day of snowfall (first Julian day snow depth > 2.54 cm) the previous fall (fsnow.y), and 4) normal (2003-2014) first day of snowfall (fall.snow; first Julian day snow depth > 2.54 cm).

Density considers that abundance is a function of the density of the host (moose). Variables that measure this relationship (directly or indirectly) are moose density (moose/km^2) and habitat (% of town in 4-16 forest age class).

Table 13: Candidate models for regional prediction of winter tick abundance in Maine, New Hampshire, and Vermont.

Model #	Scenario	Candidate Model
1	Spring Snow:Density	sex + s(re: year) + s(density:s2snow.y)
2	Spring Snow:Density + Habitat	sex + habitat + s(re: year) + s(density:s2snow.y)
3	Spring Snow:Density + Late Summer Desiccation	sex + min.aug2 + s(re: year) + s(density:s2snow.y)
4	Spring Snow:Density + Late Summer Desiccation +Habitat	sex + min.aug2 + habitat + s(re: year) + s(density:s2snow.y)
5	Density:Late Summer Desiccation	sex + s(re: year) + s(density:min.aug)
6	Density:Late Summer Desiccation + Habitat	sex + habitat + s(re: year) + s(density:min.aug)
7	Density:Previous December Temperatures	sex + s(re: year) + s(density:min.dec)
8	Density:Previous December Temperatures + Habitat	sex + habitat + s(re: year) + s(density:min.dec)
9	Density:Previous Fall Snow	sex + s(re: year) + s(density:fsnow.y)
10	Density:Previous Fall Snow + Habitat	sex + habitat + s(re: year) + s(density:fsnow.y)
11	Density:Normal Fall Snow + Late Summer Desiccation	sex + min.aug2 + s(re: year) + s(density:fall.snow)
12	Density:Normal Fall Snow + Late Summer Desiccation + Habitat	sex + habitat + min.aug2 + s(re: year) + s(density:fall.snow)

s = smoothing term, re = random effect

Model selection

The "best" model was chosen by evaluating how well each model fits the data using percent deviance explained (%D; Yee and Mitchell 1991) and Akaike's Information Criterion (AIC; Burnham and Anderson 1998). The %D indicates how well the model fits the data (similar to R^2) and the highest %D should indicate the "best" model (Yee and Mitchell 1991). The smallest AIC indicates the model that fits the greatest variation while not overfitting with too many parameters. We define highly competitive models as having a Δ AIC ≤ 4 (Anderson et al. 2001). Further, it is essential for the final model to reflect the current scientific understanding of how each variable influences abundance, and that these relationships predict the location and year of known epizootic events. This was achieved by comparing the predictions for 6 GAMs using 2 epizootic (2015, 2016) and 2 non-epizootic years (2012, 2013) to explore how each model predicts abundance and how well the predictions support known abundance data.

RESULTS

Results are not presented in reference to a calendar year, but rather a “life cycle year”: 1) adult engorged winter ticks drop from the moose in April (drop season), 2) June-July egg production and development (egg season), 3) August-September larval quiescence (quiescence), 4) October-December larval questing (questing season), 5) January-April on-host (on-host season), 6) March-April high moose mortality (epizootic year), or March-April low moose mortality (non-epizootic year). The year is designated by the calendar year of the March-April mortality season. For example, late winter/early spring snow conditions in 2015 that were followed by epizootic conditions in the spring of 2016, are referenced to as: snow conditions during the 2016 drop season. Further, the term “abundance” exclusively refers to winter tick abundance, and the term “density” exclusively refers to moose density.

Comparison of abundance between epizootic and non-epizootic years

Overall, tick abundance in epizootic years on harvested adult moose in northern Maine was consistently lower than in northern New Hampshire and central Maine during non-epizootic years; bull moose consistently had higher tick abundance than adult cows. Fall abundance was 1.5X greater on males (P = 5e-09) and 2X greater on cows (P = 2e-05) in epizootic than non-epizootic years (bull = 29.3 ± 1.1 SE; cow = 14.9 ± 1.1) in northern New Hampshire and central Maine. In northern Maine, tick abundance in epizootic years was 70% higher on cows than in non-epizootic years (9.8 ± 1.1; P = 6.7e-05), but not significantly different on males (P > 0.05; Fig. 9). Abundance in epizootic and non-epizootic years was ~60% higher on males and cows in central Maine and northern New Hampshire in comparison to northern Maine.

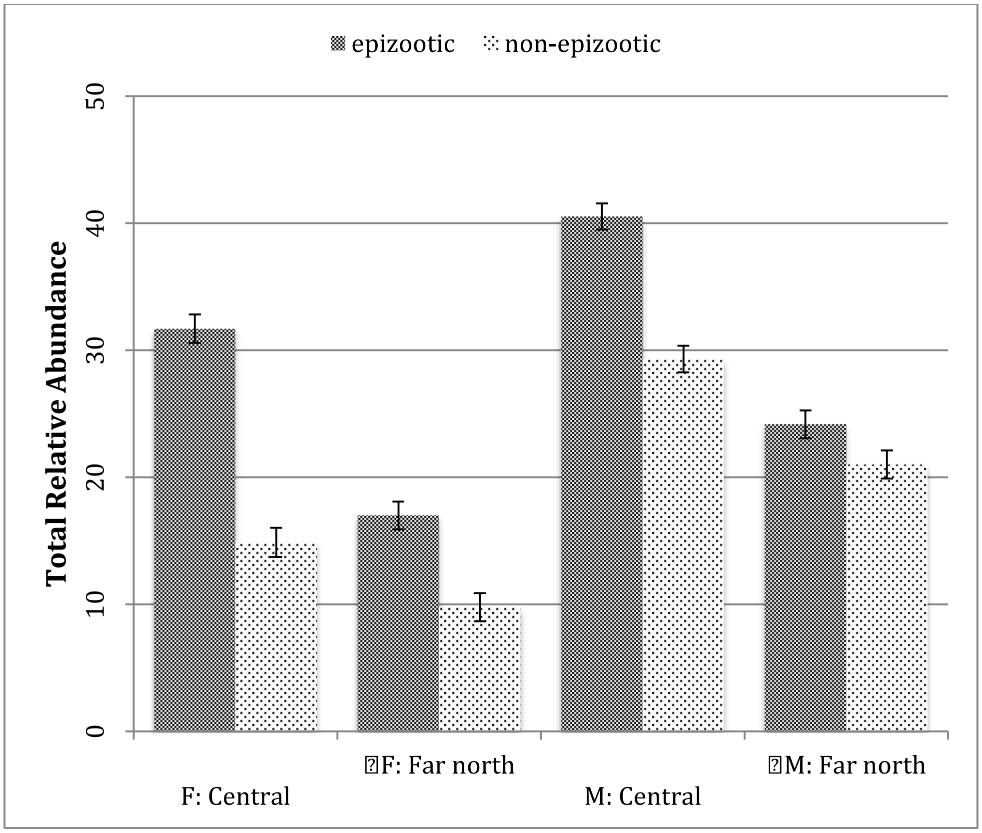


Figure 9: Comparison of total abundance on harvested moose between sex, and known epizootic years, and known non-epizootic years. Far north: northern Maine, Central: Central Maine and northern New Hampshire. Exponentiated, log transformed mean ± SE. F = adult cow, M = adult bull.

In northern New Hampshire and central Maine, shoulder and rump abundance at harvest showed increased divergence and significance between epizootic and non-epizootic years on bulls (*P* = 2e-10) and cows (*P* = 4e-12; Fig. 10). Abundance in epizootic years on bulls and cows was 1.5 and 4.8X higher, respectively. In northern Maine, abundance was higher in epizootic than non-epizootic years on cows (*P* = 6.5e-06) but not on bulls (*P* > 0.05; Fig. 10). Abundance was 1.3X higher on bulls and 1.9X higher on cows in epizootic years. Abundance on bulls during non-epizootic years was similar between the two regions, and cows always had lower abundance in each region. Abundance was ~1.5X higher on bulls and cows in epizootic years in northern New Hampshire and central Maine (Fig. 10).

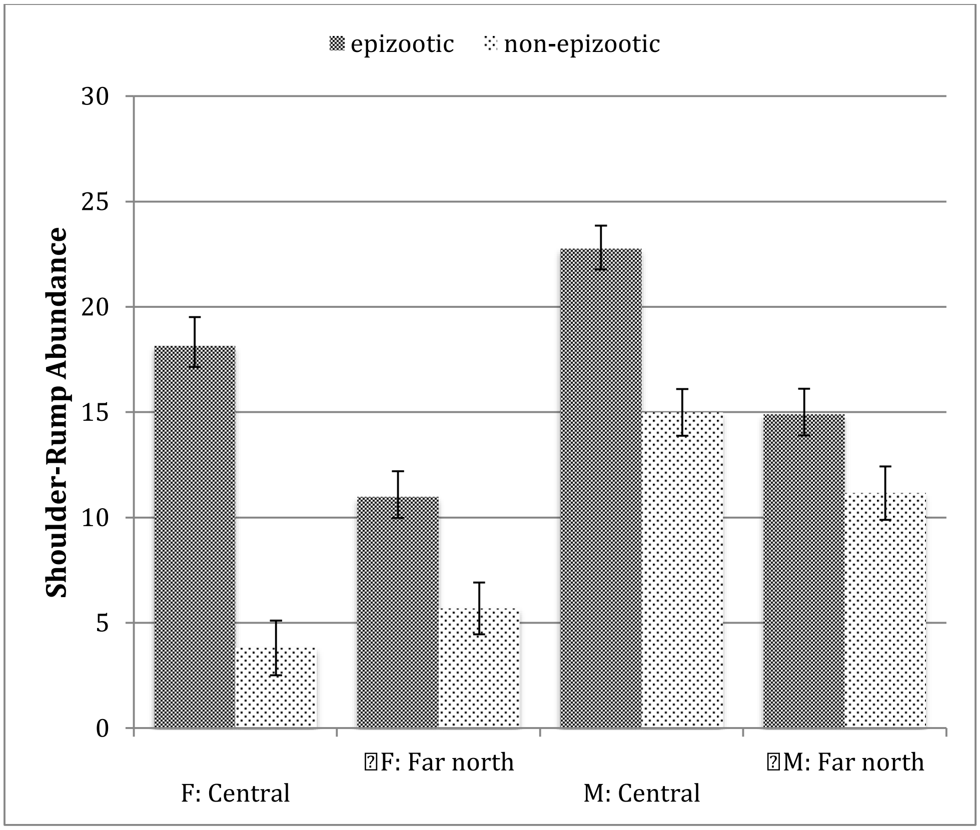


Figure 10: Comparison of shoulder-rump abundance on harvested moose between sex, and known epizootic years, and known non-epizootic years. Far north: northern Maine, Central: Central Maine and northern New Hampshire. Exponentiated, log transformed mean ± SE. F = adult cow, M = adult bull.

Latitudinal change in shoulder/rump winter tick abundance in Québec, Canada

Abundance at harvest measured on the shoulder-rump in moderate density populations in southern Québec was 4X (*P* = 4.6e-8) and 3.6X (*P* = 1.6e-6) higher than that in moderate density populations in mid- (5.5 ± 1.2) and northern Québec (5.1 ± 1.1), and 2.4X and 2.1X greater than abundances in high-density populations, respectively. Abundance in southern Québec in 2014-2016 was similar to that in northern New Hampshire and central Maine during epizootic years. In moderate and high-density populations in mid-Québec, abundance was 60% and 35% less than on bulls in northern Maine in epizootic years (Fig. 10, 11). There was no significant difference (*P* > 0.05) between tick abundance in mid- and northern Québec.

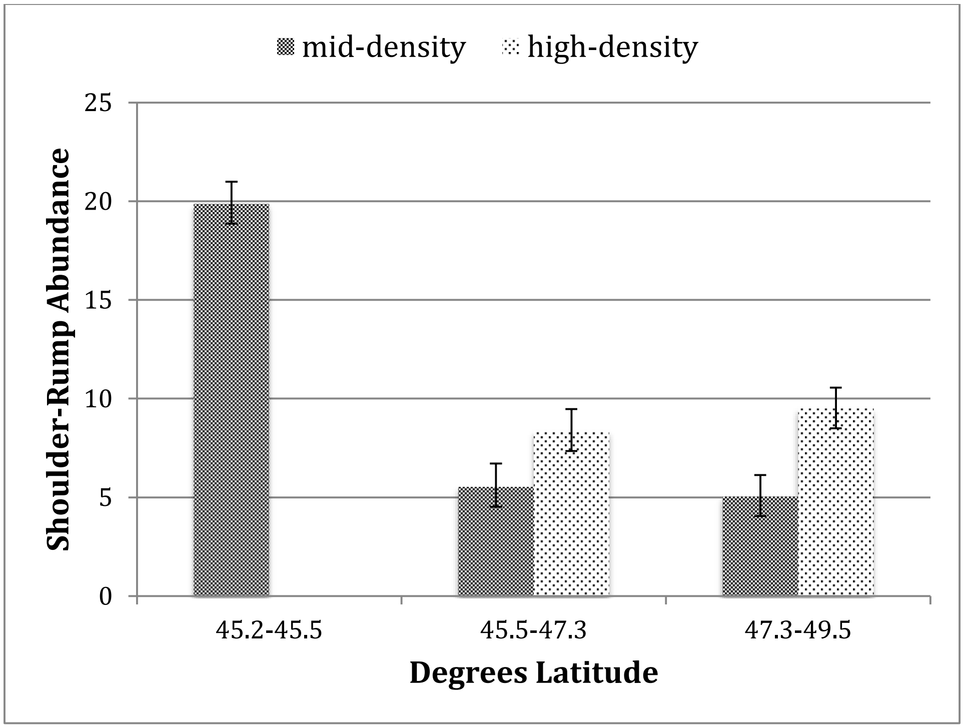


Figure 11: Comparison of shoulder-rump abundance on harvested bull moose in known epizootic years (2014-2016) in southern Québec, mid-Québec, and northern Québec. Exponentiated, log transformed mean ± SE.

Ranking fall tick abundance by year on bull moose in New Hampshire

Table 14: Abundance ranked by year on harvested bull moose in northern New Hampshire, and central Maine. Exponentiated, log transformed mean ± SE.

Rank	Year	Epizootic	State	mean	se	n	State	Rank	mean	se	n	State	Rank	mean	se	n
1	2014	Yes	Both	54.7	1.1	84	ME	1	53.4	1.1	72	NH	2	62.9	1.2	12
2	2011	Yes	Both	42.5	1.1	179	ME	2	39.3	1.1	160	NH	1	81.5	1.2	19
3	2016	Yes	Both	41.7	1.1	143	ME	3	38.9	1.1	116	NH	4	56.4	1.2	27
4	2009	No	Both	40.6	1.1	82	ME	4	34.1	1.1	55	NH	3	57.7	1.1	27
5	2012	No	Both	32.7	1.1	136	ME	5	31.2	1.1	113	NH	6	40.9	1.2	23
6	2010	No	Both	29.9	1.1	101	ME	6	28.3	1.1	79	NH	7	36.4	1.2	22
7	2015	Yes	Both	26.9	1.1	92	ME	7	25.6	1.1	83	NH	5	43.0	1.3	9
8	2013	No	Both	25.3	1.1	77	ME	8	23.4	1.1	59	NH	8	33.2	1.1	18
9	2007	No	Both	22.5	1.1	52	ME	9	22.5	1.1	52	NH				
10	2008	No	Both	20.1	1.1	50	ME	10	20.1	1.1	50	NH				

Tick abundance on bulls was consistently 1.2-2X higher in northern New Hampshire than in central Maine, ranging from 20.1 ± 1.1 to 54.7 ± 1.1 in 10 years of sampling. The 3 highest abundances (mean > 41.7 ± 1.1) were also epizootic years, with the other epizootic year (2015) ranked 7 of 10 (26.9 ± 1.1; Table 14). Mean abundance in non-epizootic years ranged from 20.1 ± 1.1 to 40.6 ± 1.1 ticks, with abundance < 32.7 in 5 of 6 years.

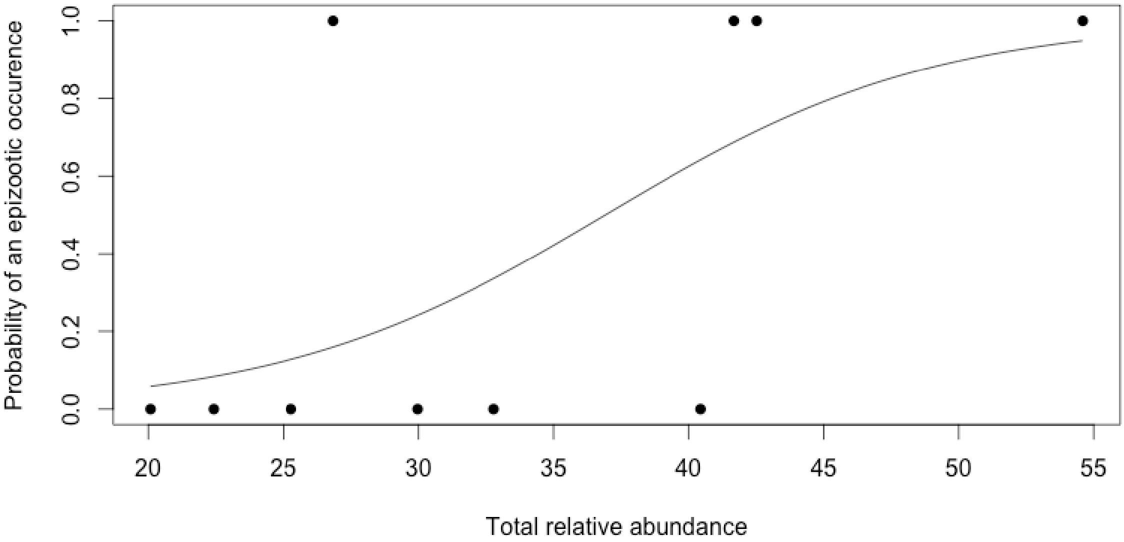


Figure 12: Probability of an epizootic occurrence using tick abundance on harvested bull moose in northern New Hampshire and central Maine from 2007-2016.

A logistic regression using the ranked mean fall abundance on bulls (Table 14) indicated that the probability of an epizootic occurrence is 0.3, 0.5, and 0.7 (± 0.1) when abundance is 31.8, 36.9, and 42.2 ticks (log = 3.46, 3.61, 3.74; Fig. 12), respectively. For example, if the average abundance in the epizootic region (Fig. 8) on bulls is 42.2 ticks, there is a 0.7 probability of an epizootic event the following spring. Overall, tick abundance in epizootic year 2015 was ~50% less than other epizootic years, although abundance was high in southern regions of the epizootic region. In non-epizootic year 2009, abundance was 1.2-2X that in other non-epizootic years. Excluding 2009 and 2015, the remaining 8 years indicate that the average tick abundance of 36.9 in the epizootic region is a 0.5 probability threshold for an epizootic. In northern Maine, the average abundance on bulls was always < 36.9 (Fig. 9, 10).

Comparison of tick abundance on captured moose

Tick abundance was 1.7X (*P* = 7e-07) and 1.5X (*P* = 0.0004) higher on cow and bull calves (31.3 ± 1.2) than adult cows in epizootic years. Cow calves had 1.2X higher abundance than bull calves (46.5 ± 1.12; Table 15), but this difference was not significant (*P* > 0.05).

Table 15: Shoulder-rump abundance on captured moose by age, and sex for in the North Region of New Hampshire, and Districts 8 of Maine.

Age	Sex	mean	se	n
Adult	Female	31.3	1.2	113
Calf	Female	53.6	1.1	122
Calf	Male	46.5	1.2	100

Abundance on all captured moose in Maine District 2 was ~50% of that measured in Maine District 8 in the same year (62.7 ± 1.22), and 75% of that measured in the North region of New Hampshire (48.8 ± 1.3). In 2014-2016, relative abundances in Maine District 8 were 1.4, 1.2, and 1.3X greater than in the North Region of New Hampshire (31.48 ± 1.5, 40.1 ± 1.2, and 48.8 ± 1.3; Table 16).

Table 16: Shoulder-rump abundance on moose captured in January by location, and year, for in the North Region of New Hampshire, and Districts 2 and 8 of Maine.

	New Hampshire			Maine District 8			Maine District 2		
Year	n	mean	se	n	mean	se	n	mean	se
2014	46	31.5	1.5	55	45.0	1.2	NA	NA	NA
2015	43	41.0	1.2	53	48.5	1.2	NA	NA	NA
2016	48	48.8	1.3	36	62.7	1.2	54	33.7	1.2

Temporal comparison of tick abundance in September, mid-October, and January

Bull moose in the early fall (~23 Sept 2015) harvest in New Brunswick had only 10% (1.9 ± 1.1) of the tick abundance measured on bulls in mid-October in central Maine and northern New Hampshire in 2015 (~ 20.2 ± 1.1), whereas abundance on calf and cow moose captured in Maine in January was ~24X higher (Fig. 13).

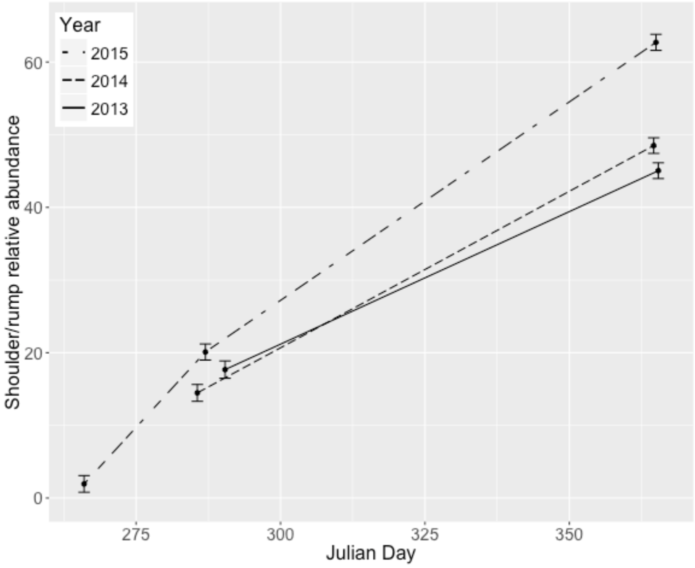


Figure 13: Shoulder-rump abundance on moose harvested in New Brunswick, Canada (~23 September) and Maine (districts: 8, 9, and 14; mid-October), and on moose captured in Maine district 8 (~January, 2014-2016). Exponentiated, log transformed mean ± SE.

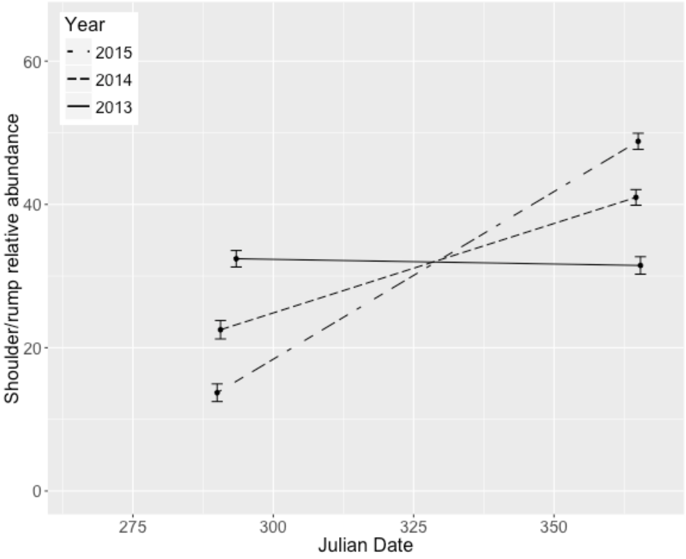


Figure 14: Shoulder-rump abundance on moose harvested in mid-October (2013-2015) and on moose captured in January (2014-2016) in the North and CT Lakes Regions in New Hampshire. Exponentiated, log transformed mean ± SE.

In Maine and New Hampshire, average tick abundance on moose captured in January was 2.3X higher than on moose harvested in October. In Maine, abundance on captured moose was ~3X higher than at harvest (17.41 ± 1.1). Abundance on captured moose in New Hampshire in 2014, 2015, and 2016 was equal, 2X, and 3.5X higher than at harvest (32.4 ± 1.1, 22.5 ± 1.1, and 13.8 ± 1.1; Fig. 14). On average, 43% of ticks were attached by mid-October.

Abundance on moose harvested in mid-October by year and WMU

Table 17: Number of observations, abundance mean, and standard error by epizootic year on moose harvested in Maine, New Hampshire, and Vermont. Exponentiated, log transformed mean ± SE.

		2007			2008			2009			2010			2011		
State	Region	n	mean	se	n	mean	se	n	mean	se	n	mean	se	n	mean	se
Maine	1	0			1	22.0	NA	0			3	8.4	1.7	0		
Maine	2	0			2	21.6	2.4	0			0			0		
Maine	3	7	8.3	1.7	4	8.2	1.7	0			0			0		
Maine	4	0			0			5	35.5	1.2	5	23.2	1.3	1	67.0	NA
Maine	5	0			2	28.1	2.6	0			1	8.0	NA	0		
Maine	6	4	27.4	1.7	7	10.8	1.5	0			0			0		
Maine	7	18	24.5	1.3	18	25.3	1.3	9	45.9	1.4	29	35.1	1.1	40	56.3	1.1
Maine	8	21	21.7	1.2	20	17.9	1.2	30	27.9	1.1	18	26.1	1.1	87	32.9	1.1
Maine	9	3	14.5	1.7	7	19.7	1.3	13	44.7	1.2	23	32.6	1.2	8	33.8	1.2
Maine	10	0			2	6.5	1.1	1	40.0	NA	0			0		
Maine	11	0			2	4.6	1.5	0			0			0		
Maine	12	3	23.9	2.2	0			1	27.0	NA	10	11.0	1.4	8	48.6	1.3
Maine	13	2	40.7	1.9	0			0			0			14	35.7	1.2
Maine	14	6	19.0	1.5	5	14.8	1.4	2	36.6	1.7	3	5.8	1.8	8	42.8	1.2
Maine	17	0			0			3	18.3	1.5	0			7	19.1	1.5
Maine	18	0			6	14.3	1.6	0			0			0		
Maine	19	0			2	8.5	1.4	0			0			0		
Maine	23	0			0			0			0			0		
Maine	25	0			0			0			0			0		
Maine	28	0			1	15.0	NA	0			0			0		
Maine	all regions	64	20.4	1.1	79	16.4	1.1	64	33.3	1.1	92	24.8	1.1	173	38.0	1.1
New Hampshire	C							1	63.0	NA	0			0		
New Hampshire	CT							32	17.9	1.2	30	13.2	1.3	16	45.3	1.2
New Hampshire	N							34	41.3	1.2	20	31.2	1.2	19	87.5	1.2
New Hampshire	SE							0			0			0		
New Hampshire	SW							0			0			0		
New Hampshire	WM							20	28.3	1.3	11	26.3	1.3	9	46.6	1.3
New Hampshire	all regions							87	28.0	1.1	61	19.9	1.2	44	60.5	1.1
Vermont	E															
Vermont	EC															
Vermont	GM															
Vermont	NC															
Vermont	SE															
Vermont	all regions															
all states	all regions	64	20.4	1.1	79	16.4	1.1	151	30.1	1.1	153	22.7	1.1	217	41.7	1.1

Table 18: Number of observations, abundance mean, and standard error by epizootic year on moose harvested in Maine, New Hampshire, and Vermont. Exponentiated, log transformed mean ± SE.

		2013			2014			2015			2016			all years		
State	Region	n	mean	se	n	mean	se	n	mean	se	n	mean	se	n	mean	se
Maine	1	0			3	9.9	1.4	16	16.6	1.1	19	24.6	1.2	44	18.0	1.1
Maine	2	10	8.8	1.2	3	11.8	1.7	35	14.9	1.2	37	19.8	1.2	89	15.5	1.1
Maine	3	21	12.5	1.2	2	3.7	3.7	12	31.3	1.3	22	22.7	1.2	73	15.2	1.1
Maine	4	12	17.3	1.3	19	34.0	1.3	20	19.7	1.3	13	20.6	1.3	86	22.2	1.1
Maine	5	6	10.4	1.4	0			1	22.0	NA	2	46.0	2.1	12	16.4	1.3
Maine	6	32	15.5	1.2	0			5	16.8	1.6	0			56	15.7	1.1
Maine	7	11	32.3	1.2	26	75.4	1.2	29	31.5	1.1	29	55.8	1.1	236	40.6	1.1
Maine	8	34	21.1	1.1	24	38.9	1.2	23	25.5	1.2	44	37.2	1.1	351	28.9	1.0
Maine	9	4	26.3	1.3	7	35.2	1.3	11	24.6	1.3	20	43.5	1.2	100	32.9	1.1
Maine	10	0			0			0			0			3	11.9	1.8
Maine	11	1	82.0	NA	0			0			0			3	12.0	2.7
Maine	12	1	35.0	NA	8	15.7	1.9	8	14.0	1.3	5	27.4	1.4	69	22.9	1.1
Maine	13	3	39.5	1.3	9	108.0	1.2	8	28.2	1.2	4	28.6	1.2	47	41.5	1.1
Maine	14	8	17.3	1.3	5	21.9	1.2	4	17.6	2.6	14	22.1	1.2	61	20.2	1.1
Maine	17	0			2	30.7	1.3	1	15.0	NA	2	37.8	2.7	16	19.6	1.3
Maine	18	0			0			0			0			6	14.3	1.6
Maine	19	0			0			0			1	10.0	NA	3	9.0	1.2
Maine	23	0			0			0			2	84.1	1.6	2	84.1	1.6
Maine	25	0			0			0			1	30.0	NA	1	30.0	NA
Maine	28	0			0			0			0			1	15.0	NA
Maine	all regions	143	17.3	1.1	108	38.9	1.1	173	21.3	1.1	215	30.3	1.1	1259	26.0	1.0
New Hampshire	C	10	27.6	1.2	14	25.8	1.4	5	6.2	2.3	9	6.8	1.7	54	15.3	1.2
New Hampshire	CT	13	21.3	1.2	10	49.1	1.2	4	46.9	1.5	13	34.7	1.3	135	24.0	1.1
New Hampshire	N	17	32.2	1.1	17	64.1	1.2	10	34.3	1.3	27	39.5	1.3	164	42.5	1.1
New Hampshire	SE	0			1	9.0	NA	0			0			1	9.0	NA
New Hampshire	SW	0			3	21.7	1.7	2	12.4	1.4	2	1.0	1.0	10	6.1	1.5
New Hampshire	WM	12	25.2	1.2	12	42.4	1.3	8	26.3	1.3	18	23.6	1.2	99	27.6	1.1
New Hampshire	all regions	52	26.6	1.1	57	40.9	1.1	29	23.1	1.2	69	24.1	1.2	463	27.8	1.0
Vermont	E				28	37.6	1.1	33	19.0	1.2	32	24.4	1.2	93	25.5	1.1
Vermont	EC				6	5.7	1.1	16	7.8	1.4	6	10.1	1.7	28	7.7	1.3
Vermont	GM				8	3.1	1.6	27	2.1	1.2	21	2.7	1.3	56	2.4	1.1
Vermont	NC				22	13.3	1.3	48	10.3	1.2	32	8.8	1.2	102	10.4	1.1
Vermont	SE				3	2.6	1.7	0			0			3	2.6	1.7
Vermont	all regions				67	14.9	1.2	124	8.3	1.1	91	9.7	1.2	282	10.0	1.1
all states	all regions	195	19.4	1.1	232	29.9	1.1	326	15.0	1.1	375	22.0	1.1	2004	23.1	1.0

An assessment across all wildlife management regions, and all years (2006-2015) using the threshold of 36.9 ticks predicted no epizootic occurred in Vermont (excluding Region E), in Maine Districts 1-6, or south and east of the White Mountains in New Hampshire. Conversely, epizootic conditions were predicted for Maine Districts 7, 8, 9, 12, 13, and 14, the White Mountain, North, and CT Lakes Regions in New Hampshire, and Region E in Vermont (Tables 17, 18). The remaining Regions and Districts had too few samples (n < 5) to assess. The North region of New Hampshire, and Maine Districts

7 and 13 consistently have the highest abundances and similar latitude and estimated moose density.

Moose density and optimal habitat by town in northern New Hampshire

Moose density was positively correlated (0.038) with % optimal habitat of a town; the relationship was significant ($P = 0.0019$) but moderately weak ($R^2 = 0.34$). When the towns of Dixville and Dix's Grant (both outliers) were removed, the relationship was substantially stronger ($R^2 = 0.67$). This relationship included a moose density range from 0.06-2.31 moose/km^2 and an optimal habitat range from 5-35% (Fig. 15).

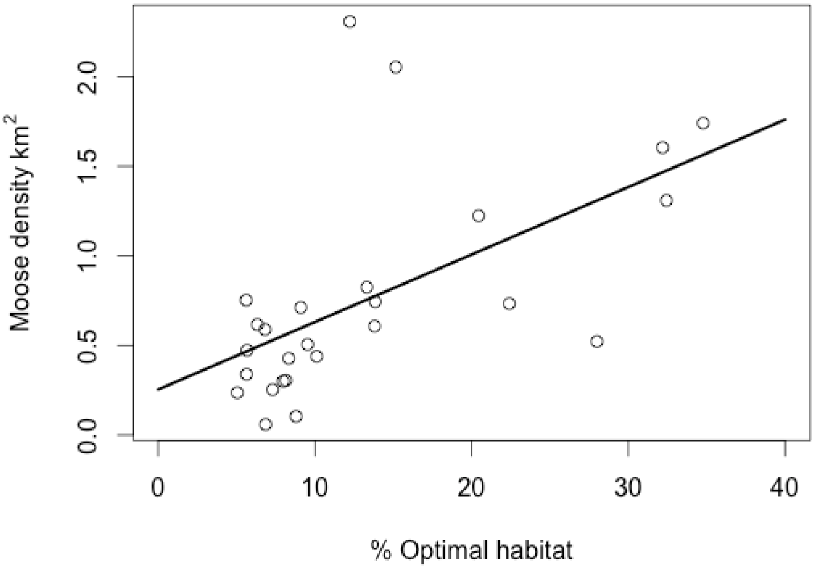


Figure 15: The % optimal habitat in 2015 versus estimated moose density in northern New Hampshire towns in 2010-2015. Optimal habitat is defined as the proportion of the town in the 4-16 year forest age class.

Case study in Berlin, New Hampshire

Results are given using the variable code names described in Tables 10 and 11 in Methods.

i. Late winter-early spring

Late winter-early spring tended to be colder, especially in March, in years preceding an epizootic event. Snow events occurred earlier in the drop season of non-epizootic years, although the number of days of snow cover was generally similar. Approaching May, maximum temperatures were higher preceding an epizootic year, although minimum temperatures were similar.

Mean depth.day in the drop season of epizootic years was 17 April (± 3.5 d), with 1 of 5 years earlier than the long-term mean (11 April ± 1.4 d) ranging from 9-28 April (19 days); the non-epizootic mean was 14 April (± 7.9 d) ranging from 28 March - 13 May (46 d). Epizootic years had 2X the number of days of snow cover (snow) from April-May including 2002 (23 d); the data were similar excluding 2002. Within the long-term data (1938-2015), there was only one day in the drop season when the minimum temperature (cold) was < -17 °C (Table 19).

Table 19: Comparison of variables between epizootic years (2002, 2011, 2014, 2015, and 2016), non-epizootic years (2003, 2004, 2005, 2012, and 2013), and long-term data (1938-2015); long-term linear trend and R^2 provided. See Table 10 for code description.

			Epizootic		Non-epizootic			Long-term: 1938-2015			
Season	**Stage**	**Variable**	mean	se	mean	se	ρ-value	mean	se	trend	r^2
Late Winter/Early Spring	**Females off-host, prior to laying eggs**	depth.day	107.2	3.5	103.8	7.9	0.708	101.5	1.4	-0.019	0.00
		snow	8.8	3.9	4.6	2.2	0.386	4.9	0.6	0.024	0.01
		cold	0.0	NA	0.0	NA	NA	0.0	NA	NA	NA
		snow.cold	0.0	NA	0.0	NA	NA	0.0	NA	NA	NA
		avg.min.mar	-10.1	2.5	-7.5	1.0	0.375	-8.7	0.3	0.009	0.01
		avg.max.mar	2.7	1.3	5.1	1.1	0.214	3.6	0.3	0.007	0.01
		avg.min.apr	-1.1	0.7	-0.6	0.4	0.646	-1.1	0.2	0.013	0.04
		avg.max.apr	11.6	0.8	11.4	0.6	0.809	10.9	0.2	0.021	0.06
		avg.may.min	5.9	0.2	6.0	0.6	0.911	4.8	0.2	0.021	0.12
		avg.may.max	20.4	0.7	18.4	0.7	0.074	18.5	0.3	0.018	0.04

Mean avg.min.mar and avg.max.mar in the drop season of epizootic years were 3 °C colder than in non-epizootic years (mean min = -7.5, ± 2.5°C, mean max = 5.1, ± 1.3 °C; Table 19). Mean avg.min.apr and avg.max.apr were similar in epizootic and non-epizootic years (-1.0 °C and 11.5 °C). Mean avg.max.may was ~2 °C (20.4 ± 0.7°C) higher in epizootic than non-epizootic years (mean = 18.4° C ± 0.7 °C) and the long-term (mean = 18.4 ± 0.7 °C); mean avg.min.may were similar (5.9 °C).

ii. Early summer

Early summer variables were generally similar between epizootic and non-epizootic years. Mean cool.egg was ~1.1X higher during the egg season of non-epizootic than epizootic years (46.4 ± 3.9 d; Table 20). Mean hot.egg was similar (~6 d) between epizootic and non-epizootic years, and 2 days less than the long-term (~8.5 ± 0.5 d). Mean prec.egg was ~24.1 cm (± 1.4), with epizootic and non-epizootic years consistently higher than the long-term (19.3 ± 0.6 cm). Mean prec.egg in non-epizootic years was variable, ranging from 12.7-31.7 cm.

Table 20: Comparison of variables between epizootic years (2002, 2011, 2014, 2015, and 2016), non-epizootic years (2003, 2004, 2005, 2012, and 2013), and long-term data (1938-2015); long-term linear trend and R^2 provided. See Table 10 for code description.

			Epizootic		Non-epizootic			Long-term: 1938-2015			
Season	**Stage**	**Variable**	mean	se	mean	se	ρ-value	mean	se	trend	r^2
early summer	**Egg**	cool.egg	46.4	3.9	51.6	1.5	0.270	50.0	0.6	-0.046	0.04
		hot.egg	6.2	1.5	6.0	1.4	0.923	8.5	0.5	-0.077	0.16
		prec.egg	24.1	1.4	21.2	3.3	0.457	19.3	0.6	0.057	0.06

iii. Late summer-early fall

Late summer-early fall conditions in non-epizootic years tended to be drier and hotter from mid-August through mid-September. The longest droughts were temporally concentrated, generally occurring from mid-August through mid-September in non-epizootic years (i.e., were drier). Conversely, September and August rains were heavier and concentrated on either side of this timeframe in non-epizootic years.

Mean hot.l.30 was similar (~3-4 d) in epizootic and non-epizootic years (Table 21). Mean avg.max.l was 0.6 °C higher in non-epizootic than epizootic years (23.0 °C ±

0.6); epizootic years ranged from 21.7-24.9 °C. Mean prec.l was 1.5X higher in non-epizootic than epizootic years (15.2 ± 2.4 cm), with a long-term average of 17.8 cm (± 0.8). Mean no.prec was similar in both year types (~41 d) and similar to the long-term (39.9 ± 0.6 d). The 3 longest periods of drought (defined as: periods without rain; days.nr1, days.nr2, and days.nr3) in epizootic years were 10.6 (± 1.0), 6.8 (± 0.6), and 5.6 d (± 0.6), and were similar to non-epizootic years and the long-term. Conversely, in non-epizootic years, the 3 longest droughts had tight temporal grouping with 4 of 5 starting in mid-late August and continuing until 15 September; the other began on 6 August, ending on 11 September (33 d). In epizootic years, the 3 longest droughts either had loose temporal grouping (i.e., were more spread out in 2002 and 2016), or the longest period without rain occurred earlier (end of August in 2011, 2014, and 2015). Mean days.3.nr was 23 d (± 1) in both year types. In non-epizootic years, total precipitation in September was ~33% higher, however, precipitation was 60% and 20% lower in sum.nr1.2 and sum.nr1.3, (from mid-August through mid-September), indicating that September rain was probably more frequent and/or intense after mid-September when larval questing initiates.

Mean temp.nr.max was similar (23.5 °C), yet mean temp.nr.min in non-epizootic years was 1.3 °C higher than the long-term (8.5 °C ± 0.4). For non-epizootic years, temp.nr2.min was 1.9 °C higher than the long-term (8.2 ± 0.5 °C); in epizootic years temp.nr2.min was 1.1 °C lower. Mean temp.nr3.min was similar (9 °C), but occurred 10 d earlier (mid/late August) in epizootic years. Overall, minimum temperatures in the 3 drought periods in non-epizootic years were 0.6-1.9 °C higher than the long-term.

Table 21: Comparison of variables between epizootic years (2002, 2011, 2014, 2015, and 2016), non-epizootic years (2003, 2004, 2005, 2012, and 2013), and long-term data (1938-2015); long-term linear trend and R^2 provided. See Tables 10, 11 for code description.

			Epizootic		Non-epizootic			Long-term: 1938-2015			
Season	**Stage**	**Variable**	mean	se	mean	se	ρ-value	mean	se	trend	r^2
Late Summer/Early Fall	**Larval quiescence**	hot.l.30	4.0	2.1	3.2	2.2	0.802	4.5	0.5	-0.059	0.11
		avg.max.l	23.0	0.6	23.6	0.4	0.510	22.8	0.1	-0.001	0.00
		prec.l	15.2	2.4	23.2	3.2	0.087	17.8	0.8	0.047	0.03
		no.prec	40.6	2.5	41.2	2.8	0.876	39.9	0.6	0.072	0.11
		yes.prec	20.2	2.4	19.8	2.8	0.916	21.1	0.6	-0.072	0.11
		days.nr1	10.6	1.1	10.2	1.0	0.794	10.2	0.4	0.031	0.05
		days.nr2	6.8	0.6	8.4	1.7	0.419	7.2	0.3	0.024	0.07
		days.nr3	5.6	0.6	5.2	0.5	0.620	5.3	0.2	0.019	0.11
		day.nr1.e	252.0	6.4	258.8	1.4	0.354	251.4	1.5	0.114	0.04
		day.nr2.e	252.4	8.4	245.4	5.5	0.510	247.2	1.7	0.073	0.01
		day.nr3.e	238.4	5.8	248.0	4.6	0.234	244.7	1.9	0.056	0.01
		days.3.nr	23.0	0.9	23.8	3.1	0.812	22.7	0.6	0.074	0.11
		avg.date.allnr	243.5	1.9	247.4	3.1	0.312	244.3	0.9	0.061	0.03
		sept.prec	7.6	1.6	10.1	1.0	0.248	8.5	0.6	-0.001	0.00
		sum.nr1.2	4.7	1.3	1.8	0.6	0.088	3.7	0.5	0.000	0.00
		sum.nr1.3	8.0	2.3	6.4	1.4	0.572	7.3	0.6	0.025	0.01
		temp.nr1.min	8.5	2.1	9.4	0.5	0.709	8.5	0.4	0.004	0.00
		temp.nr2.min	7.1	2.6	10.1	1.8	0.376	8.2	0.5	0.004	0.00
		temp.nr3.min	9.6	2.0	9.3	0.9	0.894	8.7	0.5	0.012	0.01
		temp.nr1.max	23.1	1.6	22.1	0.9	0.624	23.9	0.4	-0.038	0.08
		temp.nr2.max	22.4	2.6	23.7	2.3	0.722	23.1	0.5	-0.011	0.00
		temp.nr3.max	24.1	1.5	22.9	0.9	0.501	23.8	0.5	-0.037	0.04
		temp.nr.min	8.8	0.8	9.8	0.6	0.365	8.5	0.2	0.013	0.02
		temp.nr.max	23.5	0.7	23.1	1.0	0.707	23.7	0.2	-0.025	0.08

In non-epizootic years, min.10.l and min.20.l were ~1.4 °C higher than in epizootic years (15.8, 14.4 °C; $P = 0.126$, 0.129) and the temporal occurrence was similar between them and with the long-term (Table 22). Mean and temporal occurrence of min.10.l, min.20.l, max.10.l, and max.20.l were similar among year type and the long-term (Table 22). Mean min.10.aug was 1.5° C higher in non-epizootic than epizootic years (15.0 ± 0.5 °C; $\rho = 0.074$) and the long-term (15.3 ± 0.2 °C). Mean max.10.aug was 0.8° C higher in non-epizootic than epizootic years (28.1 ± 0.8 °C), and similar to the long-term (29.0 ± 0.2 °C). Mean min.10.sept was 1.5° C higher in non-epizootic than epizootic years (12.9 ± 0.5 °C), and 2.5 °C higher than the long-term (11.9 ± 0.2 °C). Mean max.10.sept was 1.4 °C higher in epizootic than non-epizootic years (25.5 ± 0.7 °C) and the long-term (25.8 ± 0.2 °C).

Mean avg.aug.min was 1.1 °C higher in non-epizootic than epizootic years (11.7 ± 0.4 °C; ρ = 0.071) and 1.5 °C higher than the long-term (11.2 ± 0.2 °C). Mean avg.aug.max was ~1 °C higher in non-epizootic than epizootic years (24.7 ± 0.8 °C), and 1.7 °C higher than the long-term (24.9 ± 0.2 °C). Mean avg.sept.min was 1.2 °C higher in non-epizootic than epizootic years (7.8 ± 0.6 °C) and 2.2 °C higher than the long-term (6.8 ± 0.2 °C); avg.sept.max was similar in all (~21 °C).

Table 22: Comparison of variables between epizootic years (2002, 2011, 2014, 2015, and 2016), non-epizootic years (2003, 2004, 2005, 2012, and 2013), and long-term data (1938-2015); long-term linear trend and R^2 provided. See Tables 10, 11 for code description.

Season	Stage	Variable	Epizootic		Non-epizootic			Long-term: 1938-2015			
			mean	se	mean	se	ρ-value	mean	se	trend	r^2
Late Summer/Early Fall, cont.	Larval quiescence	min.10.l	15.8	0.5	17.3	0.8	0.126	15.8	0.2	0.012	0.04
		min.20.l	14.4	0.4	15.7	0.7	0.129	14.2	0.2	0.015	0.06
		avg.date.l.min	234.5	2.0	234.0	1.7	0.871	233.6	0.5	0.000	0.00
		max.10.l	29.3	0.8	29.1	0.8	0.901	29.5	0.2	-0.025	0.12
		max.20.l	27.8	0.8	27.9	0.7	0.937	28.0	0.2	-0.019	0.08
		avg.date.l.max	235.9	1.8	231.4	1.6	0.098	233.3	0.6	-0.012	0.00
		min.10.aug	15.0	0.5	16.8	0.7	0.074	15.3	0.2	0.012	0.03
		max.10.aug	28.1	0.8	28.9	0.7	0.449	29.0	0.2	-0.023	0.10
		min.10.sept	12.9	0.5	13.6	0.6	0.397	11.9	0.2	0.018	0.05
		max.10.sept	26.9	0.7	25.5	0.7	0.202	25.8	0.2	-0.008	0.01
		avg.aug.min	11.7	0.4	12.8	0.4	0.071	11.2	0.2	0.024	0.16
		avg.aug.max	24.7	0.8	25.7	0.4	0.318	24.9	0.2	-0.005	0.01
		avg.sept.min	7.8	0.6	9.0	0.3	0.148	6.8	0.2	0.031	0.18
		avg.sept.max	21.3	0.7	21.4	0.4	0.936	20.6	0.2	0.003	0.00

iv. Fall

Mean avg.oct.min was 1.9 °C higher in non-epizootic than epizootic years (2.0 ± 0.7 °C), and 2.3 °C higher than the long-term (1.6 ± 0.2 °C; Table 23); mean avg.oct.max was similar for both and the long-term (14.5 ± 0.3 °C). Mean avg.nov.min was 1.5 °C higher in non-epizootic than epizootic years (-3.3 ± 0.7 °C) and the long-term (± 0.2). Mean avg.nov.max was 0.8 °C higher in non-epizootic than epizootic years (7.1 ± 1.0 °C) and 1.2 °C higher than the long-term (6.6 ± 0.2). Mean avg.dec.min was 2.1 °C higher in epizootic than non-epizootic years (-9.6 ± 1.2 °C) and 3.4° C higher than the long-term (-

11.2 ± 0.4 °C). Mean avg.dec.max was similar in non-epizootic and epizootic years and 1.5° C higher than the long-term (-0.4 ± 0.3 °C).

Table 23: Comparison of variables between epizootic years (2002, 2011, 2014, 2015, and 2016), non-epizootic years (2003, 2004, 2005, 2012, and 2013), and long-term data (1938-2015); long-term linear trend and R^2 provided. See Table 11 for code description.

			Epizootic		Non-epizootic			Long-term: 1938-2015			
Season	**Stage**	**Variable**	mean	se	mean	se	ρ-value	mean	se	trend	r^2
Fall	**Larval Questing**	avg.oct.min	2.0	0.7	3.9	1.7	0.358	1.6	0.2	0.027	0.12
		avg.oct.max	14.4	0.6	14.8	1.4	0.809	14.2	0.3	-0.015	0.03
		avg.nov.min	-3.3	0.7	-1.8	0.7	0.194	-3.4	0.2	0.021	0.08
		avg.nov.max	7.1	1.0	7.8	1.3	0.637	6.6	0.2	0.012	0.02
		avg.dec.min	-7.6	1.4	-9.7	1.2	0.301	-11.2	0.4	0.055	0.14
		avg.dec.max	1.2	1.4	0.9	1.1	0.873	-0.4	0.3	0.025	0.05
		perm.snow.1	366.6	15.2	356.6	14.3	0.645	360.1	3.7	0.230	0.03
		days.b.perm	24.3	11.3	17.0	10.5	0.654	20.9	2.9	0.216	0.05
		max.snow.b	5.8	2.4	4.0	1.8	0.582	8.0	1.0	0.016	0.00
		snow.1	328.8	10.1	315.6	9.4	0.373	318.3	2.0	0.100	0.02
		last.b.perm	365.8	16.9	345.4	16.4	0.417	356.2	4.0	0.282	0.04
		avg.temp.snow	347.3	12.8	330.5	11.8	0.369	337.3	2.5	0.191	0.05
		frost.0.25ft	348.0	6.6	349.0	5.2	0.908	341.3	1.1	0.138	0.11
		frost.0.5ft	356.4	5.9	353.8	5.3	0.752	349.5	1.1	0.143	0.12
		frost.1ft	365.4	6.1	361.4	5.4	0.637	357.3	1.2	0.137	0.09
		days.min.l.17	3.0	1.7	4.0	1.5	0.670	7.4	0.6	-0.084	0.13
		min.1.l.17	513.8	106.9	432.6	84.7	0.569	378.2	14.0	1.851	0.13
		fall.hot.20.min	5.3	0.5	7.0	1.4	0.308	4.8	0.2	0.027	0.12
		fall.hot.20.date.min	294.4	4.0	293.0	2.7	0.786	294.5	0.7	-0.048	0.03
		fall.hot.20.max	18.3	0.7	18.4	0.9	0.921	18.1	0.3	-0.018	0.04
		fall.hot.20.date.max	290.0	2.1	292.1	1.2	0.422	292.3	0.6	0.012	0.00
		week3.nov.mean.temp	1.4	1.2	2.7	0.6	0.380	0.6	0.3	0.011	0.01
		week4.nov.mean.temp	-0.8	1.8	1.4	1.6	0.375	-1.0	0.4	0.036	0.06
		week1.dec.mean.temp	-0.7	2.0	-3.0	2.4	0.479	-3.3	0.5	0.036	0.04
		week2.dec.mean.temp	-3.2	2.3	-3.4	1.9	0.932	-5.5	0.5	0.018	0.01

Mean week3.nov.mean.temp was 1.1 °C higher in non-epizootic than epizootic years (1.3 ± 1.2 °C), and 2 °C higher than the long-term (se ± 0.3 °C). Mean week4.nov.mean.temp was ~2.4 °C higher in non-epizootic than epizootic years and the long-term (~1 °C). Mean week1.dec.mean.temp was 2.4 °C (± 2.0) higher in epizootic than non-epizootic years (-3.0 ± 2.4 °C) and the long-term (± 0.5 °C). Mean week2.dec.mean.temp in non-epizootic and epizootic years were similar and 2 °C higher than the long-term (-5.5 ± 0.5 °C). The 20 hottest minimum and maximum ambient temperatures from October through December and the temporal location were similar in the 3 conditions.

Mean snow.1 was 12 November (± 9.3 d) in non-epizootic years and 25 November (± 10.1 d) in epizootic years, with the normal first day of snow on 14 November (± 2 d). The first day of permanent snow was 1 January (± 15.2 d) in epizootic years and 21 December (± 14.3 d) in non-epizootic years, although both categories were influenced by one outlier that polarized the means; if excluded, they would be similar to the long-term date (25 December ± 3.6 d). Mean frost.0.25ft, frost.0.5ft, and frost.1ft were 15, 20, and 27 December (± 5 d) in non-epizootic years and 14, 22, and 31 December (± 6 days) in epizootic years.

v. Fall conditions in relation to ranked abundance

Overall, fall tick abundance was an effective indicator of epizootic events, but was influenced (positively or negatively) by fall conditions (e.g., snow events) that influence infestation level in either direction. In 10 consecutive years of winter tick sampling, the 3 highest abundances (mean > 41.7) were followed by epizootic events in 2011, 2014, and 2016. In the 2014 questing season, high tick loads were followed by a frost to a depth of 7.6 cm 10 days earlier than the long-term conditions (7 December); however, the first snowfall was on 11 December, 27 days later than the long-term date. In non-epizootic year 2010, the questing season had similar abundance and timing of frost to a depth of 7.6 cm as in 2014, but the first snowfall was more than a month earlier (25 November). The first snow event in 2012, a non-epizootic year, occurred 16 days earlier than the long-term date (14 November).

Tick abundance was relatively low (< 36.9) in the 2013 and 2015 questing seasons, with early snow and frost in 2015, and an "extended" larval questing season in 2013; however, an epizootic event was documented in 2015 but not suspected in 2013. Conversely, subsetting data from NH suggests that abundance was high in 2015 but not in 2013, although sample sizes were low (18 in 2015, 9 in 2013). The questing seasons of 2007 and 2008 were the lowest abundances measured in the 10 years and despite an extended larval questing season in 2007 and typical fall conditions in 2008, an epizootic was not suspected in either year suggesting that the desiccating conditions in late summer were more influential than length of the questing season in those years.

Predictive model for northern New England

Using an information-theoretic approach, independent and interacting hypotheses were modeled to evaluate how sex, weather/ground conditions, and moose density/habitat influence the abundance of winter ticks on harvested moose. The habitat parameter consistently improved fitness and competitiveness, reducing the AIC by ~25 indicating that "habitat" influences the response variable and increases predictive power while not overfitting the model. The 6 models containing "habitat" each represent a different hypothesis and/or combination (Table 24). Predicted abundance in 2 non-epizootic and 2 epizootic years was evaluated to determine if they fit current spatial and temporal trends observed in existing data.

The 12 candidate model's AIC ranged from 17786.5-17844.5. Each model had a low deviance explained (%D) ranging from 18.7-21.0%, suggesting that accuracy is low and likely reflects the high variance in the dataset. The "best" statistical fit was model 4 which had the highest %D and had no competitive (Δ AIC < 4) alternative model, but models 1-4 and 7-10 did not reflect one or more of the fundamental ecological relationships: 1) lower abundance at higher latitudes (Fig. 9, 10, 11), 2) higher abundance during the questing season in epizootic years (Table 14), and 3) positive correlation between tick abundance and moose density (Blyth 1995, Pybus 1999, Samuel 2004).

Predictions using models 5, 6, 11, and 12 best supported these spatial and temporal fundamental abundance changes. Model 12 was accepted as the "best" overall model given that models 5, 6, and 11 were not highly competitive with model 12 (Δ AIC: 9.5-39.7).

Table 24: Results of 12 candidate negative binomial generalized additive models for regional prediction of winter tick abundance in northern New England; %D, AIC and Δ AIC.

Model #	Scenario	%D	AIC	Δ AIC
model4	Spring Snow:Density + Late Summer Desiccation +Habitat	21.0	17786.5	0.0
model2	Spring Snow:Density + Habitat	20.5	17799.0	12.5
model10	Density:Previous Fall Snow + Habitat	20.3	17803.7	17.2
model12	Density:Normal Fall Snow + Late Summer Desiccation + Habitat	20.3	17804.3	17.9
model3	Spring Snow:Density + Late Summer Desiccation	20.0	17811.6	25.1
model8	Density:Previous December Temperatures + Habitat	20.0	17813.0	26.5
model6	Density:Late Summer Desiccation + Habitat	19.7	17820.2	33.7
model1	Spring Snow:Density	19.4	17826.8	40.3
model11	Density:Normal Fall Snow + Late Summer Desiccation	19.4	17829.3	42.8
model9	Density:Previous Fall Snow	19.2	17832.9	46.5
model7	Density:Previous December Temperatures	18.9	17843.0	56.6
model5	Density:Late Summer Desiccation	18.7	17844.5	58.0

Predictions of 6 models

Model 2 used the weather variable spring snow persistence but was not competitive (Δ AIC > 4) with the highest ranked model (4), and tended to overestimate tick abundance, especially in northern Maine and southern New Hampshire in the fall of 2012 that had low abundance (Fig. 16). Relative to the late winter-early spring conditions hypothesis, the model did predict a negative relationship between years of high spring snow persistence and low tick abundance. Conversely, it did not predict lower abundance in the questing season of non-epizootic years (fall 2011 and 2012) or higher abundance in the questing season of epizootic years (fall 2014 and 2015). Habitat was positively correlated (log value: 0.016X) with abundance.

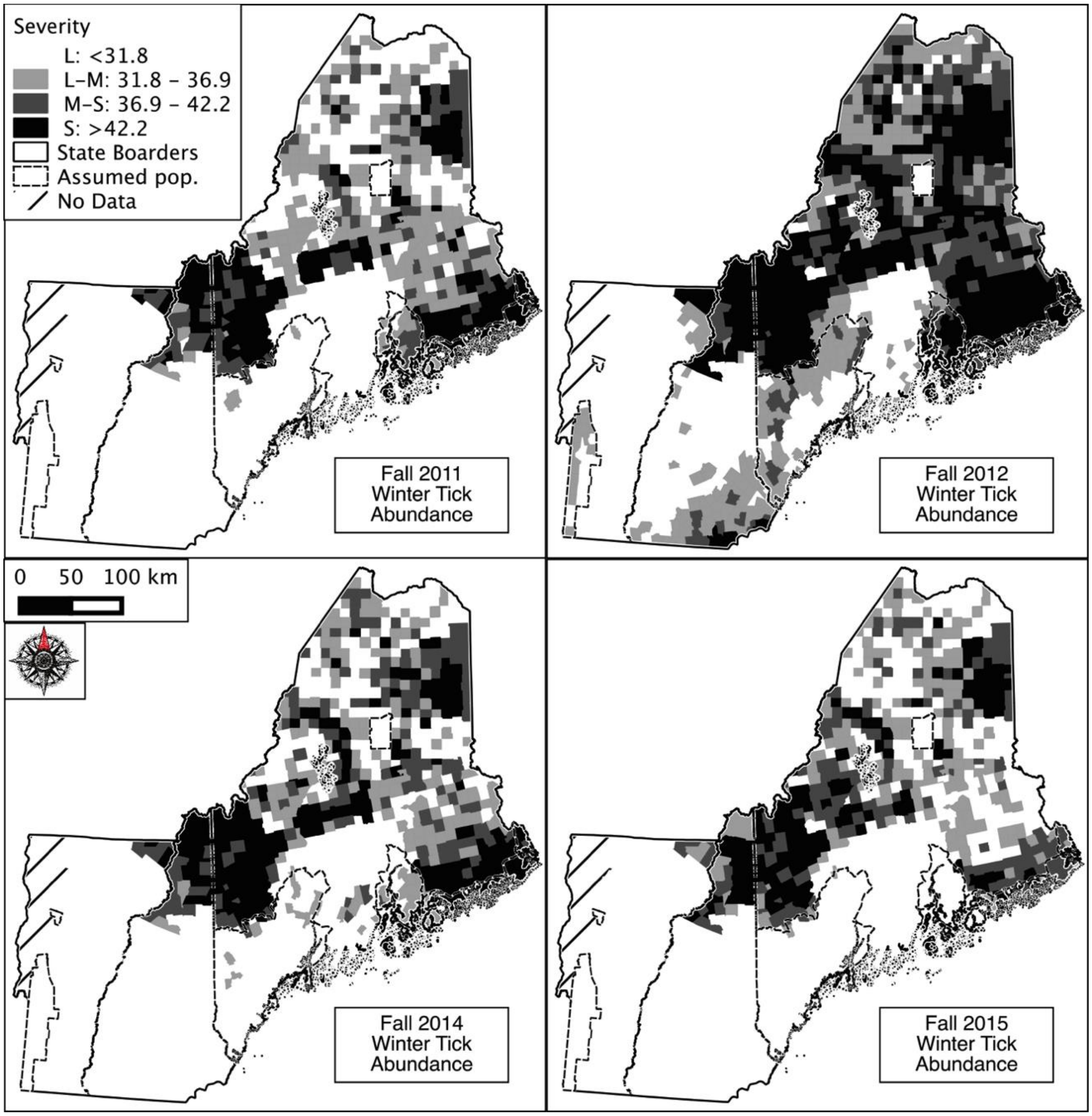


Figure 16: Model 2 predictions for relative abundance of winter tick on harvested bull moose. Falls 2011, and 2012 were followed by "non-epizootic" years, and falls 2014, and 2015 were followed by "epizootic" years. L = Light, M = Moderate, S = Severe.

Model 4 used the weather variables spring snow persistence and minimum August temperatures. With the lowest Δ AIC (0.0), model 4 predicted lower abundance in northern Maine, but not in the fall of 2012 which was described with low abundance. As indicated by the late winter/early spring conditions hypothesis, the model did predict a negative relationship between years of high spring snow persistence and low tick abundance. Conversely, it did not predict lower abundance during questing in non-epizootic years (fall 2011 and 2012) or increased abundance in epizootic years (fall 2014 and 2015; Fig. 17). Minimum August temperatures were negatively correlated (log value: -0.07X) and habitat was positively correlated (log value: 0.016X) with abundance.

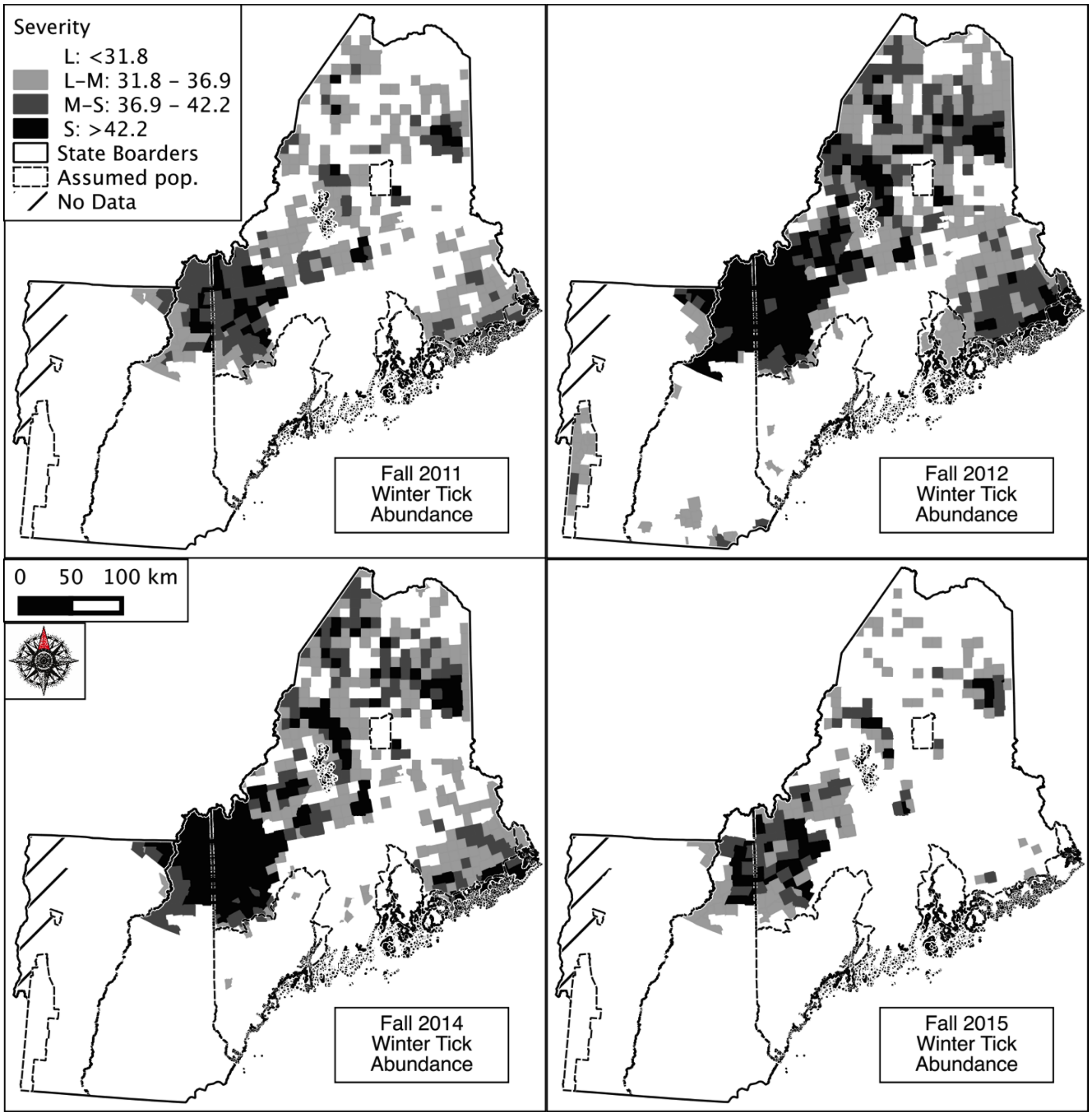


Figure 17: Model 4 predictions for relative abundance of winter tick on harvested bull moose. Falls 2011, and 2012 were followed by “non-epizootic” years, and falls 2014, and 2015 were followed by “epizootic” years. L = Light, M = Moderate, S = Severe.

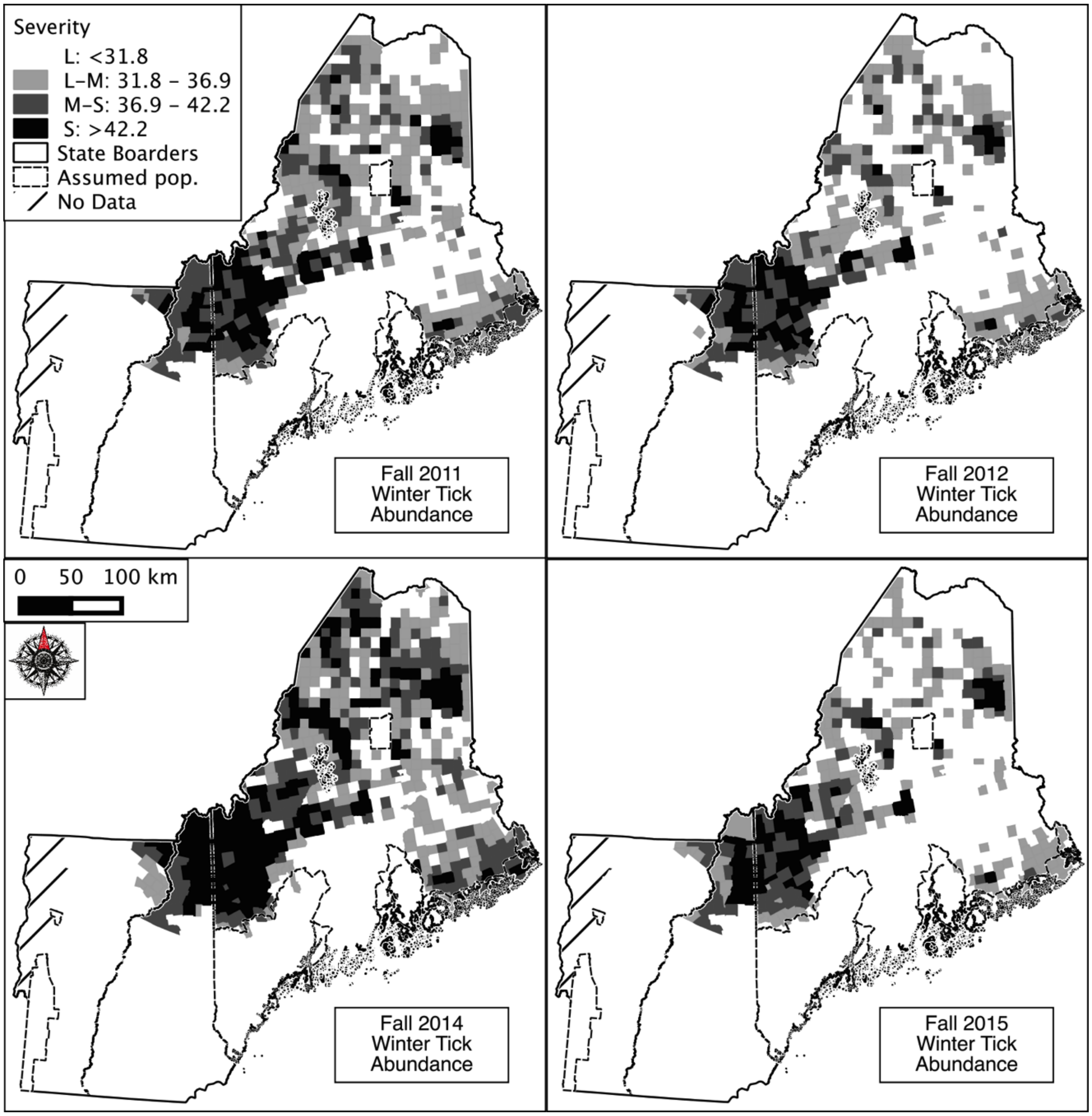


Figure 18: Model 6 predictions for relative abundance of winter tick on harvested bull moose. Falls 2011, and 2012 were followed by "non-epizootic" years, and falls 2014, and 2015 were followed by "epizootic" years. L = Light, M = Moderate, S = Severe.

Model 6 used the weather variable minimum August temperatures, but was not competitive (Δ AIC > 4) with the highest ranked model (4). It predicted lower abundance in northern Maine, but did not indicate increased abundance in the fall of 2015 which was described with high abundance. As indicated by the late summer desiccation hypothesis, the model predicted a negative correlation between August ambient temperatures and tick abundance. Excluding 2015, predictions also supported temporal and spatial abundance trends (Fig. 18). Minimum August temperatures were negatively correlated (log value: -0.07X) and habitat was positively correlated (log value: 0.016X) with abundance.

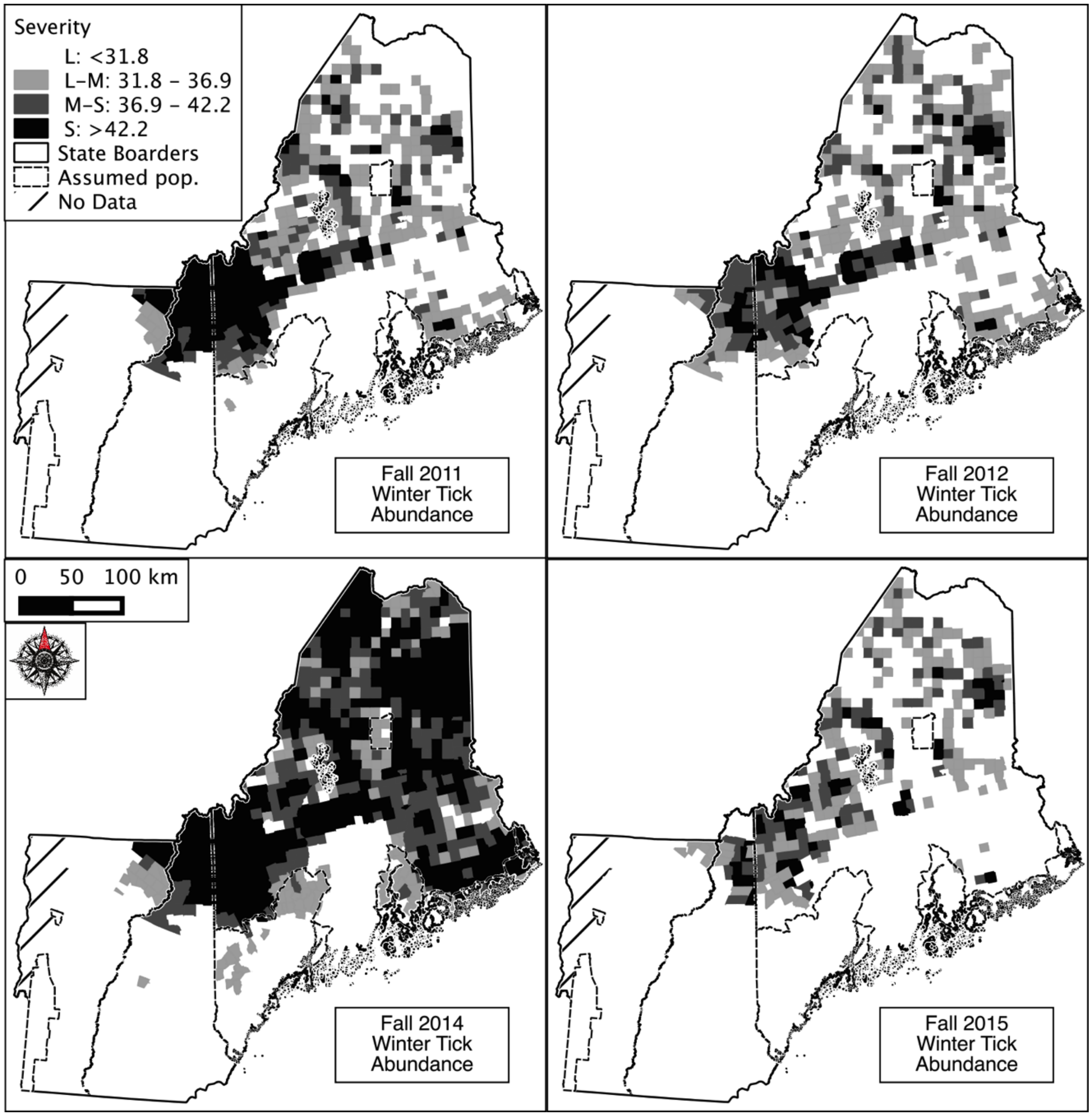


Figure 19: Model 8 predictions for relative abundance of winter tick on harvested bull moose. Falls 2011, and 2012 were followed by "non-epizootic" years, and falls 2014, and 2015 were followed by "epizootic" years. L = Light, M = Moderate, S = Severe.

Model 8 used the weather variable previous minimum December temperatures and with a high Δ AIC (26.5) was not competitive (> 4) with the highest ranked model (4), but did not predict lower abundance in northern Maine in fall 2014, and light-moderate abundance in fall 2015 which was described with high abundance (Fig. 19). It predicted a positive correlation between the larval questing period and tick abundance and habitat was positively correlated (log value: 0.018X) with abundance.

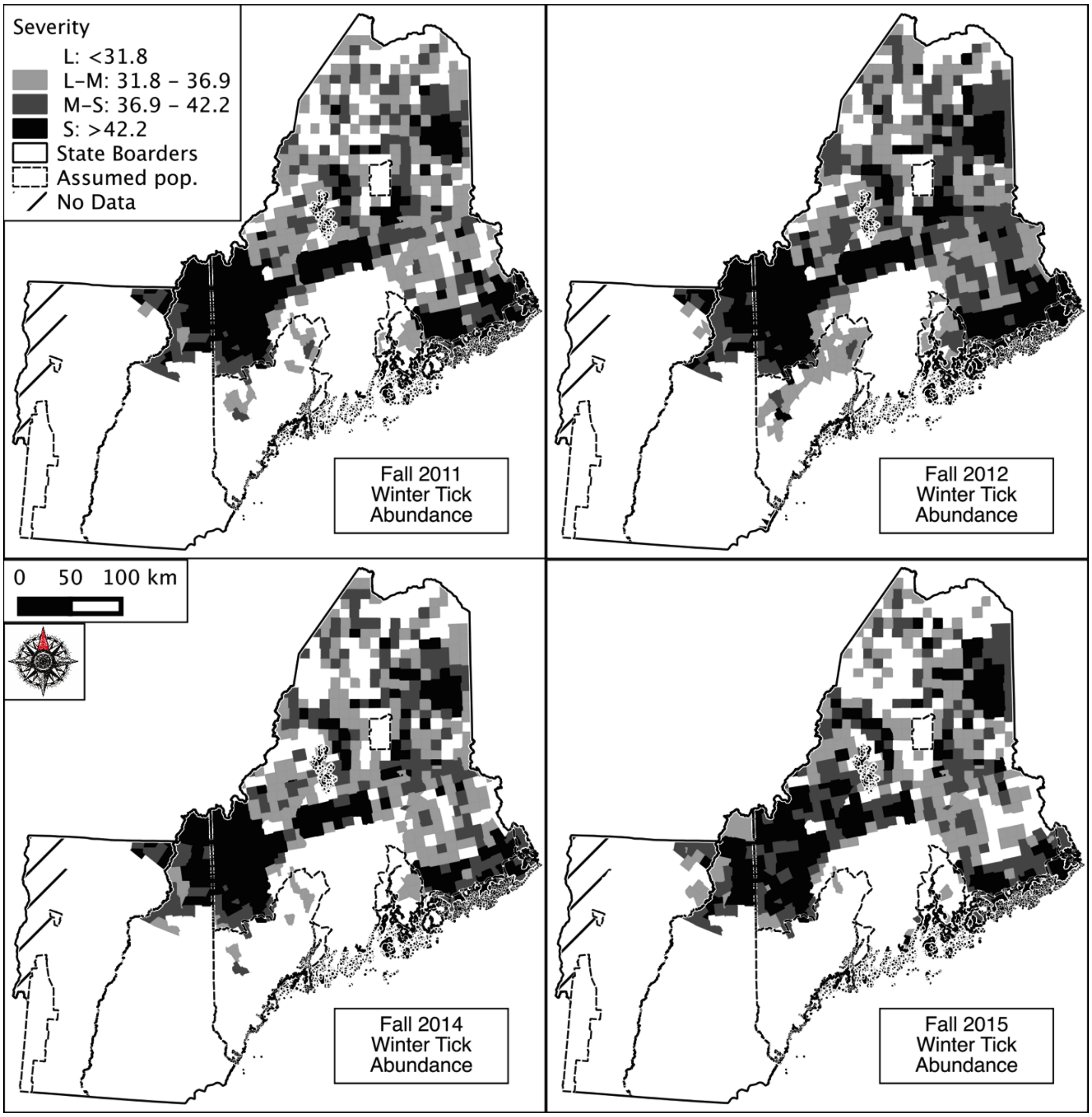


Figure 20: Model 10 predictions for relative abundance of winter tick on harvested bull moose. Falls 2011, and 2012 were followed by "non-epizootic" years, and falls 2014, and 2015 were followed by "epizootic" years. L = Light, M = Moderate, S = Severe.

Model 10 used the weather variable snowfall timing in the previous fall to predict abundance and with a high Δ AIC (17.2) was not competitive (> 4) with the highest ranked model (4). It did not predict lower abundance in the questing season of non-epizootic years (fall 2011 and 2012) or higher abundance in the questing season of epizootic years (fall 2014 and 2015; Fig. 20). The model did predict a positive correlation between the larval questing period and tick abundance and habitat was positively correlated (log value: 0.018X) with abundance.

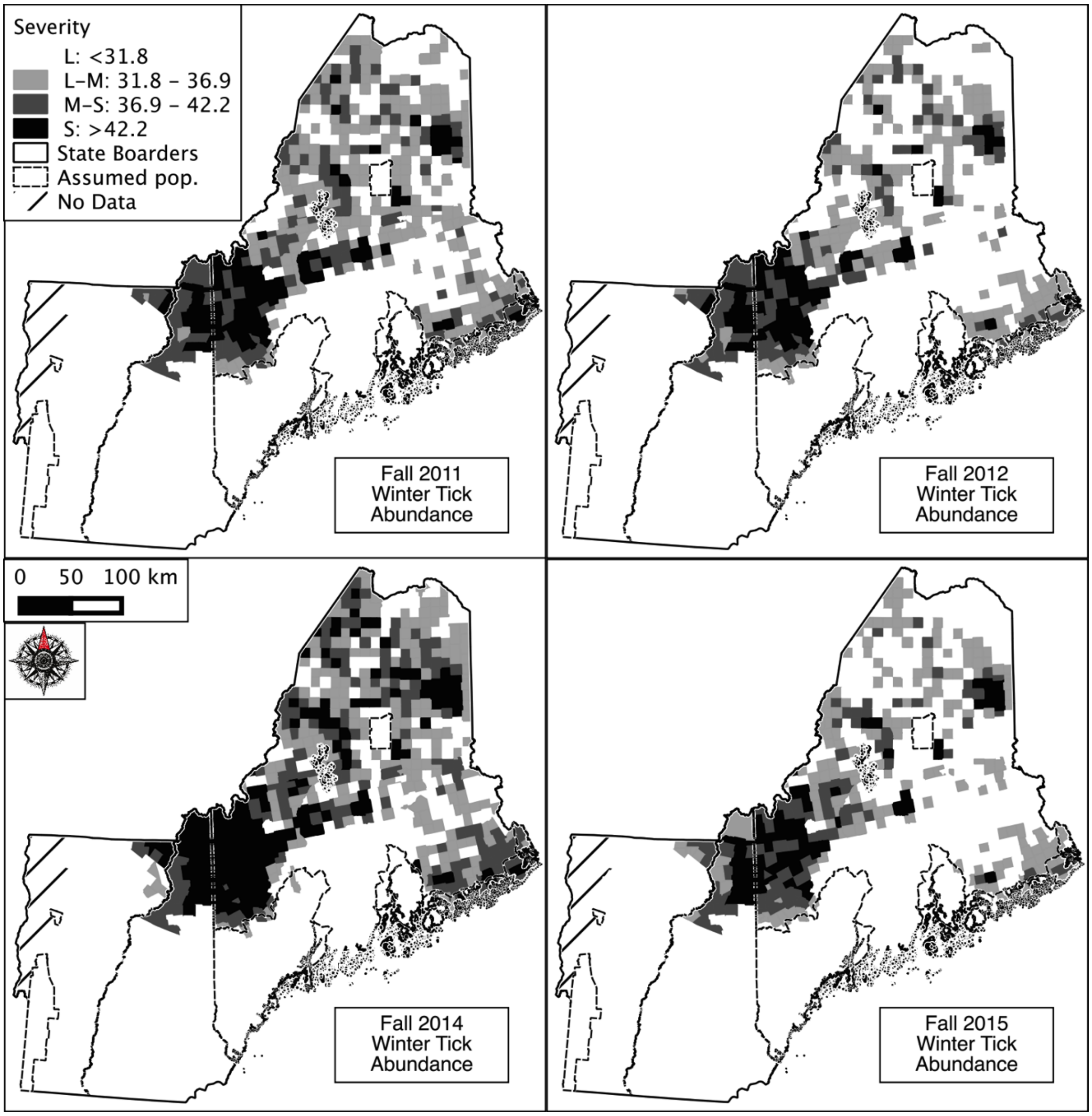


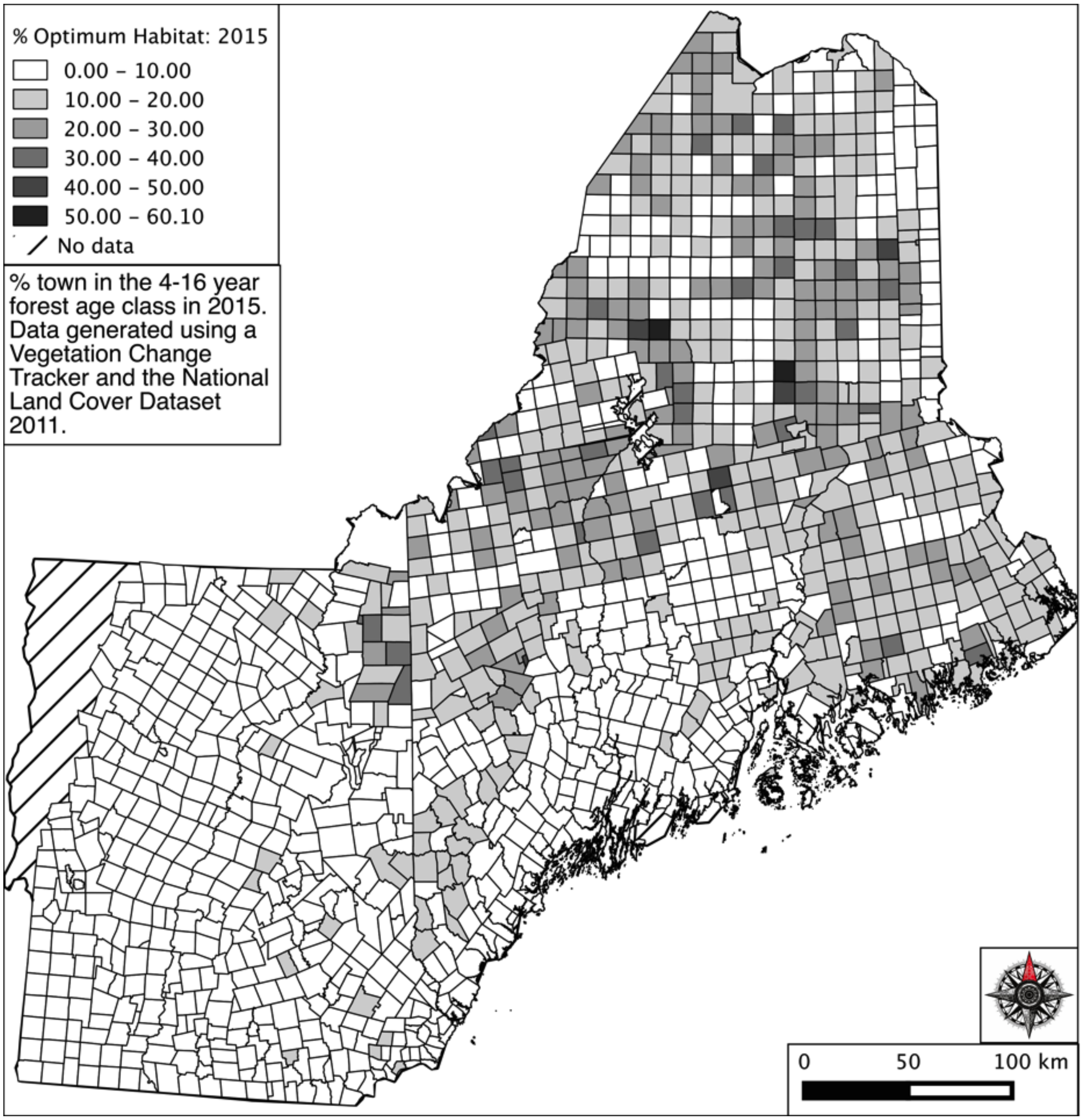
Figure 21: Model 12 predictions for relative abundance of winter tick on harvested bull moose. Falls 2011, and 2012 were followed by "non-epizootic" years, and falls 2014, and 2015 were followed by "epizootic" years. L = Light, M = Moderate, S = Severe.

Model 12 used the weather variables normal snowfall timing in the fall and minimum August temperatures to predict abundance and with a high Δ AIC (17.9) was not competitive (> 4) with the highest ranked model (4). It predicted lower abundance in northern Maine, but did not predict increased abundance in the fall of 2015 which was described with high abundance. It did predict a positive correlation between the larval questing period and tick abundance. Excluding 2015, predictions supported temporal and spatial abundance trends (Fig. 21). Minimum August temperatures were negatively correlated (log value: -0.07X), and habitat was positively correlated (log value: 0.016X) with abundance (Table 25).

Table 25: Model 12: Parametric parameter coefficients, standard errors, and significance. Smoothed terms degrees of freedom, Chi squared, and significance.

Parametric terms	coefficients	se	z value	Pr(>|z|)
intercept (sexF)	3.980	0.500	7.94	2.05E-15
sexM	0.520	0.047	10.88	2.20E-16
min.aug2	-0.067	0.023	-2.90	3.70E-03
habitat	0.16	0.003	5.28	1.27E-07
Smoothed terms	edf	Ref.df	Chi.sq	*P*-value
s(density):fall.snow	4.92	4.99	116.56	2.20E-16
re(year)	8.49	9.00	175.72	2.20E-16

Excluding 2015, model 12 predictions supported temporal and spatial abundance trends. It was accepted as the "best" overall model given that models 1-4 and 7-10 did not predict spatial and temporal abundance relationships, and that models 5, 6, and 11 were not highly competitive with model 12 (Δ AIC: 9.5-39.7). All models using optimal habitat indicated a positive correlation with tick abundance. Optimal habitat >10% is primarily located in northern New Hampshire as well as central and northern Maine, and is almost absent in Vermont (Fig. 22). The smoothed interaction between moose density and the normal first fall snow event (> 2.54 cm) indicated that abundance peaks at a density of ~0.8 moose/km (Fig. 23). Where moose density is < 0.8 moose/km, tick abundance is strongly influenced by host density. Density > 0.8 moose/km only occurs farther north where tick abundance is presumably limited by the onset of winter that reduces the length of the larval questing season (Fig. 24).



% town in the 4-16 year forest age class in 2015. Data generated using a Vegetation Change Tracker and the National Land Cover Dataset 2011.

Figure 22: % optimal habitat (4-16 year age class) by town in 2015.

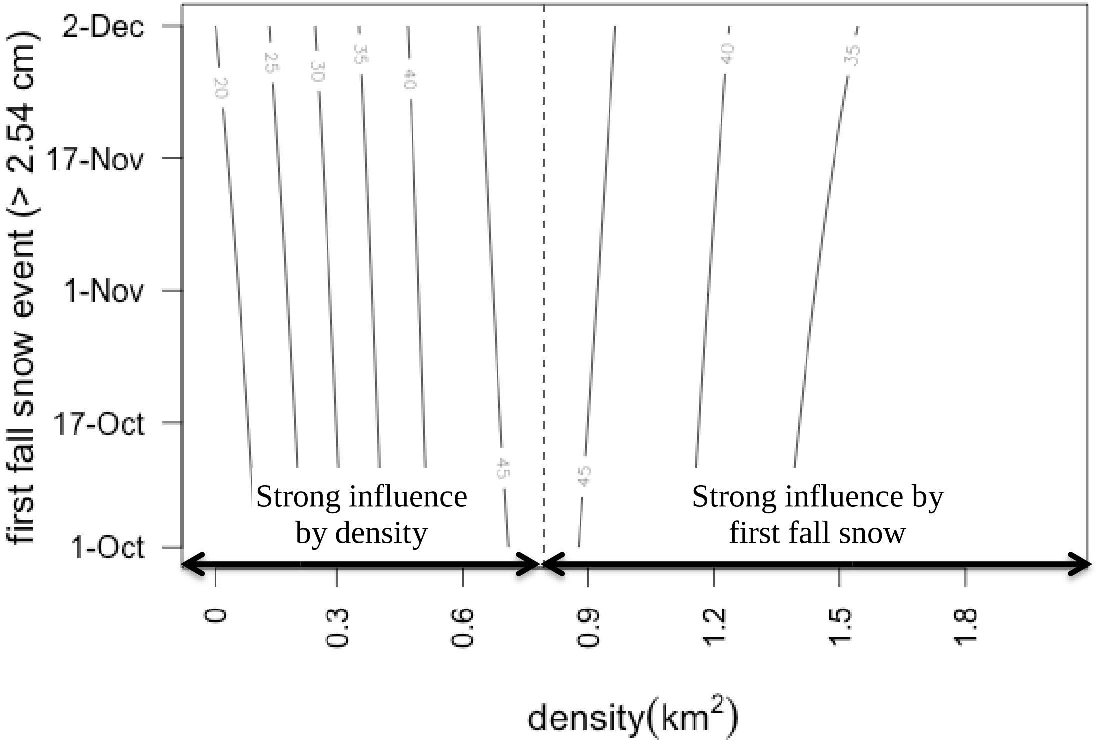


Figure 23: Predicted abundance by moose density and first fall snow event.

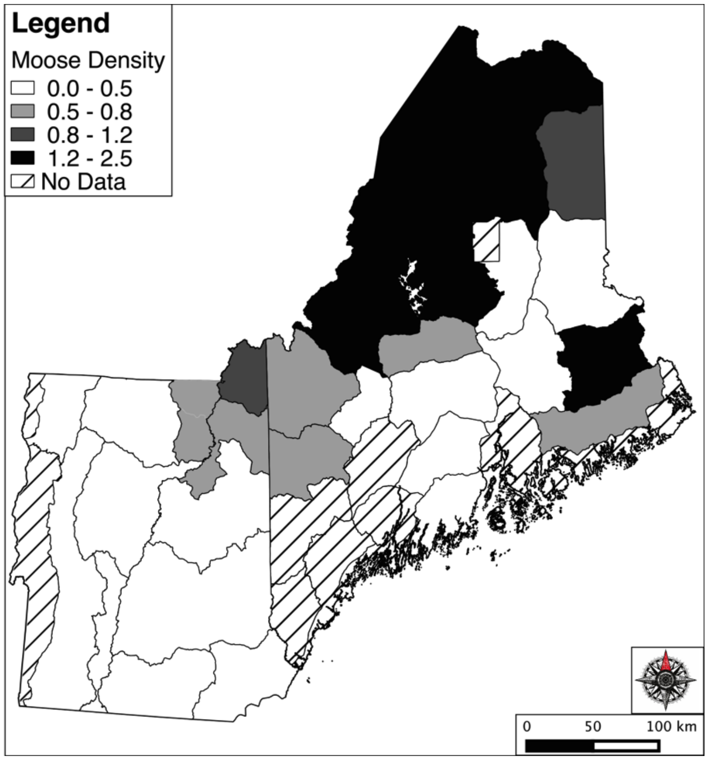


Figure 24: Estimated moose density (km^2) in 2015 by region in Maine, New Hampshire and Vermont

DISCUSSION

Winter tick abundance trends in northern New England

Winter tick epizootics are known to occur in the region between the White Mountains of New Hampshire and Moosehead Lake in Maine. They are uncommon in northern Maine, Vermont, and southern New Hampshire and Maine. Two environmental gradients are found along this latitudinal change in abundance. First, the longer duration and earlier start of winter at higher latitudes is suspected to shorten the season for questing larvae, while at lower latitudes the questing season is longer allowing more time for larval attachment. The second environmental gradient, moose density, is related to the duration and timing of winter, and is likely a product of its influence in conjunction with habitat availability. Lower moose density in southern latitudes reduces the probability of larval attachment to a host, and high density in northern Maine increases the probability for larval attachment. The interacting environmental gradients create a unimodal response curve in which tick abundance is low at southern latitudes (low moose density), high at mid latitudes (moderate density and moderate winter length), and low at northern latitudes (longer winter; Fig. 25).

The regional model indicated a “realized abundance” peak at a WMU density of 0.8 moose/km^2. Tick abundance on harvested moose in the “epizootic region” of northern New Hampshire and central Maine (mid-latitude) was ~1.5X higher than in northern Maine. Similarly abundance on captured moose was 1.4-1.8X greater in the “epizootic region” in 2016. In northern Maine, the average winter tick abundance on bull moose during epizootic years was below the predicted threshold for an epizootic event (< 36.9). Tick abundance in southern Québec in mid-density (0.4-0.8 moose/km^2) moose populations was ~4X greater than comparable densities in mid and northern Québec, and ~2X greater than abundances on high-density (0.8-3.3 moose/km^2) populations in mid and northern Québec. This suggests that tick abundance at higher latitudes is primarily limited by the onset and duration of winter that influence the length of the larval questing season. Although higher moose density can increase tick abundance at higher latitudes, this data suggests it must be substantially higher than at lower latitudes.

In a moose density < 0.8 moose/km^2 the probability of attachment is presumed lower (Fig. 23, 24). Epizootics are considered uncommon in Vermont, as well as to the south and east of the White Mountains in New Hampshire and Maine where regional moose densities are < 0.5 moose/km^2; at such densities, tick abundance is below the epizootic threshold (Tables 17, 18).

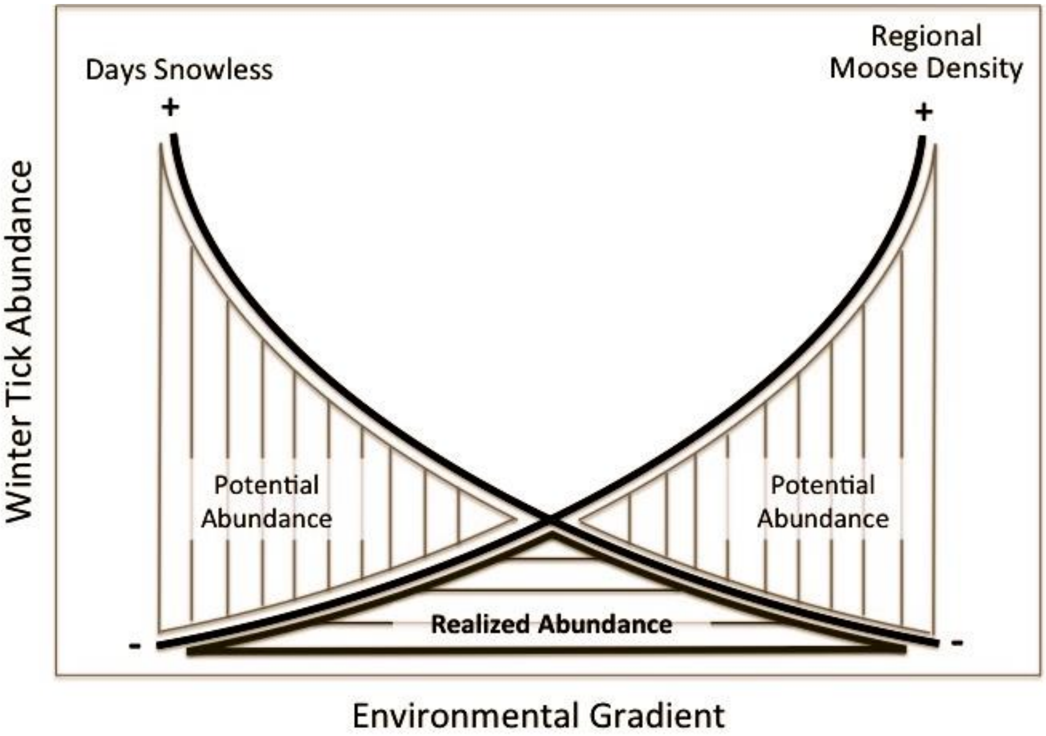


Figure 25: Conceptual model of the spatial variation in winter tick abundance in northern New England

Late winter-early spring conditions

Low daily temperatures in April (< -17 °C) and snow persistence into late April reduces the survival of replete adult female winter ticks as they drop from moose, thereby reducing egg production and presumably the abundance of the following generation (Drew and Samuel 1985, 1986, Wilton and Garner 1993, Samuel 2004, 2007). However, the 2002 epizootic in the North Region of New Hampshire followed a winter with substantial April snow (> 20 cm), and a low mean temperature (~4° C); conversely no epizootics occurred in the winters of 2008 and 2009 that had minimal April snow (< 5 cm) and higher temperature (>6 °C; Bergeron 2011). Bergeron (2011) suggested that spring snow persistence may be more influential at higher latitudes, and weather and ground conditions during the fall questing period were more influential southward.

Northern New Hampshire

The comparison of drop season weather conditions in Berlin, New Hampshire in 5 epizootic and 5 non-epizootic years indicated that min and max temperatures in March were 3 °C warmer preceding non-epizootic years. Conversely, temperatures during the peak of dropping engorged female in April were categorically similar. Snow generally persisted later in epizootic years (17 April) in comparison to the long-term (11 April) and non-epizootic years (14 April). Further, the number of days with snow cover (April-May) in epizootic years was 2X that in non-epizootic years; the threshold temperature for adult female survival (< -17 °C) occurred only once in Berlin, New Hampshire from 1938-2015.

The absence of temperatures < -17 °C and low persistent snow cover during epizootic years suggest that it is unlikely that either cold temperatures in March-April or snow persistence in April-May have substantial negative influence on the survival of adult replete females in northern New Hampshire. It seems more likely that late winter conditions might influence the timing of oviposition. Field experiments in Oklahoma (Patrick and Hair 1975, 1979), where drought condition in late summer substantially influence laval survival, inferred that cooler conditions in spring delay oviposition in both winter ticks and lone star ticks, thereby reducing the duration of larval pre-activity (quiescence) in summer, and consequently, increasing longevity by avoiding potentially desiccating conditions. Shorter winters would produce earlier oviposition and hatch, and increase larval exposure to drought and high ambient temperatures in August and September, potentially increasing mortality from desiccation (Yoder et al. 2015, Addison et al. 2016).

Northern New England

Spring snow persistence produced the highest %D in the predicted models, but overestimated winter tick abundance. Models 2 and 4 predicted extremely high tick abundance throughout Maine in fall 2012 (Fig. 16, 17). Given the spring snow persistence hypothesis, the abnormally short winter of 2012 should increase abundance, but the spring of 2013 is not suspected of being an epizootic year, and fall 2012 abundance was ranked 8 of 10 and was below the threshold for an epizootic event (Table 14). Four epizootic years (2002, 2014-2016) followed 4 moderate-severe winters in northern New Hampshire and central Maine, suggesting that the mechanism(s) controlling epizootic events may differ in Alberta (Bergeron 2011), and these condition may actually delay oviposition, quiescence, and therefore reduced larval desiccation (Patrick and Hair 1975, 1979). Overall, the hypothesis that snow persisting into late April limits tick abundance was not supported, and it is possible that it might delay oviposition and increase larval survival in late summer in the epizootic region.

Early and late summer conditions

Cold temperatures and dry conditions in early summer (June-July) reduce egg survival with lower and upper critical thresholds of 15 and 30 °C for successful egg production (Aalangdong 1994, Samuel 2004). Late summer (August-September), drought (dry) conditions, and high ambient temperatures adversely affect (kill) winter tick larvae (Addison et al. 2016). Ticks can tolerate acute mid-day extremes, but persistent dry conditions are deleterious and can produce mortality (Knülle 1966, Yoder et al. 2015, Addison et al. 2016).

Northern New Hampshire

The hypothesis that early summer weather conditions negatively affect egg production was not evident. In non-epizootic years, the amount of precipitation and the number of days breaking the low (min ≤ 15 °C) and high temperature thresholds (max ≥ 30 °C) were similar. Average minimum temperature in August was ~1 °C higher in non-epizootic than epizootic years and 1.5 °C higher than the long-term. Average minimum temperature in September was ~1 °C higher and ~2 °C higher than in non-epizootic years and the long-term. Further, minimum August and September temperatures increased at a rate of ~0.02 and 0.03 °C per year ($R^2 = 0.16, 0.18$; 1938-2015); trends for maximum temperature were stable. If the minimum temperature continues to increase, the prevalence of desiccating conditions during late summer may also increase, especially in abnormally dry and/or hot years, presumably increasing the probability of larval desiccation.

Wet conditions and high relative humidity are correlated with increased larval longevity (Knülle 1966, Koch 1984), and total precipitation in August and September was higher in non-epizootic years. However, from mid-August through mid-September when quiescent winter ticks are susceptible to desiccation, conditions tended to be hotter with highly concentrated droughts in non-epizootic years. High desiccation rates appear to be associated with a pattern of dry conditions starting in mid-August and leading into ~18 days of drought starting at the end of August, with low rainfall (< 3 cm). August-September rains are heavier in non-epizootic years but concentrated before and after this period of drought.

Northern New England

High winter tick abundance on harvested moose was a reasonable predictor of epizootic events. For example, if late summer conditions are wet and cool, fall abundance is high, and if a normal or long larval questing season follows, an epizootic event is likely. The weather pattern typically associated with epizootics in northern New England is the combination of a cool and wet late summer and a warm snowless fall.

Using minimum August temperature (Model 6) alone was not competitive with the selected candidate model (12), but models 6 and 12 predicted reduced tick abundance in fall 2012 as well as lower abundance in northern Maine. Predictions using minimum August temperatures more accurately represented the spatial and temporal changes in abundance observed on harvested moose. Again, it seems reasonable that tick abundance varies throughout the region based on an interaction between the regional moose density, and the duration and onset of winter. Given that tick abundance on moose harvested in October predicted epizootics reasonably well, it is likely that annual changes in abundance are primarily related to how severe late summer desiccating conditions are and the length of the larval questing season in northern New England. An early winter (late October-early November) should prevent severe infestation on moose.

Minimum rather than mean or maximum temperature was selected for use in the regional model for 4 related reasons: 1) the local analysis of weather conditions in northern New Hampshire indicated a larger separation between epizootic and non-epizootic years using minimum temperatures, 2) maximum ambient temperatures alone are not extreme enough to cause acute desiccating conditions, 3) low nocturnal temperatures in high relative humidity and dew formation allows a tick to recharge its water balance to avoid desiccation, whereas high nocturnal temperatures may be more effective at identifying persistent desiccating conditions, and lastly, 4) the local analysis indicated an increasing trend in minimum and not maximum temperatures from 1938-2015. Interestingly, using minimum temperature in the model would arguably be more effective at identifying abundance in the future given the predicted changes in climate.

Fall conditions

Winter ticks reduce movement at ambient temperatures < 10 °C, stop movement at < 0 °C, and temporary snow cover reduces larval questing and permanent snow terminates it (Drew and Samuel 1984, Aalangdong 1994, Samuel 2004, 2007). Musante et al. (2006) attributed the 2002 epizootic in New Hampshire to a prolonged larval questing period the previous fall (2001), and Bergeron (2011) suggested that fall conditions that dictate the length of the questing season influence tick abundance on moose more than ground conditions in spring.

Northern New Hampshire

Fall conditions in northern New Hampshire associated with epizootics were snowless and warm, often stretching into December; the first snow event seems to be the key indicator. In non-epizootic years the first snowfall generally occurred ~12 November and in epizootic years ~25 November; the long-term date was ~14 November. The first day of permanent snow occurred 12 days earlier in non-epizootic years (21 December). Temperature in October and November was lower in epizootic years and higher in December, suggesting that December is more influential in extending the larval questing period. But, considering that the average maximum ambient temperature in December is just above the threshold where tick activity terminates (0 °C) it seems unlikely that ambient temperature has a strong influence on the rate of attachment.

When considering abundance, it is clear that fall weather and ground conditions can temper or exacerbate the larval attachment rate. An early fall (late October-early November) snowstorm can effectively prevent an epizootic event despite high harvest abundances (e.g., 2009). The inverse might also occur where low-moderate tick abundance could result in a high attachment rate due to an abnormally long questing period. Although this was not observed, it may have happened in 2001 when late summer conditions were extremely dry, but were followed by an extended larval questing season and an epizootic in 2002. The fall of 2014 did not fit either of these patterns as tick abundance on harvested moose was low in Maine and high in New Hampshire, but epizootics occurred in both in 2015. Fall conditions were not abnormal, but abundance on captured moose in January were consistent with the epizootic years prior and after. Local weather conditions in Maine District 8 may have differed from those in Berlin. For example, the last day of snow cover in Berlin, NH in 2015 was April 15 but the winter condition were longer at the Moosehead Lake Weather Station in Maine District 8 was April 25, which could lead to increased mortality.

Northern New England

Larval questing generally begins in September (Drew et al. 1986, Addison et al. 1988 a, 2016), and abundance measured in late September in New Brunswick was 90% lower than on harvested moose in mid-October in Maine and New Hampshire. Abundance on calf and adult cow moose captured in January was 2.3X higher than moose harvested in mid-October. Assuming, conservatively, that larval questing begins in late September, it follows that 43% of the tick load on average is acquired from 20 September through mid October (~1 month).

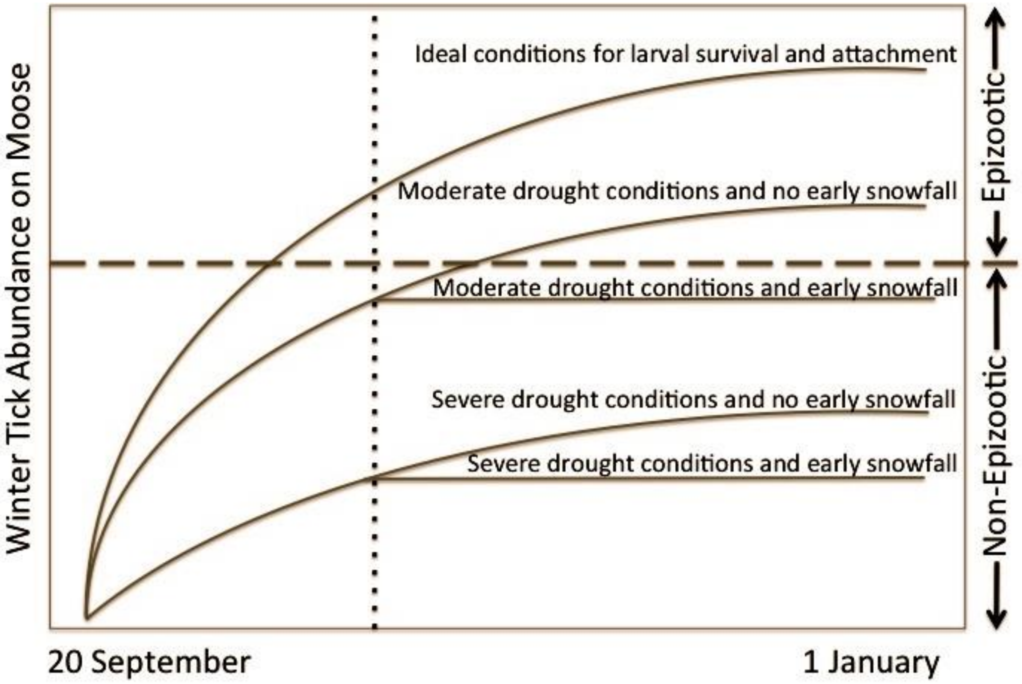


Figure 26: Conceptual model of winter tick abundance on moose through the fall. The dotted vertical line represents a mid-November snow event

Winter ticks are poikilothermic and each fall there is a finite number of larvae questing; therefore, as temperature declines and more ticks attach to a host, the rate of attachment declines as fall progresses (Fig. 26; Drew 1984). Thus, it is likely that the remaining potential (57%) of total abundance in an epizootic year is acquired at a decreasing rate over the remainder of the questing period; in this case, to mid-December. Using the average tick load estimated on dead calves in March-April (~46,800; Jones 2016), and assuming an additional 35% of tick load attaches over the next month, a "normal" mid-November snowstorm truncating the questing season would reduce the total load 22% from 46,800 to 36,500 ticks. Aalangdong (1994) and Bergeron (2011) found that early snow events ended larval questing and presumably stopped larval attachment before it could lead to an epizootic event. In concurrence, my analysis indicated that the first snow event in non-epizootic years was earlier (12 November) than in epizootic years (25 November). Additionally, the linear trend suggests that the mean first snow event (14 November) is gradually shifting to the end of fall at a rate of 0.1 days per year, although the goodness of fit ($R^2 = 0.02$) was poor.

Regardless of the relative impact of conditions in late winter-early spring or fall on winter tick abundance, on a continental scale it is length of winter that probably dictates the latitudinal difference in abundance (Fig. 25). Assuming that climate change creates a persistently shorter winter, abundance should gradually increase over time along the southern range of moose where density exceeds 0.8 moose/km^2 (Fig. 23, 27). Assuming that the frequency of epizootics also increases, a declining moose population seems inevitable.

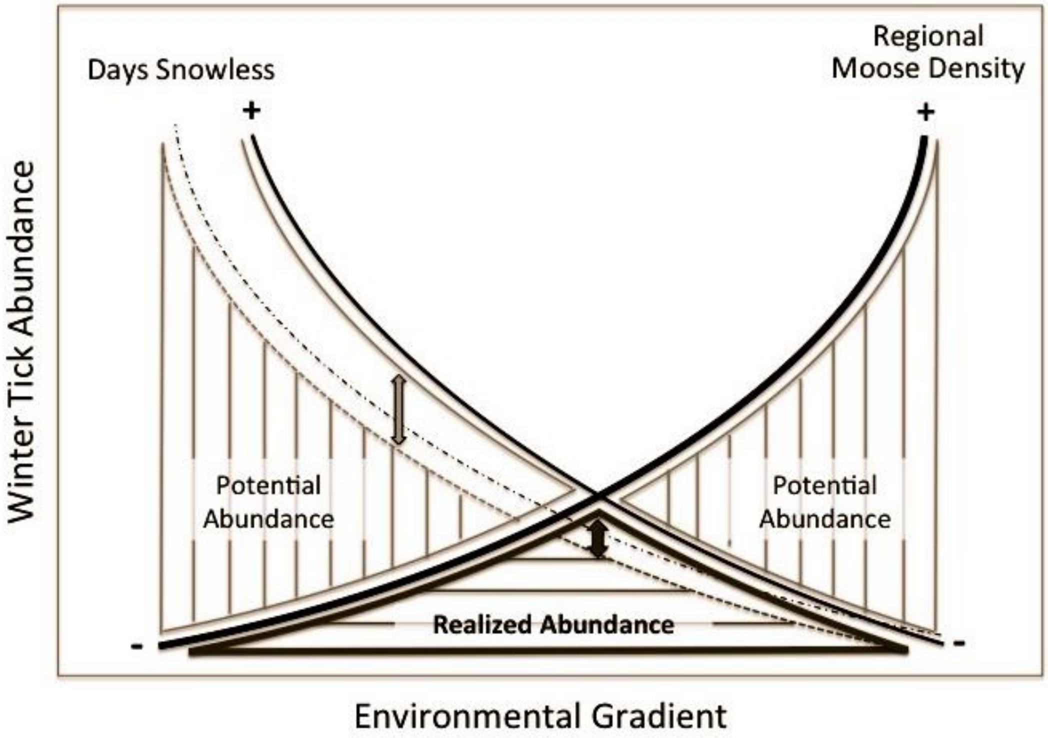


Figure 27: Conceptual model of how global climate change and shorter winters influence winter tick abundance in northern New England.

Density and optimal habitat

Winter tick abundance and distribution is correlated with moose density; with increased moose density there is a greater probability of successful larval attachment (Blyth 1995, Pybus 1999, Samuel 2004, 2007). Moose density generally corresponds to the proportion of disturbed forest (Peek et al. 1976, Schwartz and Franzmann 1989) and Daniel et al. (1977) suggested that ticks are distributed in relation to host (moose) activity. Large area cuts with preferred forage increase local moose density, concentrate where replete females drop, and facilitate the attachment of larvae given that moose use the same habitat in fall and spring (Scarpitti 2006).

Density

Density of a species that exhibits avoidance behavior, such as moose, is inherently difficult to sample, estimate, and model. Understanding the accuracy of the New Hampshire population index is fundamental to this study given our assumption that density estimates are accurate within the range of error (± 27.5%). Density estimates used in this study are primarily derived from deer hunter surveys, and to use these estimates it was assumed: 1) reinstituting the moose hunt did not affect avoidance behavior by moose, and 2), that deer hunter behavior has not changed despite a possible increase in the use of bait and less hunter movement. Anecdotally, it is likely that both of these assumptions have been violated and that the actual density is higher than predicted, but there is no quantitative evidence to assess these presumed behavioral changes.

Epizootic events occurring in the North Region of New Hampshire and Maine District 8 are outliers given their moose densities (~0.5-1.7 moose/km^2; NHFG unpublished data; Kantar and Cumberland 2013). Moose density was much higher in epizootics in Ontario, Canada on Isle Royale (3.1 moose/km^2; DelGiudice et al. 1997) and in Elk Island National Park, Alberta (2.9 moose/km^2; Samuel 2004). Yet, there was no mention of winter ticks associated with the low productivity of moose in Michigan at a lower density (0.29 moose/km^2; Dodge et al. 2004). Anecdotally, this suggests that moose density might be underestimated in the study area because epizootics are occurring, and density is presumably higher than estimated. Conversely, it is possible different mechanisms influence epizootic events in northern New Hampshire and central Maine and they allow for epizootics to occur at a lower regional density.

Since the peak population in 1998, moose density in the North and CT Lakes Regions of New Hampshire has declined by 33% and 60% while optimal habitat increased by 10% and 30%, respectively. Critically, these two relatively small regions support ~1/2 of the state's moose population (NHFG unpublished data). With a high rate of vehicular collisions, management objectives were set from 2006-2015 to reduce moose density (~1.5 moose/km^2) by 30% in the CT Lakes Region; however a 55% reduction was realized. Concurrently, in adjacent Region E in Vermont, a similar density reduction was implemented to reduce the impact of moose browsing on forest regeneration (VTFW 2009). In 2010, an aerial density estimate in Vermont Zone E1 was only 5% lower than the population index, indicating that the index was still reasonably accurate, although the study did not validate sightability with marked moose (Millette 2010). Management objectives in the North Region of New Hampshire were to increase moose density from 1998-2006, and maintain a stable population from 2006-2015 (NHFG 1998, 2005). A ~10% decline occurred from 1998-2006 with the population dropping a further ~25% afterwards.

If moose behavior and deer hunter behavior have changed and assumptions of the population index have been violated, the question becomes: is there a point in time where estimates were valid so that we can assume a reliable benchmark? The density estimates from aerial infrared surveys conducted in New Hampshire (WMUs A1, A2, B, C1, C2, D1; Bontaites et al. 2000) during that time period (1998-2000) would arguably be the most reliable. These surveys yielded an average moose density per flight of ~1.0 moose/km^2, with 67% of the flights producing a density < 1.0 moose/km^2; Samuel (2004, 2007) observed light tick effects in Alberta at this density. Only 10% of the flights had a density > 2.9 moose km^2, a density associated with epizootic events (Samuel 2004, 2007).

Critically, aerial density estimates represent a “snapshot in time” and can be influenced by weather, visibility, and observer experience, and consequently, their interpretation can be difficult; however, the data suggests that overall density (90% of observations) was below the threshold associated with an epizootic event in Alberta. The population index, productivity, and population models all indicate that moose density has declined since the aerial surveys, further indicating that regional density estimates are below the density thresholds associated with epizootic events (Musante et al. 2010, Bergeron et al. 2013, Jones 2016, NHFG unpublished data). However, it is important to recognize that on a local scale density can often exceed this threshold, and it is the local seasonal density when the adult female ticks drop and the larvae quest that ultimately dictate abundance on moose.

In defense of the population index, following 1998’s peak population, increased winter tick abundance and more frequent epizootic events triggered a decline in cow health and productivity, and increased tick-related mortality. High tick abundance has persistently caused high calf mortality, productivity by yearling cows is non-existent, and adult cow productivity has declined measurably since the mid-2000s; modeling with such data predicts a declining population (Musante et al. 2010, Bergeron et al. 2013, Jones 2016). It is possible that a density-related tipping point occurred in the 1990s exponentially increasing tick abundance to a level unrealized in this region, and the current frequency and intensity of epizootics are the residual affects of this tipping point.

In northern New Hampshire, average abundance on tick-related moose mortalities is 44% higher than in Ontario (Samuel 2004, Jones 2016), suggesting that epizootic events are more severe in northern New Hampshire. From the perspective of the density dependent hypothesis, moose density estimates would have to be substantially higher in northern New Hampshire than in Ontario (2.9 moose/km^2; Samuel 2004) to achieve 44% greater tick load. However, no estimate based on aerial surveys in the epizootic region approach this density; therefore, other variables must strongly influence the system. With decreasing tick abundance north of the epizootic region, there is likely an interaction between moose density and the onset and duration of winter. For example, consistently longer winters in northern Maine, which is at a similar latitude to Elk Island National Park, Alberta, allow for moose density to achieve ~2.5 moose/km^2 without evidence of an epizootic. An epizootic threshold of 2.9 moose/km^2 (Samuel 2004) may be more applicable for northern Maine than in northern New Hampshire and central Maine. Mild winters in northern New Hampshire support a longer questing season and would increase attachment rates, the moose density is still an extreme outlier for where epizootic events typically occur.

Optimal habitat

Why do epizootic events occur at lower regional densities in northern New England? Is there a different mechanism that controls tick abundance in this area? This study indicates that tick abundance in northern Maine and Québec is limited by the onset and length of winter, in central Maine and northern New Hampshire by late summer drought conditions and the onset of winter, and in Vermont (excluding WMZ E1) and to the south and east of the White Mountains by moose density. These mechanisms categorically differ from those associated with the spring snow persistence theory supported in Ontario (Samuel 2004, 2007), and indicate that different interactions and relationships exist in the study area. One common quality that Maine and northern New Hampshire share, but differs in Vermont, Elk Island National Park, and Isle Royale is large area forest disturbance created by timber harvesting.

In a mature forest the quantity and quality of browse per unit area is lower than in the 2-20 years following an intensive logging operation (Peek et al. 1976). Prior to the logging operation there may be minor changes in density across an unbroken forest, but with increased availability of food resources, moose are drawn to these areas to browse creating a clustered, rather than diffuse population, and a high localized density. Schwartz and Franzmann (1989) provided a conceptual relationship between one forest disturbance (fire) and the density of moose suggesting that densities in forest age classes 0-5 and >40 years are low with peak densities occurring approximately 15 years after the disturbance event. Peek et al. (1976) found moose densities to be ~2.5 times greater in recently logged areas relative to surrounding older forests.

Moose populations in northern New England rebounded following salvage operations in the 1970s-1980s that increased carrying capacity; it may be that moose are, in part, victims of their own success. If browsing in a recently cut area is an incentive, then behavior will dictate that the moose will exploit this resource and consequently cluster in a density greater than indicated by the regional density. Moose are known to feed in recently cut habitats during the drop (April) and fall questing seasons (Scarpitti 2006) creating a localized area where replete females drop and their larvae eventually attach to a host. Abundance in forest openings are highly influenced by weather conditions in late summer; in a cool and wet late summer, larval production per gram of engorged female in forest openings was 2X higher than in a mature forest, but there was no difference in larval survival in the mature forest habitat in hot and dry versus cold and wet summers (Addison et al. 2016). This suggests that production of tick larvae in mature forests is constant, or at least more constant annually, whereas abundance in more open habitat (e.g., clearcut) is susceptible to variation in microclimate where the maximum surface (< 0.5 m) soil temperature can be 3.2° C higher (Hashimoto and Suzuki 2004). It follows that in the "epizootic region", variation in annual tick abundance would be influenced by late summer weather conditions in recently logged areas.

The estimated moose density in the North Region was 0.58 moose/km^2 in 2010-2015, but the estimated moose density in WMU C2 (the study area) was 33% higher and in D1 38% lower than the regional density, indicating the uneven population distribution. At a finer scale, a pattern emerges in that towns with a higher proportion of optimal habitat have higher moose density (Fig. 15). For example, in 2015 optimal habitat in Success and Cambridge was ~2X higher than the regional estimate (~15%) and the estimated moose density was 3X higher than the regional estimate. Similarly, optimal habitat in Dalton and Stratford was 50% lower and the estimated moose density was 50% less than the regional estimate in Dalton, and similar in Stratford.

This suggests that moose density in a given area is proportional to habitat type and composition, indicating that density in optimal habitat is predicted to be ~4 moose/km^2 and in mature forest ~0.25 moose/km^2 (Fig. 15). In northern New Hampshire, tick abundance should be limited by the regional moose density, but the density in optimal habitat may not be indicative of the regional density, it is possible that this local density window is the scale at which the moose-tick relationship functions. A higher regional density may simply suggest an increased likelihood of high local tick concentrations, if optimal habitat is available (Fig. 28).

Anecdotally, in comparison to a mature forest, the probability of larval attachment may be higher in clearcuts where movements force moose against saplings at the ideal height for attachment. Both larval production and the probability of attachment would increase as moose preferentially use optimal foraging habitat during the questing and drop seasons, effectively creating a high localized moose density; such behavior would facilitate and perpetuate high winter tick abundance in local density windows in northern New England (Fig. 28).

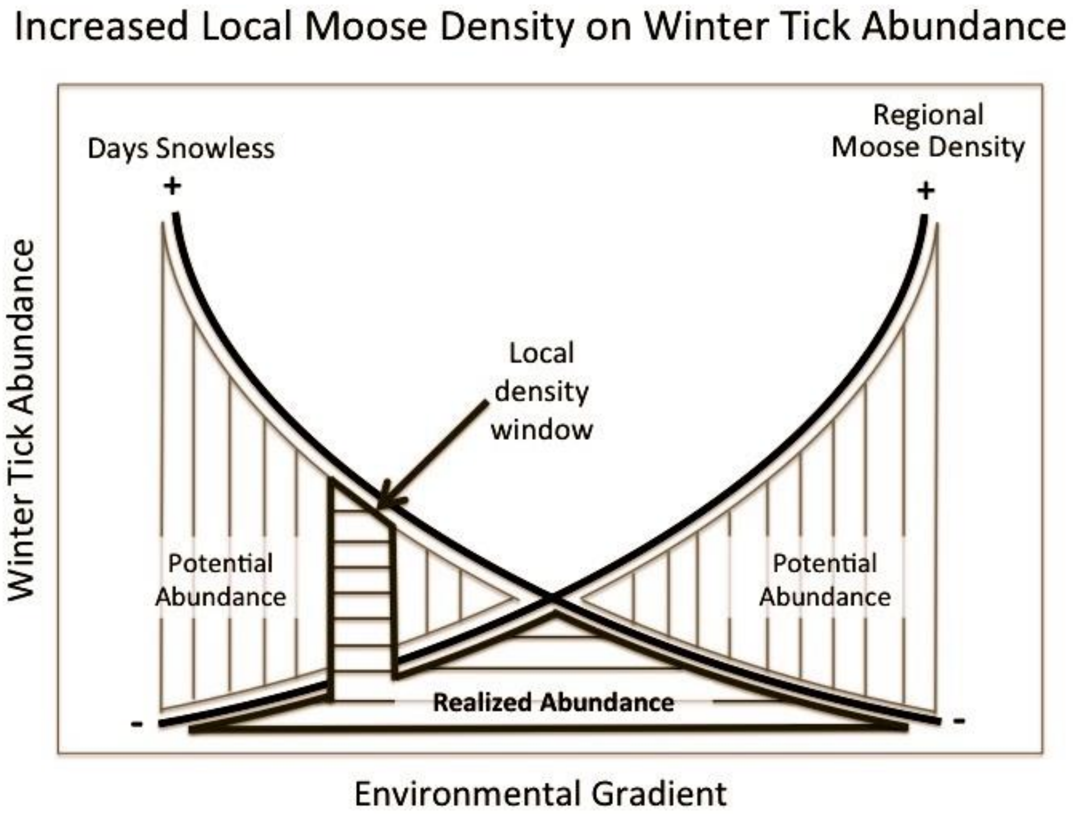


Figure 28: Conceptual model of how a high local moose density increases winter tick abundance and serve as platforms for the exchange of this ectoparasite in northern New England.

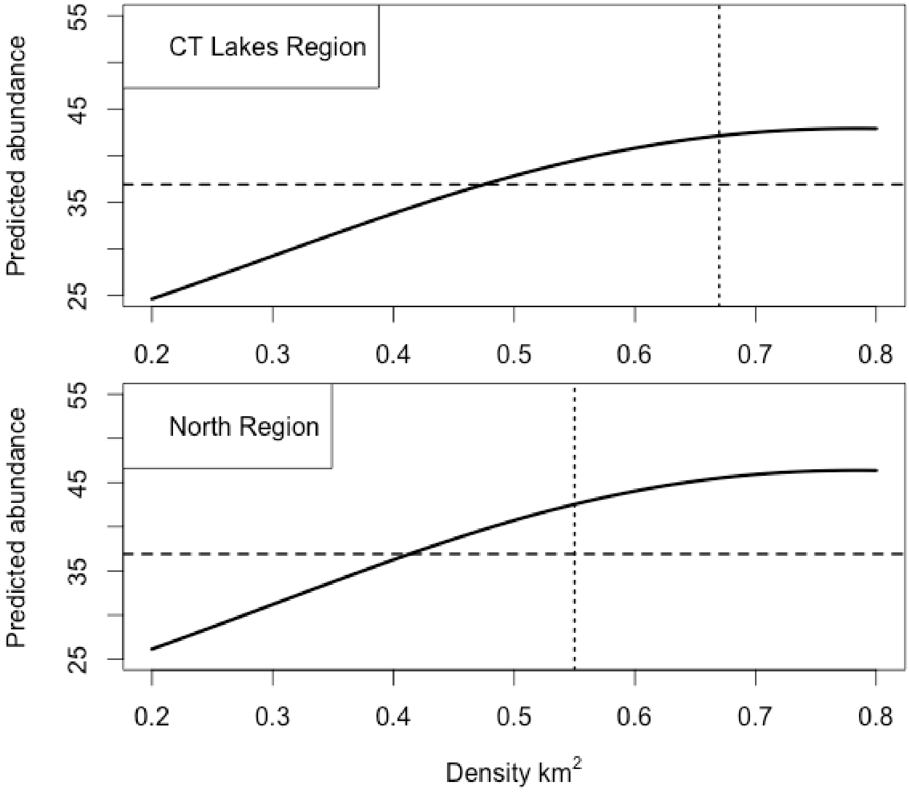


Figure 29: Predicted abundance versus moose density in 2015 in the CT Lakes and North Regions in New Hampshire. Respective horizontal and vertical lines indicate epizootic probability threshold and current moose density.

Prior to the 1990s, it is unlikely that epizootics occurred in northern New England given the lower moose density; anecdotally, 1992 is the first year of suspected tick-related die-offs in Maine and Vermont (MDIFW 1998, Samuel 2004). As the moose population peaked in 1998 concurrent with a decline in productivity and increased calf mortality in New Hampshire, it seems likely that this year serves as a temporal divide between a period of infrequent “tick-related moose die-offs” and the current period of “frequent and severe epizootics”. Samuel (2004) documented known tick-related die-offs and found the majority lasted 1-2 consecutive years; the extreme was 6 consecutive years on 2 separate occasions in Ontario. Clearly, understanding the normal frequency of epizootic events is paramount to interpreting moose population dynamics in northern New England.

Predicted abundance was severe in northern New Hampshire even in non-epizootic years, indicating that early snowfalls are critically important to prevent epizootics. Alternatively, the model also indicates that low abundances are directly related to moose density as in Vermont and the White Mountains (Fig. 29). Although counter intuitive, increased harvest to reduce moose density may be a strategy to reduce tick abundance on both the individual moose and the landscape. Do you gamble on weather and earlier winters, or be proactive and increase harvest rates to reduce moose density and return tick abundance to lower levels? Presumably, with lower tick abundance, individual health and productivity would increase and a healthier moose population could result; maintaining moose density below a threshold that produce epizootic conditions would be ideal.

For example, Fig. 29 illustrates the relationship between moose density, tick abundance, and the probability of an epizootic. To reduce the likelihood of an epizootic event in northern New Hampshire higher harvest could maintain reduced moose density such that weather conditions that support an epizootic event are less influential. By creating a moose density-limited environment parasite abundance could be reset to that in the 1990s, and a constant harvest, albeit one that controls the density should result. Overall, a more productive, healthier, and constant moose population would be maintained.

Model effectiveness

Overall, statistical attributes of the regional models did not effectively or strongly (%D 18.7-21.0) support one model over another, and the attributes show that the models did not fit the data well despite using a flexible model type (GAM). The data are extremely variable and the poor fit presumably reflect such. Model 12, although deemed “the best”, is not considered highly effective statistically, but provided a quantifiable comparison of the competing hypotheses and interpretation as to how the variables affect tick abundance spatially and temporally. Therefore, it is considered “supportive” rather than “conclusive”.

Summary

This study found that the spatial distribution of winter tick abundance on a continental scale is primarily controlled by an interaction of the onset and duration of winter, and moose density. Larval questing and attachment in northern latitudes, such as northern Maine and Québec, are limited by consistently earlier snow events, whereas in the most southern range, moose density limits tick abundance. Late summer conditions strongly influence annual changes in winter tick abundance; cool and wet conditions lead to larval survival, and hot and dry conditions to larval desiccation. The onset of winter (first snow) also affects annual tick abundance on moose. It is probable that the “epizootic region” currently has enough annual egg production to support an epizootic every year. Snow events play an important role in moderating or exacerbating late season larval attachment. If late summer conditions are cool and wet leading to high winter tick abundance, an early first snowfall can negate the occurrence of an epizootic; if late summer conditions are hot and dry leading to low-moderate winter tick abundance, a late first snowfall can extend the larval questing season and lead to an epizootic. The occurrence of either event or their interaction are key influences.

Considering the future, as the climate warms and winters become mild, local density windows will likely support high abundance in regions that do not historically have epizootic events, and presumably, the “epizootic region” will expand northward into higher density regions while limiting density in the southern part of the moose range. Increasing long-term temperatures in both late summer and late fall will lead to a more extreme and oscillatory annual tick abundance; certain years will have extremely low abundance from increased minimum late summer temperatures and increased desiccation, whereas other years will have extremely high abundance with longer falls extending the larval questing season. This study indicates that in northern New England the moose-tick interaction is perpetuated by high localized moose density, and therefore, management efforts should focus on WMUs and towns in which optimal habitat is increasing and > 10%.

Future Research

Many questions are unanswered or remain unclear after this analysis including: 1) how accurate is the current population density index, 2) What is the actual moose density in the North Region, 3) what is the effective local moose density that likely dictates tick availability and abundance, 4) does moose density/use of habitats relate directly to local larval availability, 5) What are the predominant influences and parameters to best predict annual tick abundance

Tick abundance on moose harvest in mid-October reasonably predicted whether not an epizootic occured in 8 of 10 years, suggesting that late summer desiccation is a primary influence. For example, an extended drought in August and September 2016 was followed by reduced (~50% less than 2015) abundance measured on harvested moose in October 2016 in Maine and 50% less on captured moose in New Hampshire, consequently, it seems unlikely that an epizootic in spring 2017 will follow. Epizootic year 2002 was the driest quiescent season of any epizootic or non-epizootic tested but there was a warm extended questing period, indicating that fall conditions play an important role in annual variation. This study suggests that conditions in the quiescent and questing seasons interact but their relative importance may vary annually. Continued measurement of tick abundance on harvested moose is warranted to better interpret and document these relationships.

The model used in this study utilized monthly data, local weather; specifically the timing and extent of drought conditions that desiccate larvae are not necessarily described by monthly averages. Abundance can be affected by 2-3 weeks of specific weather conditions within or across 2 months. PRISM offers daily weather data and may prove more effective in identifying critically important short-term weather events. Further, PRISM supports vapor pressure deficit data which could be more specific to, and better predict tick desiccation.

CONCLUSIONS

I. Winter tick abundance and spatial distribution on the continental scale is primarily controlled by an interaction of the onset and length of winter, and moose density.

II. In the "epizootic region", where the interaction between the onset of winter and moose density are greatest, drought conditions in the quiescent season and the onset of winter in the questing season principally influence annual winter tick abundance.

III. In the "epizootic region", average (log transformed) winter tick abundance on moose harvested in mid-October indicated a threshold of 36.9 ticks (exponentiated), above which an epizootic is like to occur unless an early snowfall event shortened the fall questing season.

IV. In northern New Hampshire, winter tick abundance is strongly limited by moose population density; regional density > 0.8 moose/km^2 tends to occur farther north where onset of winter is more influential in limiting tick abundance.

V. With a warming climate and as the length of winter shortens, tick abundance on moose will gradually increase in regions with a density > 0.8 moose/km^2 without epizootic events, specifically in regions to the north of the current "epizootic region".

VI. With increasing long-term temperatures in both late summer and extended falls, it seems plausible that winter tick abundance will become more extreme and oscillatory, and if desired, require specific harvest strategies to counteract its negative affect on moose populations.

VII. Habitat that concentrates moose in the drop (spring) and questing (fall) seasons can result in effective "local" moose densities that are much higher than a regional average, and likely lead to higher winter tick abundance, increased epizootic frequency and intensity, and negative impacts on moose.

VIII. In northern New Hampshire, snow persisting into late April was not associated with lower winter tick abundance and non-epizootic events in successive fall and spring seasons, respectively.

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APPENDIX A: INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE APPROVAL