ABUNDANCE OF WINTER TICKS (*DERMACENTOR ALBIPICTUS)* IN TWO REGENERATING FOREST HABITATS IN NEW HAMPSHIRE, USA

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ABSTRACT: Recent decline in New Hampshire's moose (*Alces alces*) population is attributed to sustained parasitism by winter ticks (*Dermacentor albipictus*) causing high calf mortality and reduced productivity. Location of larval winter ticks that infest moose is dictated by where adult female ticks drop from moose in April when moose preferentially forage in early regenerating forest in the northeastern United States. The primary objectives of this study were to: 1) measure and compare larval abundance in 2 types of regenerating forest (clear-cuts and partial harvest cuts), 2) measure and compare larval abundance on 2 transect types (random and high-use) within clear-cuts and partial harvests, and 3) identify the date and environmental characteristics associated with termination of larval questing. Larvae were collected on 50.5% of 589 transects; 57.5% of transects in clear-cuts and 44.3% in partial cuts. The average abundance ranged from 0.11–0.36 ticks/m^2 with abundance highest ($P < 0.05$) in partial cuts and on high-use transects in both cut types over a 9-week period; abundance was ~2 × higher during the principal 6-week questing period prior to the first snowfall. Abundance (collection rate) was stable until the onset of < 0°C and initial snow cover (~15 cm) in late October, after which collection rose temporarily on high-use transects in partial harvests during a brief warm-up. The higher abundance of winter ticks on high-use transects indicates that random sampling underestimates tick abundance and relative risk of infestation of moose. Calculating an annual index of infestation of winter ticks on moose is theoretically possible by integrating 3 factors: the infestation of harvested moose in October, the length of the questing period, and assuming a stable collection rate during the questing period.

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The influence of winter ticks (*Dermacentor albipictus*) on population dynamics of moose (*Alces alces*) in the northeastern United States (northeast) is well documented (Musante et al. 2010, Bergeron et al. 2013, Jones et al. 2017, 2019, Ellingwood et al. 2020). The physiological impact of blood loss on moose is directly associated with infestation level of winter ticks (Musante et al. 2007), and recent research has addressed the physiology, ecology, and etiology of winter ticks (e.g., Yoder et al. 2016, 2017a, 2017b, Holmes et al. 2018). Further, the presumed influence of climate change in the winter tick-moose relationship is that longer autumns and later onset of winter weather will extend the questing period of winter ticks (Dunfey-Ball 2017, Jones et al. 2019). Potential outcomes would include higher infestation levels, more frequent epizootics (>50% calf mortality), reduced productivity in yearling and adult cows, and sustained tick abundance on the landscape (Musante et al. 2010, Bergeron and Pekins 2014, Healy et al. 2018, 2020, Jones et al. 2017, 2019). However, few studies have attempted to measure field abundance of winter ticks (Drew and Samuel 1985, Aalangdong 1994, Addison et al. 2016), with only a single study in the northeast (Bergeron and Pekins 2014).

As in typical host-parasite relationships, host density is directly related to parasite density with several studies indicating that increased moose density increases tick distribution and relative abundance (Blyth 1995, Pybus 1999, Samuel 2007, Bergeron and Pekins 2014). Field studies indicate that 85% of adult winter ticks are located within 60 cm of a moose carcass (Drew and Samuel 1985, 1986), and >95% of larvae are typically found within 1–2 m of the hatching location (Drew and Samuel 1985, 1986, Addison et al. 2016) and ascend proximal vegetation the following autumn to quest for a host (Drew and Samuel 1985). Likewise, in laboratory conditions Yoder et al. (2016) found that larval ticks have limited mobility, crawling only ~1 m. Recruitment of larval ticks is higher in open habitat than closed-canopy deciduous forest, except in hot and dry conditions (Addison et al. 2016). Therefore, distribution and questing location of winter ticks is where adult ticks drop from moose in March-April, and the relative infestation risk is a function of environmental conditions and habitat use by moose.

Moose preferentially use young, regenerating forest habitat (4–16 years old) more than other cover types in spring and autumn (Scarpitti et al. 2005, Healy et al. 2018). Further, the same animals demonstrate overlap in use of specific cuts during spring and autumn, suggesting a positive feedback loop of infestation (Healy et al. 2018). In the single field study conducted in the northeast, larval abundance in clear-cuts was generally related to moose density, but varied among and within clear-cuts (Bergeron and Pekins 2014). It is presumed that relative tick abundance is related to the previous years' infestation level, and this earlier study was not preceded by or followed by an identified epizootic. This study was designed to measure larval abundance during autumnal questing in preferred cut habitat when tick abundance was presumably high following an epizootic in spring 2018 (61% calf mortality; Powers 2019).

STUDY AREA

The study area was in Jericho State Park located in the town of Berlin entirely within Wildlife Management Unit (WMU) C1 covering ~70 km^2 in eastern Coos County in northern New Hampshire (UTM 19 T 320970 E, 4926474 N; map in Jones et al. 2017). Moose density was estimated at 0.46–0.87 moose/km^2, down from 1.2 moose/km^2 in 1998 (NHFG 2015). Year-round access was through a network of former logging roads and off-highway recreational vehicle (OHRV)/snowmobile trails. The landscape was mostly lowland valleys with rolling hills and small water features (streams, rivers, ponds) scattered throughout. The predominant cover type was northern hardwood forest consisting of American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and paper and yellow birch (*Betula papyrifera* and *B. allegheniensis*). Conifer cover in low elevation areas consisted mostly of northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), red spruce (*P. rubens*), and balsam fir (*Abies balsamea*); high elevation stands were red spruce and balsam fir (DeGraaf et al. 1992). The larger geographical area was the focus of a comprehensive moose habitat and survival study in 2002–2005 (Scarpitti et al. 2005, Musante et al. 2010), related studies of winter ticks and forest regeneration (Bergeron et al. 2011, Bergeron and Pekins 2014), and since 2014, survival and productivity of moose

(Jones et al. 2017, 2019, Dunfey-Ball 2017, Healy et al. 2018, Ellingwood et al. 2019).

METHODS

Study plots were established in summer 2018 to measure larval abundance during the questing period in autumn 2018 (September–November). Plots were established in two cut types: clear-cuts (n = 22) and partial harvests (e.g., geometric thinning) (n = 22) (Fig. 1 and 2). Each was within an age range associated with preferred foraging habitat (4–10 years), 4.04–4.85 ha in size, and with ample sign of moose use. Moose use this area year-round and multiple radio-collared calves succumbed to infestation of winter ticks in springs 2014–2018. Epizootic conditions occurred in the larger study area in spring 2018 (61% calf mortality) and 4 of the previous 5 years (Jones et al. 2019).

Two treatments were defined in each plot: 1) random area within the plot (similar to Bergeron and Pekins 2014), and 2) high-use areas that reflected concentrated moose activity. High-use areas were obvious foraging sites and movement corridors on trails and edges proximate to uncut forest that were readily identified from visual inspection and evidence of browsing (Fig. 1 and 2). Each plot was sampled at least 12 times

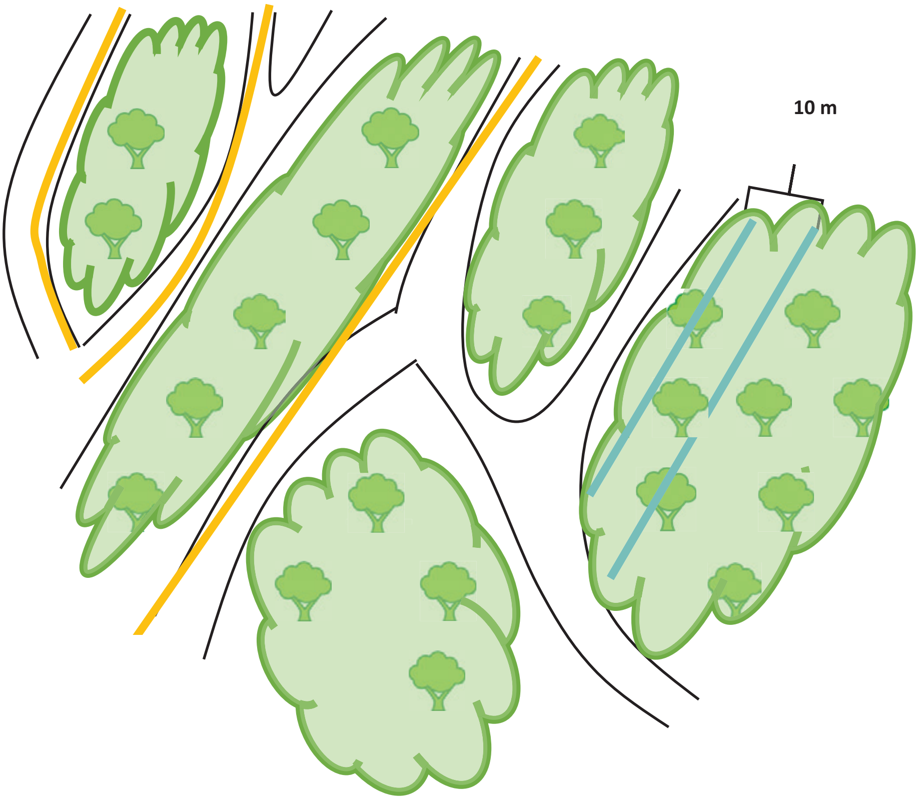

Fig. 1. Schematic illustrating the sampling design in partial harvest plots in Berlin, New Hampshire, USA. Partial harvests leave a mix of cut and uncut areas that create proximal foraging and bedding areas for moose. Green clouds depict uncut portions of trees (canopy cover) and black lines depict cut area and skid trails that serve as pathways and foraging sites. Orange lines depict typical location of high-use transects set within cut areas and skid trails. Blue lines depict typical random transects avoiding high-use areas and spaced 10 m apart.

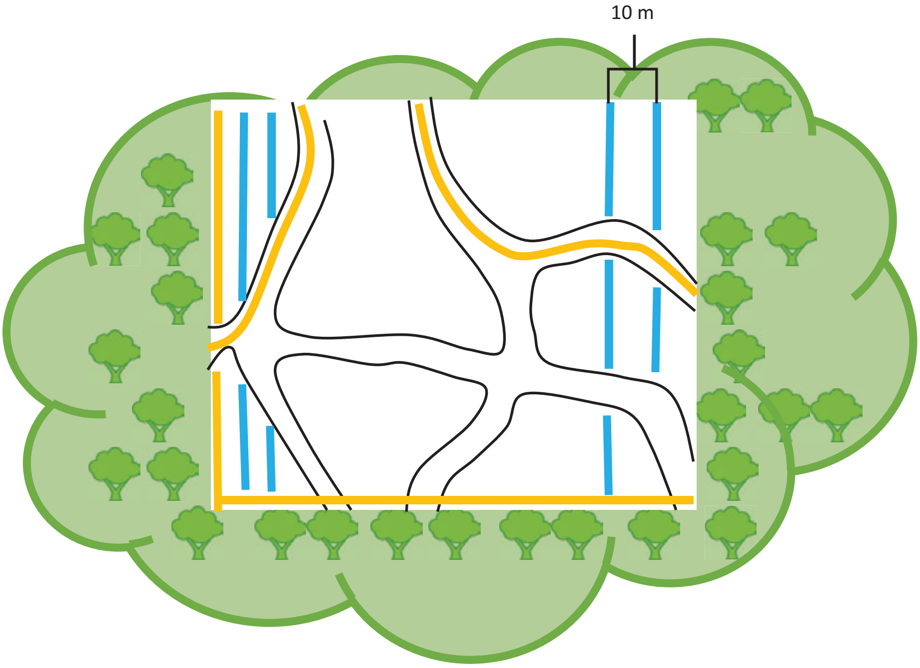

Fig. 2. Schematic illustrating the sampling design in clear-cut plots in Berlin, New Hampshire, USA. The clear-cut is white and set within a green cloud of unharvested forest; skid trails are depicted with black lines. Orange lines depict high-use transects placed within foraging and movement pathways (e.g., edges and skid trails). Blue lines depict random transects spaced 10 m apart through the uniform regenerating forest.

during the questing period (mid-September through mid-November); sampling continued until collection of larvae ceased.

Line transects were established weeks prior to sampling after visual inspections of each plot to identify random and high-use sampling locations within each plot. Transects were spaced at least 10 m apart and no repeat sampling occurred of a transect either daily or during a subsequent visit. Plots were sampled bi-weekly by flagging at least 4 transects (2 random, 2 high-use) per visit. Flagging followed the basic technique used by others (Drew and Samuel 1985, Piesman et al. 1986, Ginsberg and Ewing 1989, Aalongdong 1994, Bergeron and Pekins 2014) in which a 1 m^2 cotton cloth was dragged over vegetation to collect questing larvae. Each transect flag was bagged (plastic ziplock) separately and frozen. Subsequently, an entire count of larvae on each flag was performed to calculate abundance (ticks/m^2; area = transect length (m) × 1 m^2).

A subset of plots (4 clear-cut and 4 partial harvest) were monitored continuously with remote data-loggers that measured hourly ambient temperature (±0.5ºC) from mid-August until late November at the typical questing height (125 cm) of larvae (McPherson et al. 2000). These data were analyzed relative to collection rate and tick abundance to investigate relationships between temperature, tick abundance, and relative questing activity. Snow events were also monitored given the susceptibility of larvae to freezing/desiccation (Drew and Samuel 1985).

ANALYSIS

The raw data exhibited the typical field-sampling problem of “zero-inflated” data, as ~50% of transects were tick-less (i.e., negative transects); therefore, the data were analyzed using a hurdle or "two-stage" linear model. The first stage was a logistic model that used the binary form of all transect data including negative transects; data were not log-transformed. In the second stage, the negative transects were removed and only positive transects were analyzed. After testing for normality, these data were subsequently log-transformed to fit a normal distribution. Both were used to test if larval abundance was different between clear-cuts and partial harvests, and between random and high-use transects within cuts.

A temporal analysis of larval abundance using all transect data, ambient temperature, and questing activity was performed with a linear mixed-effects model. Fixed variables in the model included ambient temperature, transect type, date, snow depth, with plots as the random effect variable; analysis was performed in Program R (ver. 3.4.4, Austria). Basic summary statistics were used to express and analyze ambient temperature measurements. The average daily temperature and abundance data were used to analyze temporal factors possibly influencing abundance within the model. A *t*-test was used to compare ambient temperature between plot types; analysis was performed in Program R (ver. 3.4.4, Austria).

RESULTS

A total of 589 transects were measured in the 44 plots from 15 September–20 November 2018. Transect length ranged from 28–322 m (median = 177 m) in clear-cuts and 45–322 m (median = 177 m) in partial harvests (Table 1). Larval questing had initiated at the start of dragging on 15 September. The absolute number of larvae collected per transect ranged from 0–2,554 larvae. For all transects combined, the absolute average and maximum abundances were always higher on high-use than random transects in both cut types, with larger differences in partial cuts; a similar trend occurred on positive transects alone that had abundances ~1.5–2.5 × higher than the overall combined averages (Table 1).

The first stage model (all transects) indicated that abundance was 1.8 × times higher ($P < 0.05$) in partial harvests (0.24 ± 0.08 ticks/m^2) than clear-cuts (0.13 ± 0.03

Table 1. Field abundance (ticks/m^2) of larval ticks collected from 15 September–10 November 2018 in 22 clear-cut and 22 partial cut study plots, Berlin, New Hampshire, USA. Positive transects were those where larvae were collected. Random indicates transects that were distributed randomly within a plot. High-use indicates transects that were located in areas of concentrated moose activity (i.e., game trails and foraging areas).

All transects	Clear-cut (random)	Clear-cut (high-use)	Partial Harvest (random)	Partial Harvest (high-use)
# of transects	140	138	155	156
Transect length (m)	74–321	28–322	70–322	45–322
Abundance (se)	0.12 (0.02)	0.15 (0.04)	0.11 (0.03)	0.36 (0.13)
Max abundance	1.90	5.52	4.04	13.45
Range (# ticks/transect)	0–459	0–975	0–527	0–2554
Positive transects				
# of transects	74	86	66	72
Abundance (se)	0.22 (0.04)	0.25 (0.06)	0.27 (0.23)	0.81 (0.29)
Range (# ticks/transect)	1–459	1–975	1–527	1–2554

ticks/m^2) (Table 1). There was a strong trend ($P = 0.13$) toward higher abundance on high-use than random transects in both cut types. The second stage model indicated that abundance was 2.3 × higher ($P = 0.05$) in partial harvests (0.54 ± 0.35 ticks/m^2) than clear-cuts (0.24 ± 0.11 ticks/m^2 (Table 1). Abundance in clear-cuts was similar ($P = 0.47$) on random (0.22 ± 0.04 ticks/m^2) and high-use transects (0.25 ± 0.06 ticks/m^2), whereas abundance was higher ($P < 0.05$) on high-use (0.81 ± 0.29 ticks/m^2) than random transects (0.27 ± 0.23 ticks/m^2) in partial harvests (Table 1).

Two drags on high-use transects in partial harvests (13.2 and 13.4 ticks/m^2) substantially elevated the mean abundance estimates in weeks 2 (1.25 ticks/m^2) and 8 (0.98 ticks/m^2) (Table 2). These values reflected the collection of very large clusters of larvae (identified on the flags) and could be considered outliers relative to weekly estimates; their removal would more closely align the weekly estimates (0.10 and 0.05 ticks/m^2). However, these data were retained in the weekly analyses because they represent important characteristics of local variation in larval abundance and ecology.

Weekly mean abundances were used to test for a temporal relationship because the infestation rate of moose is presumably correlated with the relative abundance of larvae. Because snow and low ambient temperature at the end of week 6 measurably reduced the collection rate (abundance) in week 7 (Table 2, Fig. 4), linear regression was used to determine if abundance was constant (i.e., slope = 0) across the first 6 weeks assuming that collection rate was mostly unaffected by weather. Further, because transect type was not related to abundance in clear-cuts, the means of random and high-use transects in clear-cuts (Table 2) were averaged to produce a weekly abundance; partial harvest data were not tested because abundance differed by transect type. The slope in clear-cuts was 0.0019 (90% CI = −0.004 to 0.456) and not different than 0 ($P > 0.05$), indicating that weekly abundance was stable in the first 6 weeks (Fig. 3).

The first stage model was rerun with the 6-week data and indicated that abundance was 1.7 × higher ($P = 0.01$) in partial harvests (0.25 ± 0.08 ticks/m^2) than clear-cuts (0.15 ± 0.03 ticks/m^2) (Table 3). Similarly, higher abundance ($P = 0.02$) occurred on high-use than random transects in partial harvests (0.36 ± 0.15 vs. 0.14± 0.05 ticks/m^2) and clear-cuts (0.17 ± 0.03 vs. 0.14

Table 2. Weekly larval tick abundance (ticks/m^2) from 15 September to 10 November 2018, Berlin, New Hampshire, USA. Transect type indicated by "Random" and "High-use" within both cut types.

	Clear-cut Random	SE	Clear-cut High-use	SE	Partial Harvest Random	SE	Partial Harvest High-use	SE
Week 1	0.21	0.11	0.12	0.04	0.03	0.01	0.17	0.15
Week 2	0.03	0.03	0.13	0.04	0.43	0.40	1.25	1.31
Week 3	0.20	0.08	0.32	0.23	0.01	0.01	0.19	0.15
Week 4	0.16	0.07	0.22	0.07	0.16	0.07	0.35	0.33
Week 5	0.01	0.01	0.09	0.06	0.03	0.02	0.24	0.11
Week 6	0.20	0.10	0.22	0.08	0.19	0.12	0.19	0.08
Week 7	0.08	0.05	0.03	0.01	0.03	0.02	0.17	0.12
Week 8	0.05	0.02	0.03	0.01	0.12	0.08	0.98	0.84
Week 9	0.03	0.02	0.00	0.00	0.00	0.00	0.03	0.03

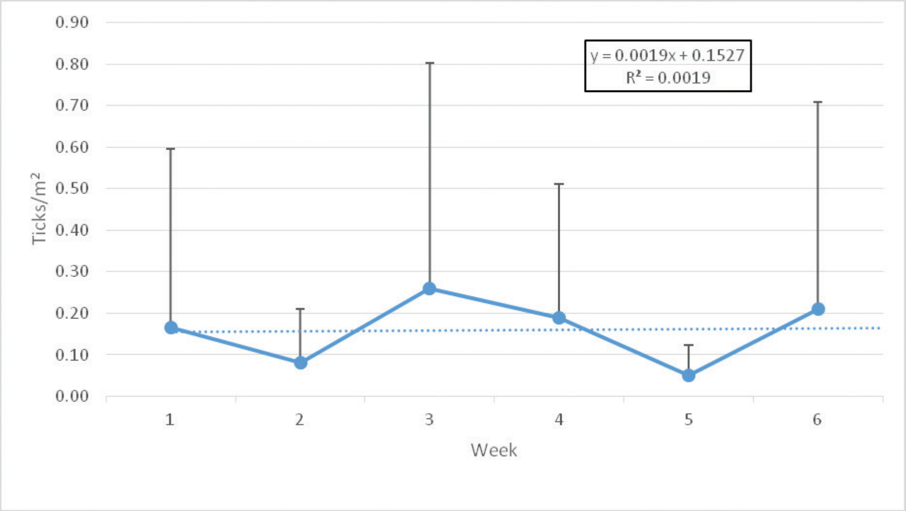

Fig. 3. The mean weekly abundance of winter ticks in clear-cuts from 15 September–26 October 2018, Berlin, New Hampshire, USA. Each point is the weekly mean prior to the snow event on 26 October that induced substantial reduction in tick abundance. The vertical line at each point represent standard error. The dotted line represents the temporal linear relationship that indicated that abundance was stable during the 6 weeks.

Table 3. The 6-week field abundance (ticks/m^2) of larval ticks collected in 15 September–27 October 2018 in 22 clear-cut and 22 partial cut study plots, Berlin, NH. Random indicates that transects were distributed randomly within a plot. High-use indicates transects that were located in areas of concentrated moose activity (i.e., game trails, and foraging areas).

	Clear-cut (random)	Clear-cut (high-use)	Partial Harvest (random)	Partial Harvest (high-use)
# of transects	105	105	106	107
Transect length (m)	74–321	28–322	70–322	45–322
Mean abundance (se)	0.14 (0.03)	0.17 (0.03)	0.14 (0.05)	0.36 (0.15)
Max abundance	1.90	5.52	4.04	13.45
Range (# ticks/transect)	0–459	0–975	0–527	0–2554
Positive transects				
# of transects	53	69	47	52
Abundance (se)	0.27 (0.06)	0.30 (0.08)	0.30 (0.10)	0.74 (0.29)
Range (# ticks/transect)	1–459	1–975	1–527	1–2554

± 0.05 ticks/m^2). Abundance was similar on random transects in both cut types (0.14 ticks/m^2) (Table 3). Interestingly, the second stage of the model indicated that abundance was 1.9 × higher ($P = 0.03$) in partial harvests (0.54 ± 0.16 ticks/m^2) than clear-cuts (0.28 ± 0.05 ticks/m^2), but transect type had no effect on abundance ($P = 0.90$) (Table 3). Absolute abundance on high-use transects was always higher than on random transects in both cut types (Table 2).

With the onset of cold temperatures and snow in late October (week 6), abundance declined in each plot and transect type in week 7 (Fig. 4). However, a temporary increase in activity and collection occurred on

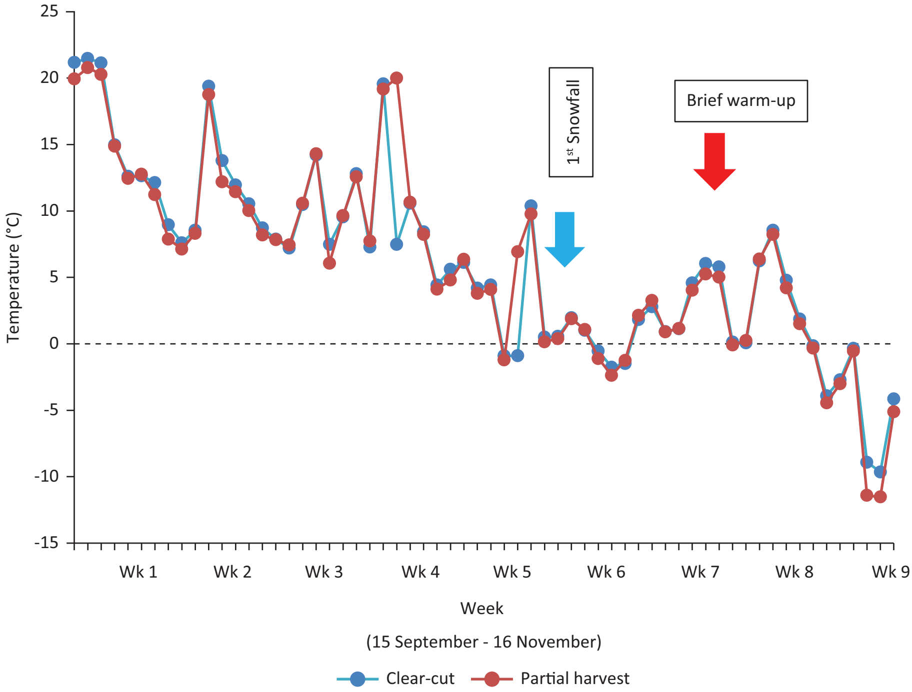

Fig. 4. Average daily temperature in clear-cuts and partial harvests from 15 September–16 November 2018, Berlin, New Hampshire, USA.

5 November (week 8) in partial cuts when ambient temperature rose to 8.5°C; abundance in clear-cuts did not increase concurrently (Table 2, Fig. 4). By 10 November (week 9, Table 2), abundance was functionally zero based on lack of collection and the obvious (observed) inability of the few collected larvae to crawl on the flag. The onset of sustained snow cover and temperatures <0°C coincided with a decline in larval abundance ($P < 0.05$). Decline in abundance in both cut and transect type from 15 September to 20 November was correlated with date ($P = 0.002$). No individual effect was found with temperature or snow depth ($P > 0.05$); however, a significant interaction effect ($P = 0.03$) indicated their negative combined effect on abundance. The termination of questing was assumed as 10 November based on lack of collection and consistent ambient temperature <0ºC. The minimal length of the questing period was 56 days based on the sampling period (15 September–10 November), but this is considered a conservative estimate because larvae were questing on 15 September.

DISCUSSION

Winter tick epizootics are typically considered sporadic events (Samuel 2004) and were undocumented in the northeast until the mid-2000s (Musante et al. 2010); more recently, the frequency of epizootics is unprecedented in the northeast – 5 in 6 years (Jones et al. 2019, Powers 2019, Ellingwood et al. 2020). Not surprisingly, winter tick abundance on the landscape is poorly understood, in part, because epizootics were infrequent or unknown, and the fieldwork associated with measuring tick abundance is labor-intensive. Similarly, little is known about the actual distribution of larval ticks on the landscape relative to the dynamic nature of multiple variables including moose density, habitat/forest diversity, habitat use and movement patterns of moose, and micro-environmental conditions that influence tick survival. This study provides novel information about tick abundance in 2 optimal foraging habitats of moose, length of the larval questing period, and conditions that terminate questing.

Although the average larval abundance on random transects in clear-cuts and partial harvests (0.12 and 0.11 ticks/m^2; Table 1) was similar to that measured previously in New Hampshire (2-year average = 0.11; Bergeron and Pekins 2014), the average abundance on high-use transects was 1.4–3.3 × higher (0.15 and 0.36 ticks/m^2, respectively; Table 1). Further, the maximum abundance on random (1.9 ticks/m^2) and high-use transects (5.52 ticks/m^2) in clear-cuts (Table 1) was considerably higher than that (0.40–0.64 ticks/m^2) measured a decade earlier, and ticks were collected in all clear-cuts whereas ~10% were without ticks in 2008–2009 (Bergeron and Pekins 2014). The average abundance was much higher in Elk Island National Park in Alberta, Canada (1.36 ticks/m^2) in the year preceding a moose die-off (Aalangdong 1994, Samuel 2007), except in week 2 and week 8 in partial harvests (Table 2). It is not clear why the abundance in Alberta was much higher than that measured after the spring 2018 epizootic, and why average abundance in clear-cuts in New Hampshire was relatively stable since 2008–2009 despite multiple epizootics. The data reflect the difficulty and variability associated with measuring larval abundance, but also indicate that larval abundance likely increased over the past decade. Furthermore, the abundance estimates provided here and in Bergeron and Pekins (2014) should be considered conservative for a number of reasons. Most importantly, we have no ability to estimate the efficiency or detection probability of a single drag, but it is improbable that all larvae are collected with a single drag regardless of time of day or environmental conditions. We encourage multiple sampling of transects in future experiments to improve accuracy and abundance estimates.

Predictably, larvae were not distributed evenly within either cut type, as not all transects produced ticks and abundance was higher on high-use transects (Table 1). Both reflect non-random or preferred habitat use by moose, and maximum abundance always occurred on high-use transects in both cut types – 13.45 ticks/m^2 in partial harvests and 5.52 ticks/m^2 in clear-cuts. The similar abundances on random transects in this and the previous regional study (Bergeron and Pekins 2014) indicates that random sampling likely underestimates tick abundance, moose-tick encounter rates, and projected infestation rates. For example, the abundance estimates on positive transects was ~ 2 × higher than the overall average during the principal 6 weeks of questing (Table 3). It is important to recognize that the earlier study reported a regional abundance, whereas this study was within a focal area of ~70 km^2 with a moderate-high moose density experiencing winter tick-associated mortality (Jones et al. 2019).

The effect of winter conditions on questing was evident due to the combined influence of temperature and weather (Drew and Samuel 1985). Specifically, overall abundance declined in both cut and transect types after the snowfall on 24 October (week 6; Table 2, Fig. 4). Although the exposure time at <0°C lasted 3 days (25–27 October), the warm-up on 5 November (weeks 7 and 8) and associated increase in collection rate in partial harvests reflects the resilience of winter ticks at these conditions (Holmes et al. 2018, Addison et al. 2019), particularly on high-use transects in partial harvests

(Table 2). The few larvae collected in week 9 were curled and immobile, characteristics consistent with thermally stressed larvae (Holmes et. al. 2018), and were presumably collected due to their claw-like appendages.

As Addison et al. (2019), we found that a short-term warmup after an initial snowfall resulted in a temporary increase in larval collection, specifically in partial harvests, indicating that prolonged (multi-day) winter weather is necessary to terminate questing. Some larvae may have been protected within insulative layers/gaps in the more complex vegetative/stand structure of partial harvests than in more open clearcuts. Eventually, sustained below-freezing temperatures and snow cover were lethal to questing ticks in all plots.

Preferential habitat use by moose is well documented in northeastern forests (Scarpitti et al. 2005, Wattles and DeStefano 2013), as is selective use of regenerating forest habitat during the autumn questing and spring drop-off seasons of winter ticks (Healy et al. 2018). Open, regenerating habitat presumably provides higher relative survival of larvae that decline in abundance and survival as canopy cover exceeds 60% (Drew and Samuel 1986, Aalangdong 1994, Terry 2015, Addison et al. 2016). Abnormally dry and drought-like conditions in late summer and early autumn can measurably reduce larval survival (Dunfey-Ball 2017), but less so in closed canopy habitat (Addison et al. 2016). Partial harvests arguably provide an optimal mix of foraging (open) and bedding (canopy) habitat for moose, an optimal mix of microhabitats to sustain egg and larval abundance of winter ticks in a range of environmental conditions, and subsequently, an optimal transmission nidus that sustains winter tick infestation of moose.

Although a moose-tick encounter rate was not measured, the stable abundance measured throughout the questing period is potentially useful to estimate the final infestation (index) at the termination of questing. Infestation is measured on the shoulder and rump of harvested moose (Sine et al. 2009, Bergeron and Pekins 2014) in October in Maine, New Hampshire, and Vermont to produce an annual harvest index that is correlated with the probability of winter tick-associated mortality of calves (Dunfey-Ball 2017). However, a stronger relationship exists between a similar index measured on January-captured calves of known fate (Ellingwood et al. 2019, Jones et al. 2019). Assuming the infestation rate is stable throughout the questing period (as reflected by the stable abundance measured here), the harvest index could be extrapolated to a final index by assuming two dates: 1) the start date of the questing period and 2) the date that questing terminates due to environmental conditions. The extrapolated final index could be substituted for the January index to better predict survival of calves, assuming that larvae and nymphs are not measurably reduced by grooming prior to early January; however, this assumption may be invalid as experimentally infested (larvae) captive moose groomed throughout autumn (Addison et al. 2019). Ongoing analyses are exploring the potential accuracy and usefulness of such an approach.

The variability in tick abundance by cut and transect type not only reflects areas of lower and higher infestation risk, but also, that relative risk reflects individual differences in activity, foraging behavior, and habitat use by moose. Likewise, the annual infestation on harvested moose varies considerably by sex and age (Samuel and Barker 1979, Drew and Samuel 1985, Bergeron and Pekins 2014), and for calves, mortality is directly related to the level of individual infestation (Ellingwood et al. 2019). Those calves surviving in an epizootic year presumably reflect local variance in tick abundance, relative infestation risk, and individual habitat use within the epizootic area.

Using previous larval abundance estimates (Bergeron and Pekins 2014) in an agent-based model based upon availability of local regenerating (cut) habitat and its use by radio-collared moose, Healy et al. (2020) predicted calf mortality similar to that measured in the field (Jones et al. 2019). The strong influence of preferential habitat use on infestation was supported by this modeling exercise that restricted moose-tick encounters to cut habitat that was <20% of the home range of moose. The higher larval abundances reported here suggest that predictions of Healey et al. (2020) were conservative and that proportionally small, yet high-use travel routes and foraging areas within cuts provide the nexus for high infestations on moose.

Interestingly, differences in moose and tick response to clear-cuts and partial harvests might lead to differences in the adjacent states of Maine and New Hampshire. Forest harvest regulations enacted in the 1989 State Practices Act of Maine effectively restricted size of clear-cuts in response to extensive salvage operations associated with the regional outbreak of spruce budworm (*Choristoneura spp.*); ironically, moose expansion in the northeast was spurred by these operations (Bontaites and Gustafson 1993, Wattles and DeStefano 2011, Dunfey-Ball 2017). However, timber removal has since increased not declined in Maine because the footprint of forest harvesting has expanded as partial harvests have increased >90% (MFS 2016). These harvest regulations may have increased and sustained high availability of more preferred/optimal habitat and moose density, while inadvertently increasing local tick abundance, infestation rate of moose, and the probability of an epizootic during warming weather and environmental conditions that simultaneously benefit winter ticks.

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