Received: 31 October 2023 | Revised: 30 May 2024 | Accepted: 2 June 2024

DOI: 10.1002/jwmg.22630

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

SPECIAL SECTION

Monitoring questing winter tick abundance on traditional moose hunting lands

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Funding information

U.S. Geological Survey, Grant/Award Number: RWO-MA-74

Abstract

An important symbolic and subsistence animal for many Native American Tribes, the moose (*Alces alces*; mos in Algonquin, Penobscot language) has been under consistent threat in the northeastern United States because of winter tick (*Dermacentor albipictus*) parasitism over the past several decades, causing declines in moose populations throughout the region. This decline has raised concern for Tribes and agencies that are invested in moose. Given this concern, it is increasingly important to effectively monitor and develop strategies to manage winter ticks to address consistent population declines of moose due to winter ticks. The Penobscot Nation developed a novel strategy to sample questing winter ticks (i.e., ticks that are actively seeking hosts) using a plot-based sampling protocol that may be suitable for heterogeneous habitats. We deployed this protocol in the northeastern United States in 2022 during the tick questing period (Sep–Dec) on Penobscot Nation sovereign trust lands, the White Mountain National Forest and Umbagog National Wildlife Refuge, and western-central Massachusetts, USA. We analyzed the data using occupancy and N-mixture models. Detection probability peaked during mid-October and tick occupancy and abundance were greatest at sites with intermediate understory vegetation height. The sampling protocol was successful at sampling ticks in Massachusetts, where abundances were expected to be low, indicating that it may be useful for studies planning to monitor winter tick distribution and abundance in areas with sub-optimal moose habitat and where winter tick abundance is expected to be low. This approach may also benefit managers or researchers intending to monitor many species of hard ticks, and where imperfect detection is expected.

KEYWORDS

Alces alces, *Dermacentor albipictus*, dragging, flagging, imperfect detection, Indigenous resource management, moose, New England

Moose (*Alces alces*) retain their Algonquian name (mos in Penobscot language) and are an important spiritual symbol and subsistence resource for Penobscot people and Indigenous Peoples throughout North America (Popp et al. 2020). The largest contiguous population of moose in the lower 48 states is in the northeastern United States (Pekins 2020), where multiple Tribes are present, including the Penobscot Nation. The Penobscot Nation has jurisdiction over 50,586 ha of sovereign trust land and reservation land, reclaimed under the Maine Indian Land Claims Settlement Act of 1980 (Public Law 96-420). The Penobscot Nation Department of Natural Resources manages these lands under the concepts of multiple use and sustained yield; however, the top priority is preserving the lands for tribal members' cultural and traditional activities. Therefore, because moose are the most important big game animal that provides sustenance, cultural, and spiritual value to the Penobscot Nation, it is up to the Tribe to protect them within their trust and reservation lands.

It is of great concern to the Penobscot Nation that moose in the northeastern United States are experiencing population declines caused by winter tick (*Dermacentor albipictus*) infestations (Drew and Samuel 1985, Addison and Mclaughlin 1988, Bergeron and Pekins 2014). The winter tick is the greatest threat to moose persistence in this region, and infestations are so severe that moose can become infested with up to 90,000 individual ticks (Jones et al. 2019). Increases in winter tick populations over the past 2 decades have caused multiple epizootics during which ticks cause high calf mortality (>50%), reduce adult calving (<60%), and lower twinning rates (<5%; Musante et al. 2007, Ellingwood et al. 2020). Although winter ticks can infest a variety of mammals, winter ticks affect moose most severely because of similarities in the life history of moose and winter ticks (i.e., ticks quest during the moose rut), an evolutionary lack of programmed grooming in moose (as there is in other deer), and habitat preferences (moose prefer successional forests, which provide adequate vegetation for winter tick questing; Mooring and Samuel 1998, Blouin et al. 2021). Negative effects of ticks include hair loss and damage, excessive grooming, weight loss, and reduced fat (Musante et al. 2007). All age classes of moose have documented mortality resulting from winter ticks, although mortality is higher for calves (Musante et al. 2007). Winter ticks engorge on moose over the winter months (Figure S1, available in Supporting Information), during which moose are already experiencing stress due to limited and nutrient-deficient forage (Musante et al. 2007). Specifically, it is the exacerbation of chronic blood loss from tick infestation in addition to poor winter diets that leads to anemia in calves, which is the leading cause (>90%) of calf mortality (Musante et al. 2007, Ellingwood et al. 2019, Pekins 2020, Blouin et al. 2021).

Larval winter ticks seek and attach to a host (quest) in fall, typically September until the first permanent snowfall (Addison et al. 2016, Powers and Pekins 2020, Blouin et al. 2021). Winter tick questing is influenced by variation in multiple environmental and habitat factors that can affect tick survival, availability, and ability to quest and attach to a host (Addison et al. 2016, Yoder et al. 2016). Tick questing is closely tied to weather (e.g., daily temperature and humidity) and photoperiod (Drew and Samuel 1985). In addition, ticks rely on appropriate habitat to survive and attach to a host. For example, ticks found on vegetation of 1–1.5 m have a better chance of attaching to a host because this is about chest height on adult moose (Drew and Samuel 1985, McPherson et al. 2000). Environmental factors may affect tick survival, questing, and the probability that an observer will encounter winter ticks during sampling bouts because ticks may not be actively questing under certain conditions. Considering the season, environmental, and site factors when sampling ticks may improve assessments of environmental drivers, abundance, and questing behavior.

Overall, winter tick survival and questing are subject to environmental factors and habitat; therefore, sampling tick abundance within the landscape is important to understanding how environmental and habitat factors lead to large infestations on moose. Winter tick abundance is known to vary by land cover type (Aalangdong 1994), and ticks occur in high abundances in clear cuts (Bergeron and Pekins 2014, Terry 2015, Powers and Pekins 2020); however, tick sampling has been targeted in areas of high moose abundance (Powers and Pekins 2020), thereby making inferences about forest management and interacting density dependence incomplete. The Penobscot Nation is therefore interested in studying factors affecting tick abundance in a variety of habitat and management scenarios to deploy mitigation efforts. After careful consideration, the Penobscot Nation deemed existing tick sampling within landscapes inadequate. Therefore, the first step toward achieving research and management goals was to implement a modified monitoring protocol designed specifically for winter ticks.

Flagging or dragging, whereby a flannel cloth is passed over questing ticks so that they attach to it as they would a passing host, is the primary method for sampling ticks from the environment (Dobson 2013). Designed for human disease surveillance, the standard method for the flagging or dragging method suggests sampling along a straight line transect for a distance ≥100 m, keeping the sampling flag flat along the ground (dragging), or waving it overtop vegetation (flagging; Carroll and Schmidtmann 1992, Centers for Disease Control [CDC] 2018, Solomon et al. 2020). Members of the Penobscot Nation were not satisfied with the standard method because it does not reflect the mechanism by which moose acquire ticks in the environment by pushing their way through the understory vegetation. Standard linear transects sampled area inefficiently (1-m flag width × x-m transect length [where x = length]). Length can vary (CDC suggests 750 m), and it was difficult to fit linear transects into small non-linear habitat and some types of forest management patches. Further, typical analytical methods for flagging data ignore imperfect detection of ticks and may underestimate abundance of ticks (Sirén et al. 2024). In response to these limitations and the threat to the moose population, individuals in the Penobscot Nation developed a method for sampling winter ticks that was built from disease surveillance dragging and flagging methods but designed specifically for sampling moose habitat. The method draws from the Tribal members' deep understanding and respect for moose and mimics the way moose move through their habitat; it efficiently samples habitat in a way that generates data about how tick abundance varies in space and time. The University of Massachusetts assisted with the revisit design and analytical methods.

We had 3 objectives. First, we deployed the Penobscot Nation winter tick sampling method in 3 study areas to demonstrate the generality of the sampling method. Second, we estimated winter tick occupancy and abundance at 3 study sites. Finally, we evaluated factors that may influence detection probability, occupancy, and abundance of questing winter ticks (Table 1). We expected to find site-level differences and predicted that the highest winter tick abundance and occupancy probabilities would be found in White Mountain National Forest and Umbagog National Wildlife Refuge, and the sovereign trust lands of the Penobscot Nation. We predicted peak winter tick detection to occur in the middle of the sampling period, and that temperature during sampling would be positively correlated with probability of detecting winter tick. We also predicted that the greatest tick abundance and probability of occupancy would be found on vegetation between 0.5–2 m.

STUDY AREA

Penobscot Nation sovereign trust lands, Maine (STL)

Our study area included approximately 29,000 ha in 5 tracts on the sovereign trust lands (STL) of the Penobscot Nation, which are spread across northern Maine, USA, where elevations range from 241–1,207 m. The study area was made up of many small mountains and rolling hills, lowland valleys, and abundant lakes, ponds, and rivers (Jones et al. 2019). Annually, mean temperatures ranged from −10–18°C and annual precipitations ranged from 70–136 cm from

TABLE 1 All covariates measured at sites where we sampled winter ticks in 3 study areas in the northeastern United States: sovereign trust lands, Maine (STL), western and central Massachusetts (WCM), and White Mountain National Forest and Umbagog National Wildlife Refuge, New Hampshire (WMU). We sampled ticks using a modified flagging technique developed by the Penobscot Nation in 4-m-radius circular plots from 6 September to 9 December 2022. We provide the variables used in either the detection or process (occupancy or abundance) sub models, a short description, and the predicted relationship.

Variable name	Sub model	Description	Predictions
Day	Detection	Survey day (Julian) from 16 Sep–09 Dec 2022	Detection of winter ticks will peak in the middle of the sampling period (quadratic)
Temperature	Detection	Air temperature (°C) at time and location of survey	Winter tick detection will be positively correlated with warmer temperatures
Relative humidity	Detection	Percent relative humidity of the air at time and location of survey	Winter ticks will be curvilinearly correlated with humidity
Wind speed	Detection	Speed of wind (mph) at time and location of survey	Winter ticks will be negatively correlated with high wind speeds
Dew point	Detection	Dew point (°C) at time and location of survey	Winter tick detection will be negatively correlated with a higher dew point
Observer	Detection	Observer who completed survey	Observer will at times be correlated with detection
Time	Detection	Time spent flagging a plot	Winter ticks will be positively correlated with longer flagging times
Vegetation height	Process	Average maximum vegetation height at a site	Winter ticks will be most abundant on understory vegetation between 0.5–2.5 m (quadratic)
Location	Process	Study site (STL, WMU, WCM)	Winter ticks abundance and occupancy probability will be higher in WMU and STL

2000–2022 (National Oceanic and Atmospheric Administration [NOAA] 2022). This area experienced the fall (Sep–Nov), winter (Dec–Feb), spring (Mar–May), and summer (Jun–Aug) seasons in which summers were mild and winters were cold and snowy (Runkle et al. 2022*a*). Fall (winter tick questing period) was generally cool, with a mean temperature during sampling of 10°C. The STL sites were in the deciduous–boreal ecotone, which consisted of conifers and mixed wood (Goldblum and Rigg 2010). Specifically red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*), and balsam fir (*Abies balsamea*) were present (Healy et al. 2018). Large-scale clear cutting was replaced with larger areas of partial harvest after the Maine Forest Practices Act (Maine Forest Practices Act, Public Law 1989, Chapter 555, §10) passed (Wiersma 2009). Consistent industrial timber harvest of large scale and partial cutting had contributed to younger forests in this region. Dominant fauna included animals typical of the boreal forest, including moose, American black bear (*Ursus americanus*), coyote (*Canis latrans*), and Canada lynx (*Lynx canadensis*). Maine had abundant contiguous optimal moose habitat (Figure 1), where moose densities were high and winter tick epizootics affect moose health in the region (Healy et al. 2018). In STL, 3 of our sites were revisited 4 times, 18 sites were revisited 5 times, and 19 sites were revisited 6 times every 1 or 2 weeks (20 Oct–9 Dec 2022).

White Mountain National Forest and Umbagog National Wildlife Refuge, New Hampshire (WMU)

The study area in New Hampshire, USA, included a 125,000-ha portion of White Mountain National Forest and the Umbagog National Wildlife Refuge (WMU). It fell in the deciduous–boreal ecotone (Goldblum and Rigg 2010). The

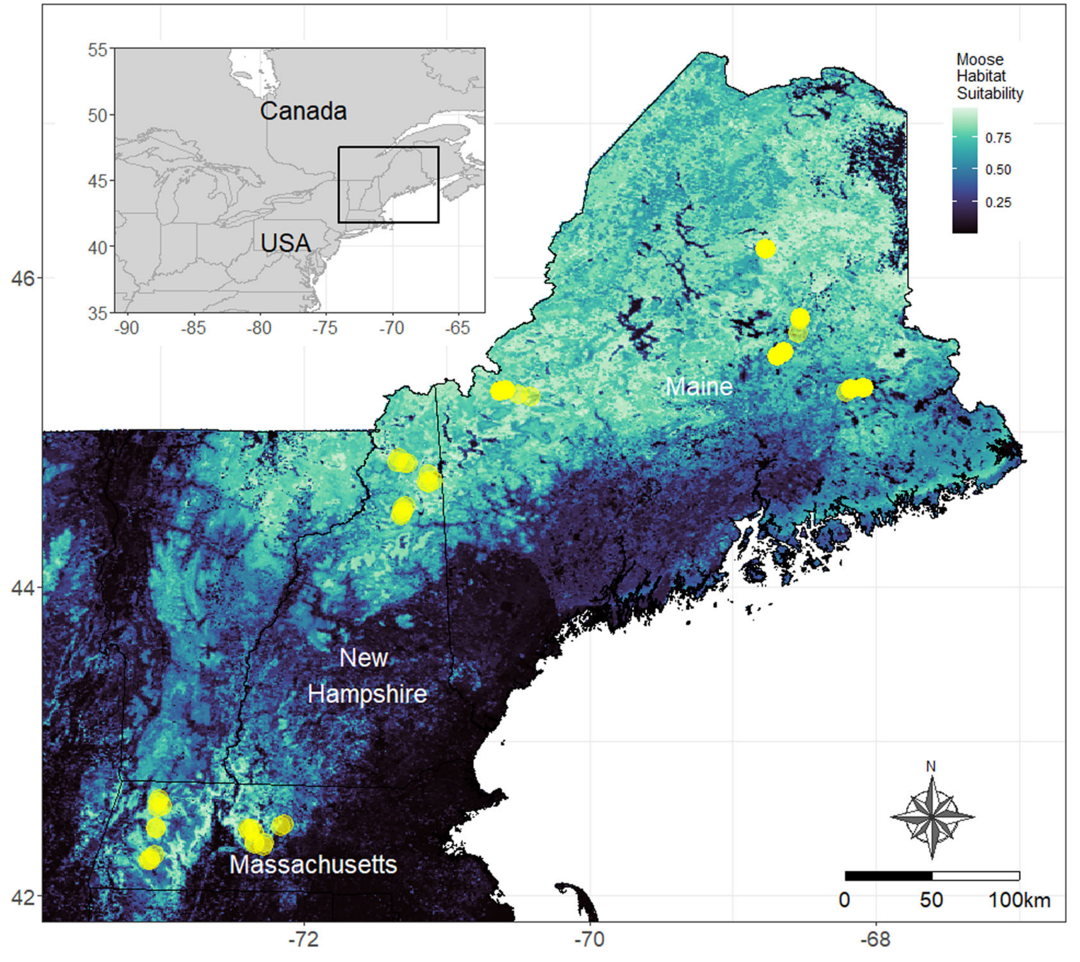

FIGURE 1 Sample sites (yellow circles) for winter ticks at 3 study areas in the northeastern United States: sovereign trust lands, Maine (STL), western and central Massachusetts (WCM), and White Mountain National Forest and Umbagog National Wildlife Refuge, New Hampshire (WMU). Sampling occurred from 6 September 2022–9 December 2022. The background map represents a modeled gradient of moose habitat suitability from black indicating low suitability to light green indicating high suitability (modified from Teitelbaum et al. 2021, © 2021 This work is openly licensed via CC BY 4.0).

forest was dominated by hardwood species like American beech, sugar maple, and yellow birch. Timber harvest was less common in the White Mountain National Forest than in the Umbagog National Wildlife Refuge, and both areas were heavily recreated. Elevation in this study rose from 350 m to 850 m. Mean annual temperature ranged from −8–19°C with precipitation between 5–53 cm (NOAA 2022). The study area experienced the fall (Sep–Nov), winter (Dec–Feb), spring (Mar–May), and summer (Jun–Aug) seasons in which summers were mild and winters were cold and snowy (Runkle et al. 2022*b*). Fall (winter tick questing period) was cool with a mean temperature of 8°C during sampling. The study area was north of the highest mountains in the region (1,917 m on Mount Washington), consisting of rolling, formerly glaciated hills containing ample wetlands, ponds, lakes, and logging roads (Bergeron and Pekins 2014). Dominant fauna included animals typical of the northern hardwood forest, such as moose, white-tailed deer (*Odocoileus virginianus*), American black bear, coyote, Canada lynx, and bobcat (*Lynx rufus*). The site had ample optimal moose habitat near the center of moose distribution in the northeastern United States (Teitelbaum et al. 2021; Figure 1) with intermediate moose densities. Winter tick epizootics affected moose at this site (Healy et al. 2018, Ellingwood et al. 2020). We visited 6 of our sites in WMU 2 times, and 5 of our sites 3 times (23 Sep–20 Nov 2022).

Western and central Massachusetts (WCM)

The Massachusetts, USA, study area (WCM) was approximately 180,000 ha north of Interstate 90, including the Berkshire mountains and hilly terrain west of Interstate 495. This area represented a forest transition zone, where deciduous-boreal forests common in northern New England shifted to southern mixed coniferous and deciduous forest types (Goldblum and Rigg 2010, Wattles and DeStefano 2013). The elevation of this site ranged from 44–230 m. Mean annual temperature was between −4–22°C with precipitation between 9–33 cm (NOAA 2022). The study area experienced the fall (Sep–Nov), winter (Dec–Feb), spring (Mar–May), and summer (Jun–Aug) seasons in which summer were warm and winters were short and cold (Runkle et al. 2022c). The fall season (winter tick questing period) was mild, with the mean temperature during sampling 13°C. The topography consisted of formerly glaciated hills, moraines, streams, lakes, and wetlands. Mixed deciduous forest of second or multiple growth with 100% closed canopy was the dominant forest type. This forest type consisted of dominant hardwoods like northern red oak (*Quercus rubra*), red maple, and American beech, transition conifers such as white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and northern conifers like spruce and balsam fir. Larger scale commercial timber harvest was uncommon; therefore, most early successional vegetation was created through small patch timber harvest or through natural disturbance (Wattles and DeStefano 2013, Wattles et al. 2018). Cooler and wetter microclimates in the form of wetlands and closed canopy forests were abundant (Wattles et al. 2018). Dominant fauna included animals typical of northern mixed-wood forest, including white-tailed deer, American black bear, coyote, and bobcat. This site was near the southern range limit of moose in the northeastern United States (Teitelbaum et al. 2021; Figure 1) where moose densities were low and winter tick epizootics were not known to affect moose (Wattles et al. 2018). We visited 11 sites in WCM 3 times, 8 sites 4 times, and 1 site 6 times with the goal of sampling each site ≥1 time per month (6 Sep–4 Dec 2022).

METHODS

We conducted tick drag surveys at 71 sample sites in the 3 study areas: 20 in WCM, 11 in WMU, and 40 in STL. There were slight differences in site selection between the 3 study areas because co-located ongoing research projects were managed separately. We chose a random sample of 20 sample sites in WCM and 11 in WMU from a regional camera network (Berube 2024). We selected 40 sites at STL in 5 regions. Each region had a 2-site × 4-site array of 8 sites spaced 50 m apart. All sampling sites were considered independent based on the limited landscape mobility of winter ticks (Addison et al. 2016). We sampled winter ticks in September–December 2022, coinciding with the winter tick larval questing period, during which ticks are active on vegetation and not yet attached to hosts.

There was a slight difference between the placement of the temporally replicated surveys at sites sampled by University of Massachusetts at the WCM and WMU sites and those sampled by the Penobscot Nation at the STL sites. On STL we sampled the same spatial coordinates during each temporal replicate, but we changed the coordinates by >4 m between replicate surveys at WCM and WMU (Figure S2, available in Supporting Information). We modeled this slight difference in replicate design by including the covariate observer in all occupancy and abundance models. To obtain comparable estimates from WCM and WMU data (4 circular plots/visit) and STL data (1 circular plot/visit), we obtained the per-visit median of data from circular plots (4) collected in WCM and WMU for use in data analysis.

Penobscot Nation tribal biologists developed a modified dragging technique that we applied at all sites (Figure 2). As is standard practice, the method samples ticks from the vegetation using a 1-m^2 white flannel sheet

FIGURE 2 Penobscot Nation tribal biologist demonstrating the circular plot-based flagging method in September 2022 used to sample winter ticks in the northeastern United States. Photo by J. Berube.

attached to a wooden dowel with binder clips (Salomon et al. 2020) but has 2 modifications. The first modification was intended to sample brushy vegetation rather than trails or lawns typical of human disease surveillance. When the site had substantial understory vegetation, we held the cloth vertically in front of our body with the bottom of the cloth touching the ground. Pushing the cloth through the brush allowed us to sample ticks from any questing height within 1 m of the ground within the canopy. At sites where the understory vegetation was absent or sparse, we dragged the cloth along the ground in a manner similar to standard practice (Salomon et al. 2020). The second modification was to use 1 or more circular plots with a fixed radius (4 m) instead of the standard *x*-m long by 1-m wide (the cloth is 1-m wide) single-pass swath (transect; Salomon et al. 2020). This modification made it easier to standardize effort and was more likely to minimize habitat heterogeneity within a single sample unit. To sample the circular plot, we walked in 4 concentric circles starting at the center moving outwards 1 m after each rotation until the whole circular plot (~50 m^2) was surveyed. We used brightly colored flagging tape, the dowel (1-m wide), and landmarks (e.g., trees and rocks) to guide the subsequent passes to obtain complete coverage of a relatively uniform radius. At the end of each circular plot, we placed the flannels in 1-gallon plastic bags labeled with the date, unique site ID, and unique sample ID. Upon returning to the laboratory, we froze sample bags at −17°C until we processed them.

To process samples, we used a lint roller to remove all ticks from each flannel and returned the lint roller sheets to the labeled plastic bag unless they were counted right away. We counted ticks with a tally counter for each sample directly from the lint roller sheets to record total abundance and presence-absence. To keep track of ticks during counting, we counted each individual tick on the lint roller sheets through the plastic bags they were stored in and crossed off each tick with a permanent marker on the bag to avoid repeat counting. We identified all present ticks to the species level using the Clifford et al. (1961), Brinton et al. (1965), and Dubie et al. (2017) dichotomous keys. This laboratory method was consistent between Penobscot Nation and University of Massachusetts.

Covariates

We chose covariates that we expected would influence detection probability, occurrence, or abundance (day of year, relative humidity, and understory vegetation height, among others; Table 1) because of possible effects on tick survival, questing behavior, or both (Drew and Samuel 1985, Samuel 2007, Dunfey-Ball 2017, Healy et al. 2018). Because time in the field was limited, it was important to make habitat measurements as time efficient as possible. Therefore, we used a variety of manual and automated tools for quick collection and data storage. We used an iPad to record all variables at every visit. We measured understory vegetation after the flagging was completed, so as not to incidentally remove ticks prior to collection.

We used a handheld weather station (Kestrel 3000 Pocket Weather Station; Nielsen-Kellerman, Chester, PA, USA) to measure weather variables during each visit to all sites (Table 1). We measured the understory vegetation height at every circular plot using a thin metal rod marked in 3 increments to represent 0-50 cm, 51-100 cm, and 101-200 cm. We took 16 total measurements within the plot by taking 4 steps 1 m apart, in each cardinal direction and placed the rod at the toe of one's boot on each 1-m step to record all segments in which any vegetation touched the rod. For analysis at the site level (process sub model), we summed each measurement of the maximum height from each 1-m step at a plot, then calculated the mean for the site from each summed plot result.

Data analysis

We analyzed occupancy using hierarchical models with 2 sub models: process (e.g., occupancy [ψ]) and detection (ρ), which were appropriate for use with detection and non-detection data where imperfect detection is expected (MacKenzie and Bailey 2004, Kéry and Royle 2016). The process sub model returned estimates of the ecological process of interest, including the probability of occurrence (occupancy) or true abundance (N-mixture), and the detection sub model returned the probability of observing the species of interest given it was present (Kéry and Royle 2016). In this study we applied both site occupancy and N-mixture models to measure winter tick occurrence and abundance. Both models assumed that the ecological process of interest (occupancy or abundance) is constant during the season that sampling took place. We assumed that variation in availability (whether or not ticks were available to be sampled) could be modeled by including date in our detection model. To accommodate these assumptions we interpreted our ecological process of interest and the covariates applied to the process model in the superpopulation framework, which considers replicated visits to be samples from a latent superpopulation of ticks questing at the site over the entire sampling period (Hartley and Sielken 1975, Schmidt et al. 2013). We fit single-season occupancy and N-mixture models in program R (R Core Team 2020) with the package unmarked (Fisk and Chandler 2011).

Although we collected spatial replicates at WCM and WMU, we did the following actions to make our data comparable to that from STL: 1) we considered a site to be occupied if we found a tick at any of the circular plots (occupancy); 2) we used median counts for N-mixture models, 3) we used median per-visit measurements for detection sub model covariates; and 4) we used median measurements from all site measurements for the ecological process sub model. We determined sampling occasion by number of visits, so that occasion ranged from the first visit (1) to maximum number of visits to a site (6). We summarized site-level covariate data, such as vegetation height, by the median value across all replicates and visits of a site to result in 1 value for each site and occasion. We zero-centered and standardized all numeric variables. To successfully run models with different numbers of occasions (ragged array), we filled in missing data with zero (mean).

We used a 2-step model-selection process by fitting all possible combinations of the detection process covariates (28 models; Table S1, available in Supporting Information) while holding the state process (occupancy, abundance) at a constant intercept. We ranked models with Akaike's Information Criterion (AIC) for comparison (Akaike 1974) and a likelihood ratio test to choose the top detection models. We excluded a model if it contained the lower-ranked model and one or more covariates that were not supported by a likelihood ratio test. To somewhat mitigate the disadvantages of the 2-step model selection process (Morin et al. 2020), we used the best 2 non-nested detection models following the criteria above to create a candidate set of 16 models with the remaining process model covariates (Table S2, available in Supporting Information).To reduce problems associated with multicollinearity, we did not include covariates in the same model if the Pearson correlation coefficient between them was > 0.50. The final model set always contained the variable observer in the detection probability sub model to account for the slight difference in sampling designs between University of Massachusetts (WCM and WMU sites) and Penobscot Nation (STL sites), which may have affected the probability of detecting ticks given they were present. We ran a goodness-of-fit test with the R package AICcmodavg (Mazerolle 2020) on the most saturated model to test the parsimony of the fit (MacKenzie and Bailey 2004). If nested models had a ΔAIC < 2, we used likelihood ratio tests using R package lmtest (Zeileis and Hothorn 2002) to evaluate the added complexity of extra terms. We used the model with the lowest AIC for inference and to visualize covariate relationships.

For tick abundance, we fit an N-mixture model using the pcount function in the unmarked R package (Fiske and Chandler 2011). We used the same candidate model set as was used to model occupancy, except that the response data were the number of winter ticks collected per site per occasion. N-mixture models fit with the negative-binomial distribution outperformed the Poisson models when compared with AIC. Our tick data were overdispersed, and the negative-binomial model is more appropriate when the variance and uncertainty are larger than the mean (Kéry and Royle 2016). This model list consisted of 10 models. We compared models using AIC and goodness of fit and used the model with the lowest AIC to visualize covariate effects.

RESULTS

Naïve occupancy (proportion of sites containing ticks) was highest on the STL, and lowest in WMU (Table 2). The highest tick count obtained in a single sample was recorded in WCM at 985 individual ticks. Although it was common to sample no ticks during a visit, counts ranged from a single individual to groups of >100 (Figure S3, available in Supporting Information). The average number of ticks counted when present was 22. Between all the samples, we counted 3,530 winter ticks (Berube et al. 2024).

The top detection model (an occupancy model fit with no covariates on the occupancy sub model) according to AIC contained the Julian date covariate, in addition to observer, which was in all candidate models (Tables S2 and S3, available in Supporting Information). This model includes a quadratic effect of date, with the peak probability of detection occurring in the middle of the sampling period (Figure 3). Even though we fit all process models using the best 2 unique detection models (observer + date + date^2) and (observer + temperature), the detection models containing the quadratic effect on date always outperformed the models containing temperature (Tables S2 and 3). A likelihood ratio test supported the quadratic formulation of the variable date versus a linear formulation ($\chi^2 = 11.36$, $P < 0.01$).

TABLE 2 Summary of winter tick observations by site and sample from sampling in the northeastern United States at sites on the sovereign Trust lands, Maine (STL), central and western Massachusetts (WCM), and White Mountain National Forest and Umbagog National Wildlife Refuge, New Hampshire (WMU). We sampled ticks using a modified flagging technique developed by the Penobscot Nation in 4-m-radius circular plots from 6 September to 9 December 2022. Naïve occupancy is the observed proportion of sites occupied without taking imperfect detection into account.

Site	Number of sites	Sites with ticks	Naïve occupancy	Number of samples	Samples with ticks
STL	40	34	0.85	327	121
WCM	20	12	0.60	284	32
WMU	11	4	0.36	108	11

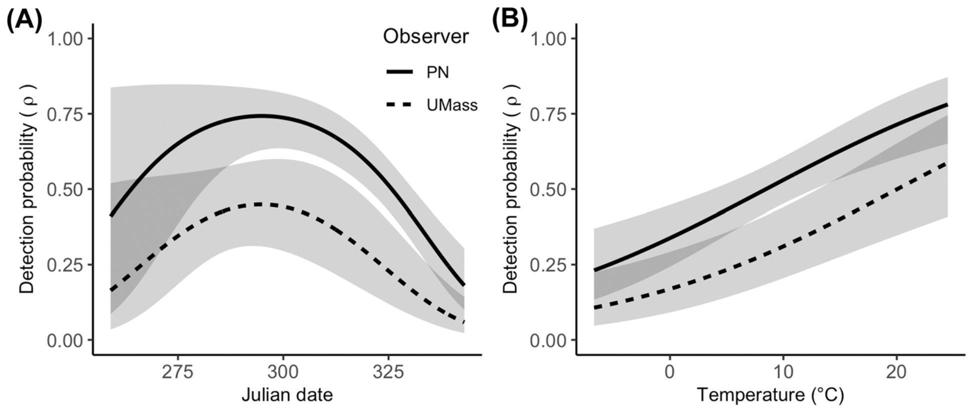

FIGURE 3 The modeled relationship between detection probability of winter ticks and A) Julian date and B) air temperature (°C) from the 2 best non-nested intercept-only occupancy models according to Akaike's Information Criterion. We sampled winter ticks from 6 September 2022–9 December 2022 using a modified flagging technique in 4-m-radius circular plots from 3 sites in the northeastern United States. The solid line represents data collected by the Penobscot Nation (PN) on the sovereign trust lands, Maine (STL), and the dashed line represents data collected by the University of Massachusetts (UMass) in western and central Massachusetts (WCM) and White Mountain National Forest and Umbagog National Wildlife Refuge, New Hampshire (WMU).

TABLE 3 Model selection results for the occupancy model of winter tick occurrence at 3 study areas in the northeastern United States. We sampled ticks using a modified flagging technique developed by the Penobscot Nation in 4-m-radius circular plots from 6 September to 9 December 2022. The 5 occupancy models with the lowest Akaike's Information Criterion (AIC) values are displayed and we provide the log likelihood (logL), the number of parameters (*K*), and the comparative weight of evidence for each model in the model set (w_i). Squared terms (e.g., date^2) indicate a second-order polynomial.

Detection (ρ)	Occupancy (ψ)	logL	*K*	AIC	ΔAIC	w_i
~Observer + date + date^2	~Vegetation	−181.24	6	374.47	0.00	52.7%
~Observer + date + date^2	~Vegetation + vegetation^2	−181.21	7	376.42	1.95	19.9%
~Observer + date + date^2	~Location	−181.63	7	377.26	2.79	13.1%
~Observer + date + date^2	~Location + vegetation	−180.85	8	377.70	3.23	10.5%
~Observer + date + date^2	~Location + vegetation + vegetation^2	−180.85	9	379.69	5.22	3.9%

Temperature had a positive relationship with the probability of detecting winter ticks, and the quadratic effect with date indicated a peak in tick detection in the middle of the tick collection period (Table 3; Figure 3).

The top occupancy model according to AIC returned vegetation height in the process sub model (Table 3; Table S4, available in Supporting Information). The model with a quadratic term of vegetation was ranked second according to AIC, but the quadratic effect was not supported by a likelihood ratio test ($\chi^2 = 0.45$, $P = 0.50$). The full occupancy model, which was ranked fourth in AIC, included location and vegetation height in the process sub model (Table 3). Using predictions from the top model, predicted occupancy increased as the understory vegetation height decreased from the maximum measurement. We used the single-variable location process sub model to depict winter tick occupancy rates across the different study sites (Figure 4; Table 4). A goodness-of-fit test on the most saturated occupancy model resulted in a chi-square of 166.10 ($P = 0.01$), indicating poor fit, and a $\hat{c}$ of 1.47, indicating slight overdispersion.

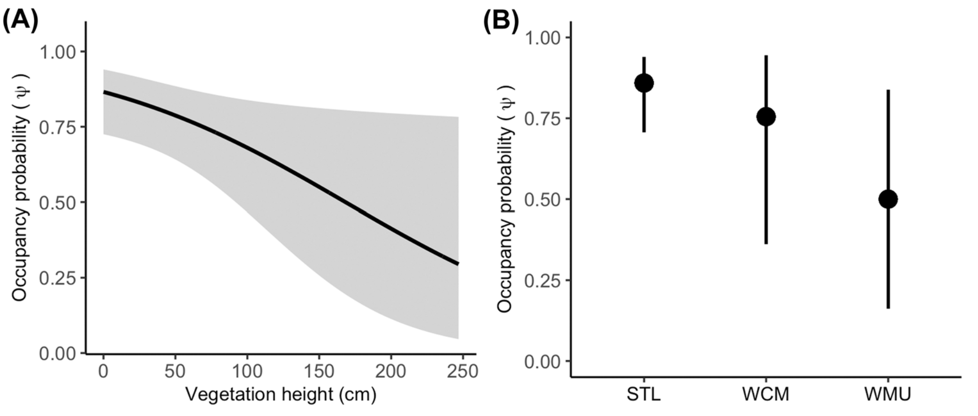

FIGURE 4 Graphs of the modeled probability of winter tick occupancy at 3 study sites in the northeastern United States. We sampled winter ticks using a modified flagging technique developed by the Penobscot Nation in 4-m-radius circular plots from 6 September to 9 December 2022. We present A) the modeled relationship (line) between winter tick occupancy and understory vegetation height (cm) and the standard error (shading) and B) winter tick occupancy at the 3 study areas: sovereign trust lands, Maine (STL), western and central Massachusetts (WCM), and White Mountain National Forest and Umbagog National Wildlife Refuge, New Hampshire (WMU). The points indicated the modeled probability of winter tick occupancy, and the lines indicate the standard error. We provide the relationship with study area (B) for illustration purposes, but models including location were not supported by Akaike's Information Criterion.

All the supported abundance models included a quadratic term of vegetation height, which was supported with a likelihood ratio test ($\chi^2 = 4.28$, $P = 0.04$). The top abundance model, which was also the full model, contained a location effect (Tables 4 and 5; Table S5, available in Supporting Information). A goodness-of-fit test on the full abundance model resulted in a chi-square of 472,660.4 ($P < 0.01$), indicating poor fit, and a $\hat{c}$ of 56.01, indicating overdispersion. The next model contained only the quadratic vegetation height term and was <1 AIC from the top model (Table 5). A likelihood ratio test did not support the location covariate ($\chi^2 = 4.83$, $P = 0.09$). Predictions from the full model are included to show that abundance was predicted to be highest with middle understory vegetation height, and to show predicted tick abundance by site (Figure 5; Table 4).

DISCUSSION

The probability of occupancy and abundance of winter ticks was similar at all sample sites. Although location occurred in the top models in the N-mixture model set, high variance masked any potential differences between study areas. We expected to find ticks at all study sites (Chenery et al. 2023), but we hypothesized that the STL and WMU study site would support the highest tick abundance and probability of site occupancy. Winter tick epizootics are hypothesized to be density dependent, and primarily affecting moose in high-density populations in New Hampshire, Vermont, and western Maine (Samuel 2004, Healy et al. 2018, Pekins 2020). We were therefore surprised to find winter ticks in WCM at high occupancy and in similar abundance to sites in WMU and STL.

The sampling protocol developed by the Penobscot Nation was designed to produce a clearer picture of what was occurring on the landscape in regard to winter tick densities. They wanted to use a method that allowed them to determine exactly where, within the study plot, they were picking up ticks and to hold the sheet in a way that would travel through the vegetation similarly to how a moose would be traveling. They created this new method to sample winter ticks in moose habitat, whereas the standard method is used most frequently for sampling deer ticks (*Ixodes scapularis*) for human disease surveillance (Centers for Disease

TABLE 4 Model coefficients from the top models of winter tick detection, occupancy, and abundance from 3 study areas in the northeastern Unites States: sovereign trust lands, Maine (STL), western and central Massachusetts (WCM), and White Mountain National Forest and Umbagog National Wildlife Refuge, New Hampshire (WMU). We sampled ticks using a modified flagging technique developed by the Penobscot Nation in 4-m-radius circular plots from 6 September to 9 December 2022. The coefficients displayed for the detection model were derived from the occupancy model formulation. Squared terms (e.g., date^2) indicate a second-order polynomial.

Model	Covariates	Estimate	SE
Detection			
~Observer + date + date^2	Observer: Penobscot Nation	0.67	0.20
~1	Observer: UMass	−1.26	0.40
	Date	−0.82	0.17
	Date^2	−0.43	0.13
	Intercept	1.65	0.45
Occupancy			
~Observer + date + date^2	Vegetation	−1.18	0.56
~Vegetation	Intercept	0.90	0.42
Abundance			
~Observer + date + date^2	Location: STL	9.21	1.50
~Location + vegetation + vegetation^2	Location: WCM	−4.07	1.41
	Location: WMU	−3.83	1.73
	Vegetation	1.64	1.02
	Vegetation^2	−5.15	1.58
	Intercept	−1.33	0.17

TABLE 5 Model selection results for the N-mixture model of winter tick abundance in the northeastern United States. We sampled ticks using a modified flagging technique developed by the Penobscot Nation in 4-m-radius circular plots from 6 September to 9 December 2022. The 5 N-mixture models with the lowest Akaike's Information Criterion (AIC) values are displayed and we provide the log likelihood (logL), the number of parameters (K), and the comparative weight of evidence for each model in the model set (w_i). Squared terms (e.g., date^2) indicate a second-order polynomial.

Detection (ρ)	Abundance (ψ)	logL	K	AIC	ΔAIC	w_i
~Observer + date + date^2	~Location + vegetation + vegetation^2	−2,476.57	10	4,973.11	0.00	57.4%
~Observer + date + date^2	~Vegetation + vegetation^2	−2,478.97	8	4,973.94	0.83	37.9%
~Observer + date + date^2	~Location	−2,481.07	8	4,978.14	5.02	4.6%
~Observer + temp	~Location + vegetation + vegetation^2	−2,925.17	9	5,868.34	895.22	0.0%
~Observer + temp	~Vegetation + vegetation^2	−2,927.41	7	5,868.81	895.70	0.0%

Control [CDC] 2018) and is primarily deployed on trails (Salomon et al. 2020). In studies of winter ticks, researchers typically employ the standard method in recent timber harvests, or on linear features such as skid roads and trails (Bergeron and Pekins 2014), where vegetation tends to be more conducive to standard drag methods. Because the Penobscot Nation method was developed specifically to sample winter ticks in

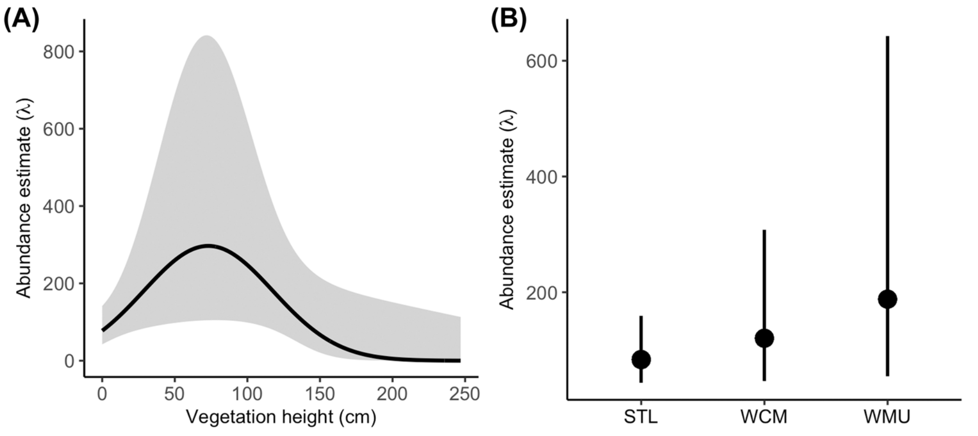

FIGURE 5 Graphs of the modeled winter tick abundance at 3 study sites in the northeastern United States. We sampled ticks using a modified flagging technique developed by the Penobscot Nation in 4-m-radius circular plots from 6 September to 9 December 2022. We present A) the relationship (line) between winter tick abundance and understory vegetation height (cm) and the standard error (shading) and B) winter tick abundance estimates for each study area: sovereign trust lands Maine (STL), western and central Massachusetts (WCM), and White Mountain National Forest and Umbagog National Wildlife Refuge New Hampshire (WMU). The points indicate the estimated abundance, and the lines denote the standard error.

heterogeneous habitats and not deer ticks in homogenous habitats, direct comparisons between this method and results from other standard flagging studies cannot be made. We show that the Penobscot Nation method successfully collected ticks in a variety of land cover types and in locations where we expected detection probability of ticks to be low because of a lack of moose epizootics (e.g., WCM). Therefore, our modified method may be more appropriate for answering questions about how ticks may affect moose because it emulates how moose realistically move through a landscape and acquire ticks by sampling ticks from within the understory rather than just the top of the plants.

Understory vegetation height was important for explaining both tick occurrence and abundance. This is expected because winter ticks are dependent on understory vegetation for questing and will typically climb 50–200 cm into the underbrush when they quest, remaining there until they attach to a host or die (Drew and Samuel 1985, McPherson et al. 2000). In addition to providing structure for questing, vegetation may provide structure that improves survival of winter ticks when they are off host (Drew and Samuel 1985, McPherson et al. 2000). We therefore expected that more winter ticks would occur at sites with vegetation within this range. The quadratic relationship with understory height was supported for abundance, and included in the top models for occupancy, suggesting a peak in abundance and occupancy when the understory vegetation was about 75 cm. The Penobscot Nation method sampled the understory from about 0 to 155 cm.

We expected to find site-level differences in both tick abundance and occupancy, but the location covariate was not among the top models selected by AIC. Ours was a regional analysis that grouped sites into large, heterogeneous study areas for analysis, which may not reflect actual differences in tick abundance and distribution caused by micro-habitat characteristics. The large variance that we observed in the location occupancy and abundance estimators may have come from unmodeled habitat heterogeneity that could be modeled had we measured additional habitat covariates. Future work may be improved by carefully measuring site-level habitat covariates that are hypothesized to affect tick occupancy and abundance.

It is common for studies of tick distribution and abundance to collect replicate samples throughout the questing period, but few use replicates to address imperfect detection using occupancy or other hierarchical modeling techniques (Sirén 2024). Occupancy and N-mixture models are a special class of hierarchical model that allows the analyst to separate factors expected to influence probability of detection from those expected to affect occupancy and abundance (Kéry and Royle 2016). We again demonstrated that the probability of collecting ticks given they are present can be substantially less than perfect and can be affected by both day of year and temperature. We used the occupancy modeling structure to accommodate potentially confounded differences in the replicate design between University of Massachusetts (WCM and WMU) and STL by fitting the observer covariate in the detection sub model and location in the process (occupancy or N-mixture) sub model. By doing so, we separated the potential differences in detectability owing to the revisit designs from real differences in occupancy or abundance at the sites. Had we not used a hierarchical model, these effects would have been entirely confounded. A trade-off to our approach is that combining datasets across observer required us to summarize data across spatially replicated samples (median) at sites in WCM and WMU, thereby reducing any benefits gained using the spatially replicated design. Future analyses of the WCM and WMU datasets would benefit from using a multi-scale occupancy model to measure differences in tick availability caused by micro-habitat variation.

Questing peaked in mid-October. Although the exact start and end dates of questing remain unknown, the seasonality of questing is undisputed and there is a peak in tick abundance during the middle of the questing season (Drew and Samuel 1985, Samuel and Welch 1991, Aalangdong 1994, Addison et al. 2016); we expected the effect to show up on our detection sub model. This result can be partially explained by tick behavior in which ticks must balance their need to find a host with risks of desiccation (Addison et al. 2016, Powers and Pekins 2020). Weather affects questing behavior in many tick species (Drew and Samuel 1985, Addison et al. 2016, Powers and Pekins 2020), but measured weather variables were not among the top detection probability models selected by AIC.

Our results are not conclusive about what could cause the observed seasonal pattern in detection because in their most basic form, occupancy models are unable to distinguish between different components of the detection process (Nichols et al. 2009). This thereby confounds the probability that ticks are actively questing and available to be detected with the ability of detecting ticks using flag or drag sampling methods (Nichols et al. 2009, DiRenzo et al 2022). We suspect both availability and detection would change throughout the tick questing season, and that this is best represented by the quadratic date effect. Furthermore, as the season progresses, ticks are either removed by hosts or lose energy to quest (Addison et al. 2016). Therefore, further refinements of the detection process model may improve our understanding of the seasonality of tick questing behavior.

There are intrinsic limitations to these data and our inference. Winter ticks are naturally patchy in distribution and difficult to detect, forcing a balance between sites and visit replicates. This study maximized the number of sites and visits as much as possible. Despite this, our dataset is still relatively small, especially in WMU, which was difficult for researchers based at University of Massachusetts to access regularly. A small number of revisits affects parameter identifiability in N-mixture models (Barker et al. 2018, Madsen and Royle 2023); therefore, estimates of WMU should be viewed with caution.

Goodness-of-fit analyses indicated poor fit for our models. This is a known problem for negative binomial N-mixture models, and we expected it given our relatively small sample size and known overdispersion of tick data (Kéry and Royle 2016, Kéry 2018). Lack of fit for standard occupancy models is also common for small datasets and is most often a characteristic of unmodeled heterogeneity in the detection sub model (MacKenzie and Bailey 2004). In our case, there were 4 sites that we suspect contributed to the lack of fit (1 from WMU and 3 from STL) as they had detection histories where ticks occurred more frequently than expected. We hypothesize that model fit for both the occupancy and N-mixture models would improve with a site-level random effect, which is only available in a Bayesian formulation.

MANAGEMENT IMPLICATIONS

The replicated circular plot method was useful for sampling winter ticks in moose habitat where habitat patches may be small, variable, or both, because the circular plots themselves were less likely to cross habitat boundaries. It has wide applicability to other tick species, including those that transmit zoonotic diseases (e.g., Lyme disease). The protocol we followed is easy to learn and carry out, and the measurement tools are readily available. We demonstrated that repeated flag or drag sampling visits throughout the questing season, a common practice for tick studies, can be used in an occupancy framework to estimate the probability of detecting ticks. Managers can target sampling during the questing period and fair-weather days for the best possible sampling conditions and success. There is still much to learn about what causes winter tick epizootics and how to best mitigate or adapt to them, and pairing regional tick monitoring with moose abundance measurements could help make progress on multiple goals.

ACKNOWLEDGMENTS

Any use of trade, firm, or product names in this publication is for descriptive purposes only and does not imply endorsement by the United States Government. We thank our technicians, J. Brenner, A. Bickford, K. Counihan, T. B. Murphy, and M. Tatro, for their indispensable help in the field. Thanks to C. F. Sullivan for answering questions about tick sampling and helping with ID. Our paper was improved by the contributions of K. Gieder, 3 anonymous reviewers, and the editorial staff at *JWM*. Funding was provided by United States Geological Survey (MA-RWO-74).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study sampled invertebrate species that do not require collection permits or Institutional Animal Care and Use Committee approval. In all cases, permission to access sampling locations was granted by the landowner.

DATA AVAILABILITY STATEMENT

Data from WCM and WMU is available at Science Base (https://doi.org/10.5066/P1ZSHPPX). Data from PNTL are property of the Penobscot Nation; please contact Ben Simpson benjamin.simpson@penobscotnation.org to inquire about their availability.

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Associate Editor: Jonathan Gilbert.

SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

How to cite this article: Berube, J. A., A. P. K. Sirén, B. D. Simpson, K. B. Klingler, and T. L. Wilson. 2024. Monitoring questing winter tick abundance on traditional moose hunting lands. Journal of Wildlife Management 88:e22630. https://doi.org/10.1002/jwmg.22630