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**Assessing the Relationships of Winter Ticks, Weather and a Declining Moose Population in
Northern New Hampshire**

BY

Brent Illig Powers

B.S., University of New Hampshire, 2009

THESIS

Submitted to the University of New Hampshire in

Partial Fulfillment of

the Requirements for the Degree of

Master of Science in

Natural Resources: Wildlife and Conservation Biology

December 2019

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:

Thesis Director, Dr. Peter J. Pekins
Professor of Wildlife and Conservation Biology

Dr. Mark Ducey
Professor of Forest Biometrics
Department Chair: Natural Resources

Dan Bergeron, New Hampshire Fish and Game
Department - White-tailed Deer Project Leader

24 October, 2019

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

Dedication

I dedicate this work in honor of my father, Michael Powers, because he is responsible for introducing me to the outdoors. He has always been my biggest supporter and pushed me to pursue my passion for wildlife conservation. Prior to embarking on the path towards a Master's degree I asked him what he thought of it, he told me I would be a fool not to take advantage of this opportunity, he was right.

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devotion to the work is truly inspiring as is his commitment to helping me see this thesis through to the end. I am honored to have had the opportunity to study under him.

I want to specially acknowledge my fellow graduate students and friends, Caroline Kanaskie, Nate Roe, Chad Hammer, and Dan Ellingwood. These individuals shared in my graduate school experience and am forever grateful for their interest in me, my research and their friendship. A very special thank you to my field technicians Owen McGovern, Pat Fitzgibbons, Robyn Parker, Cody Simmons, Brianna Bousquet, Jenna O'Del, Preston Massingham, Oliva Fortuna, Alicia Miller, Mike Voggt, Chase Cody, Garrett Phillips and Sean Skinner, without your enthusiasm and dedication this work would not have been possible. I also owe a huge thank you to my former co-workers and friends at the Massachusetts Natural Heritage and Endangered Species Program specifically, Dr. Peter Hazelton, David Paulson, and Misty-Anne Marold who pushed me to pursue a higher level of education and offered support whenever I needed it.

Lastly, I want to thank my family and Amanda Weise. Without their support I would not have had the strength to finish this work. When there was no end in sight they were my motivation and inspiration to carry on. They sacrificed as much as I have to help me see my dream come true. Words alone cannot express my gratitude and sincere thanks to them.

List of Tables

Table 1.1: Field abundance (ticks/m ²) of larval ticks collected in 15 September – 10 November 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).....	11
Table 1.2: 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).....	12
Table 1.3: Weekly larval tick abundance (ticks/m ²) from 15 September to 10 November 2018, Berlin, NH. Transect type indicated by “Random” and “High-use” within both cut types.....	15
Table 2.1: Productivity parameters of radio-collared adult cow moose in northern New Hampshire 2014-2019. Sample size in parenthesis. *denotes epizootic year	42
Table 2.2: Summary of body weights (kg) of moose calves capture din January 2016-2018 in northern New Hampshire. *Males were significantly heavier than females each year.....	45
Table 2.3: Tick abundance on cow and calf moose captured in January in northern New Hampshire (2014-2018). Abundance equals the total count on 8, 10-cm transects, 4 at the shoulder and 4 on the rump. *denotes epizootic year.....	47
Table 2.4: Proportion of moose calves with tick abundance >37 at January capture, 2014-2018. Tick abundance is the combined # of ticks counted along 8, 10-cm transects at the shoulder and	

rump. Epizootics (>50% calf mortality) occurred in 2014, 2015, 2016, and 2018. *denotes epizootic year.....48

Table 2.5: Annual percent calf and adult moose survival in northern New Hampshire from 2014-2019. *denotes epizootic year.....49

Table 2.6: Summary of UN:C ratios of snow-urine samples (n) from moose in 2014-2017, New Hampshire, USA. Original UN:C data are presented here with statistical comparisons made after data were log transformed. Dead calves had significantly higher ($P < 0.05$;) UN:C ratios from late February onwards. Table 2.6 from Ellingwood et al. 2019 (Table 1.)50

Table 2.7: Winter (January – April) survival of radio-marked male and female calves in 2014-2018. *denotes epizootic year.....52

Table 2.8: Percentage of collar loss and cause of mortality of radio-marked adult and calf moose in northern New Hampshire, 2014–2019.....53

List of Figures

Figure 1.1: Pre-established clear-cut tick dragging plots and high-use transect distribution in Jericho State Park Berlin, NH.....7

Figure 1.2: Pre-established partial harvest tick dragging plots and high-use transect distribution in Jericho State Park Berlin, NH.....8

Figure 1.3: Weekly abundance in sampled clear-cut and partial harvests from 15 September – 10 November 2018, Berlin, NH.....13

Figure 1.4: Autumn 2018 daily average snow depth in Berlin, NH from 19 October – 16 November.....	17
Figure 1.5: Average daily temperatures in clear-cuts and partial harvests from 15 September – 18 November 2018 in Jericho State Park Berlin, NH.....	19
Figure 1.6: 6-week abundance in sampled clear-cut and partial harvests from 15 September – 26 October 2018, Berlin, NH.....	16
Figure 2.1: Study area of moose research project in the North and White Mountains Region, specifically the eastern half of Wildlife Management Units (WMU) B & C1, and all of WMU C2, in Coos County, New Hampshire.....	32
Figure 2.2: Parturition date of radio-marked cows in northern New Hampshire from 2014-2019.....	37
Figure 2.3: Average tick abundance on radio-marked adult cow and calf moose at January captures (2014-2018). Abundance is equal to the total count of ticks along 8, 10 cm transects at the shoulder and rump. An epizootic occurred each year except 2017 where infestation were lowest overall.....	43
Figure 2.4: Number of radio-marked calf mortalities by month (2014-2018). Mortalities peak during the primary feeding period of adult female winter ticks (March through April).....	48
Figure 2.5: Timing of annual neonate moose mortality in northern NH from 2014 – 2019.....	52
Figure 2.6: Timing of annual adult moose mortality in northern NH from 2014 – 2019.....	54
Figure 2.7: Timing of annual adult moose mortality in northern NH from 2014 – 2019.....	55

Abstract

ASSESSING ABUNDANCE AND QUESTING BEHAVIOR OF WINTER TICKS (*DERMENCENTOR ALBIPICTUS*) IN NORTHERN NEW HAMPSHIRE.

by

Brent Illig Powers

University of New Hampshire

December, 2019

Recent decline in New Hampshire's moose (*Alces alces*) population is attributed to parasitism by winter ticks (*Dermacentor albipictus*) associated with high calf mortality and reduced adult cow productivity. Research has focused mainly on moose (host) population dynamics with minimal study of abundance and distribution of winter ticks (parasite) on the landscape. Importantly, tick location is dictated by where ticks drop from moose in April, when they principally forage in regenerating forest. This research was designed with 4 primary objectives: 1) measure and compare larval abundance in 2 types of regenerating forest habitat (clear-cuts and partial harvests), 2) measure and compare larval abundance on 2 transect types (random and high-use) within the 2 cut habitat types, 3) estimate the length of the larval questing period, and 4) measure the microclimate within cut habitats to evaluate conditions associated with termination of the larval questing period. Ticks were not evenly distributed within preferred habitat as larvae were collected on 50.5% of all transects combined; proportionally, 57.5% of transects in clear-cuts and 44.3% in partial cuts had larvae. The average abundance (by cut and transect types) ranged from 0.11-0.36 ticks/m², similar to that measured in 2008-2009

when moose density was 40% higher; however, the maximum values in individual cuts were up to 10x higher than those measured earlier. Abundance was highest on high-use transects and in partial cuts. No difference in abundance was found between cut or transect type when eliminating tickless transects. Abundance or weekly collection rate was stable until the onset of temperatures $< 0^{\circ}\text{C}$ and multiple days of snow cover, after which abundance decreased in all cut and transect types except high-use transects in partial harvests. Questing slowed during an initial snow of ~15 cm in late October but resumed on these transects during a warmup indicating the relative hardiness of larvae; it terminated permanently at the onset of permanent snow cover and prolonged cold in early November. The higher abundance of winter ticks in partial harvests suggest that moose may prefer or spend proportionally more time in partial harvests than clear-cuts. Predicting the final infestation rate on moose is theoretically possible by relating the stable collection rate, infestation level of moose harvested in late October, and length of the questing period.

Table of Contents

Dedication	iii
Acknowledgments.....	iii
List of Tables	v
List of Figures	vi
Abstract.....	viii
Chapter One. Estimating Abundance, Distribution, and Questing Period of Winter Ticks.	1
Introduction	1
Objectives.....	3
Methods.....	4
Analysis	7
Results.....	8
Discussion.....	17
Conclusions	24
Chapter Two: Population Characteristics of Marked Moose in Northern New Hampshire (2014-2019)	26
Introduction	26
POPULATION DYNAMICS OF MOOSE.....	28
WINTER TICK ECOLOGY	30
Objectives.....	34
Study Area.....	35
Methods.....	37
MOOSE CAPTURE	37
MEASUREMENTS AT CAPTURE.....	37
Weight.....	37
Tick Abundance.....	38
Physical Condition.....	38
MONITORING	38
MORTALITY.....	39

SNOW URINE COLLECTION.....	39
Results.....	40
PREGNANCY RATE (2014-2018)	40
PARTURITION (2014-2019).....	41
CALVING RATE (2014-2019)	42
SUCCESSIVE CALVING RATE (2015-2019).....	43
CALF BODY WEIGHT - JANUARY CAPTURES (2016-2018)	44
PHYSICAL ASSESSMENT OF CALVES - JANUARY CAPTURES (2014-2018).....	45
WINTER TICK INFESTATION AT CAPTURE (2014-2018).....	45
SNOW URINE ANALYSIS – UN:C RATIOS (2014-2017).....	48
CALF SURVIVAL – WINTER (2014-2018)	50
NEONATE SURVIVAL - SUMMER (2014-2019).....	52
ADULT SURVIVAL (2014-2019)	53
CONCLUSIONS & MANAGEMENT STRATEGIES.....	54
Literature Cited	61
Appendix	67
APPENDIX A: INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE APPROVAL.....	67

Chapter One. Estimating Abundance, Distribution, and Questing Period of Winter Ticks.

Introduction

The recent influence of winter ticks (*Dermacentor albipictus*) on moose (*Alces alces*) population dynamics in the northeastern United States (northeast) is well documented (Musante et al. 2010, Bergeron et al. 2013, Jones et al. 2017, 2019). 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 further 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, Healey et al. 2018, Jones et al. 2017, 2019). However, few studies have attempted to measure field abundance of winter ticks (Drew and Samuel 1985, Aalooongdang 1994, Addison et al. 2016), with only a single study in the northeast (Bergeron and Pekins 2014).

The winter tick is a single-host ectoparasite of moose throughout its range south of 60° N latitude (Samuel 2004). It also parasitizes other ungulates including elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus*); however, moose tend to have the highest levels of infestation and related impacts (Welch et al. 1991). At high infestation levels, winter ticks can consume blood volumes potentially fatal to calf/yearling moose, cause irritation and excessive grooming resulting in substantial hair loss, induce skin inflammation and

ulcers, and reduce appetite (McLaughlin and Addison 1988, Samuel 1991, Mooring and Samuel 1998, Samuel 2004, Musante et al. 2007). Although annual calf mortality associated with winter ticks is not unexpected in moderate-high density moose populations, the current frequency of epizootics in the northeast is unprecedented, occurring annually since 2014 with the stark result of ~70% annual calf (10–11 months old) mortality in northern New Hampshire and western Maine (Jones et al. 2019). Understanding the relationship between an expanded larval questing period and high infestation rates, and the influence on mortality and productivity of moose is critically important to develop effective management strategies for moose populations in the northeast.

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 2004, 2007, Bergeron and Pekins 2014). Further, Drew and Samuel (1985, 1986) found that 85% of adult winter ticks were located within 60 cm of a moose carcass, and larvae with limited mobility are typically found within 1 meter of their hatching location where they ascend nearby vegetation the following autumn (Drew and Samuel 1985). In laboratory conditions, Yoder et al. (2016) found that larval ticks displayed limited mobility and only crawled ~1 meter. Recruitment of larval ticks is highest in open habitat versus closed canopy deciduous forest, except in hot and dry weather conditions (Addison et al. 2016). Effectively, where an adult female tick drops from the host moose is the site of egg deposition, hatching, and larval questing. Therefore, the distribution and questing locations of winter ticks is where adult ticks dropped from moose the previous March-April.

In spring and autumn moose preferentially use young, regenerating forest habitat (4-16 years old) more than other cover types (Scarpitti et al. 2005, Healey et al. 2018). Therefore, the

distribution and abundance of winter ticks should be higher in this preferred habitat, and the relative exposure of moose to winter ticks is related to their seasonal habitat use. Healey et al. (2018) also demonstrated a high degree of overlap in use of specific cuts during spring and autumn by the same animals, suggesting a positive feedback loop of infestation. 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 epizootic. My study was designed to measure larval abundance in preferred cut habitat following an epizootic in spring 2018 (61% calf mortality) when tick abundance would presumably be high.

Objectives

The overall objective of this study was to measure larval abundance of winter ticks in regenerating forest habitat in northern New Hampshire, and to determine the length of the larval questing period. Specific objectives were to:

- 1) measure and compare larval abundance in 2 types of regenerating habitat (clear-cuts and partial harvests),
- 2) measure and compare larval abundance on 2 transect types (random and high-use) within the 2 types of cut habitat,
- 3) estimate the length of the larval questing period, and
- 4) measure the microclimate within cut habitats to evaluate conditions associated with termination of the larval questing period.

Methods

Study plots were established in summer 2018 to measure larval abundance during the questing period in autumn 2018 (September-November). Plots ($n = 44$) were located in Jericho State Park in Berlin, NH and classified as either clear-cut ($n = 22$) or partial harvest ($n = 22$) (Fig. 1.1 and 1.2); each was within an age range associated with preferred foraging habitat (4-10 years) and were 4.04-4.85 ha in size with ample sign of moose use. Classification of plot type was determined from aerial photos and verified by field observation. Clear-cuts were defined as areas where timber harvesting removed all living trees resulting in an even-aged stand of regenerating forest (Oliver and Larson 1996). Further, the clear-cut category also included openings with minor reserves deemed inconsequential as cover for moose and too small to categorize as a partial harvest. Partial harvests were considered analogues with geometric thinning (i.e., strips) and group selection system or similar harvest that resulted in an uneven-aged stand with at least 50% of the residual stand uncut (Oliver and Larson 1996). Field observations indicated that partial harvests almost always resemble geometric thinning or irregular shelterwood harvest systems (e.g., 3 entries with a preparatory, establishment, and final removal cut). The combination of aerial photo interpretation, ground observation, and silvicultural description was used to assign cut classifications; given this approach, reserve size in clear-cuts was not measured. 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).

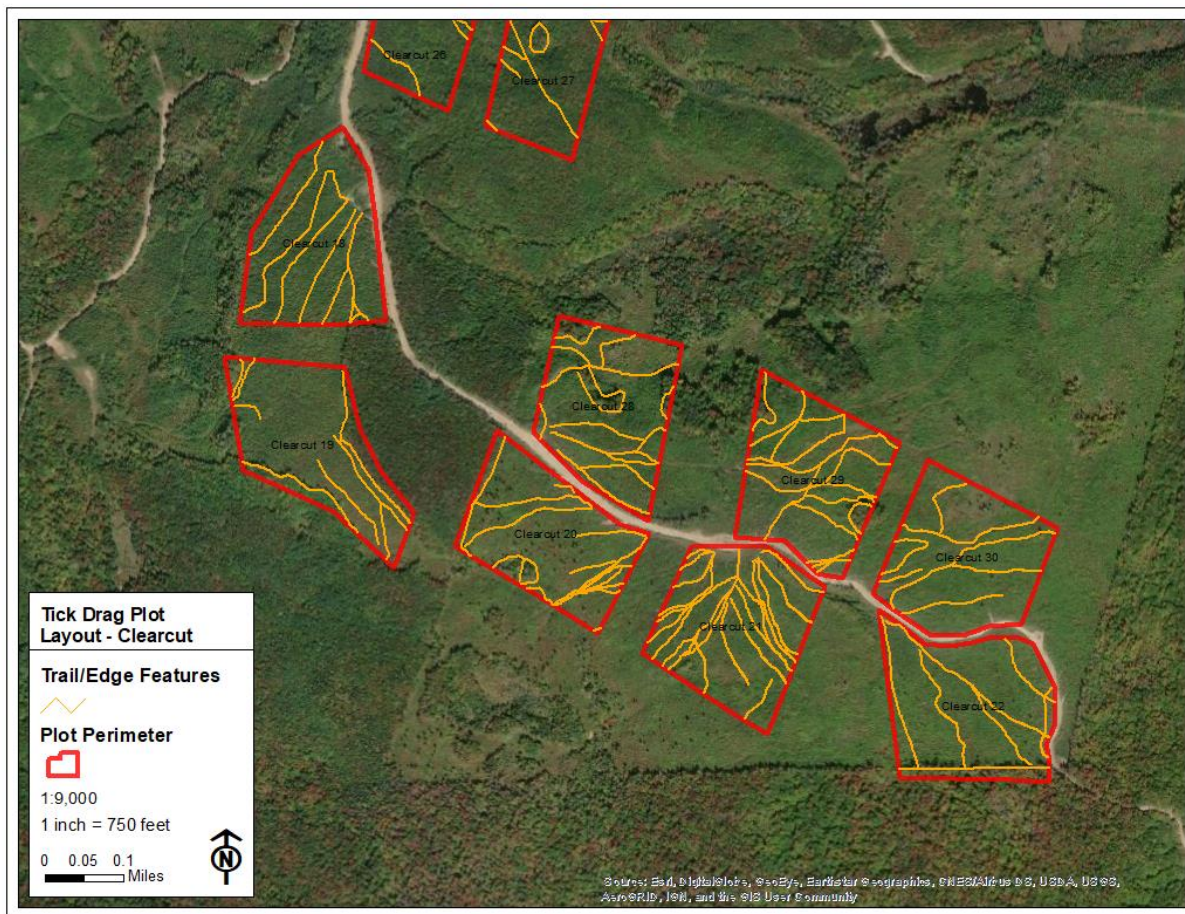


Figure 1.1 Pre-established clear-cut tick dragging plots and high-use transect distribution in Jericho State Park Berlin, NH.

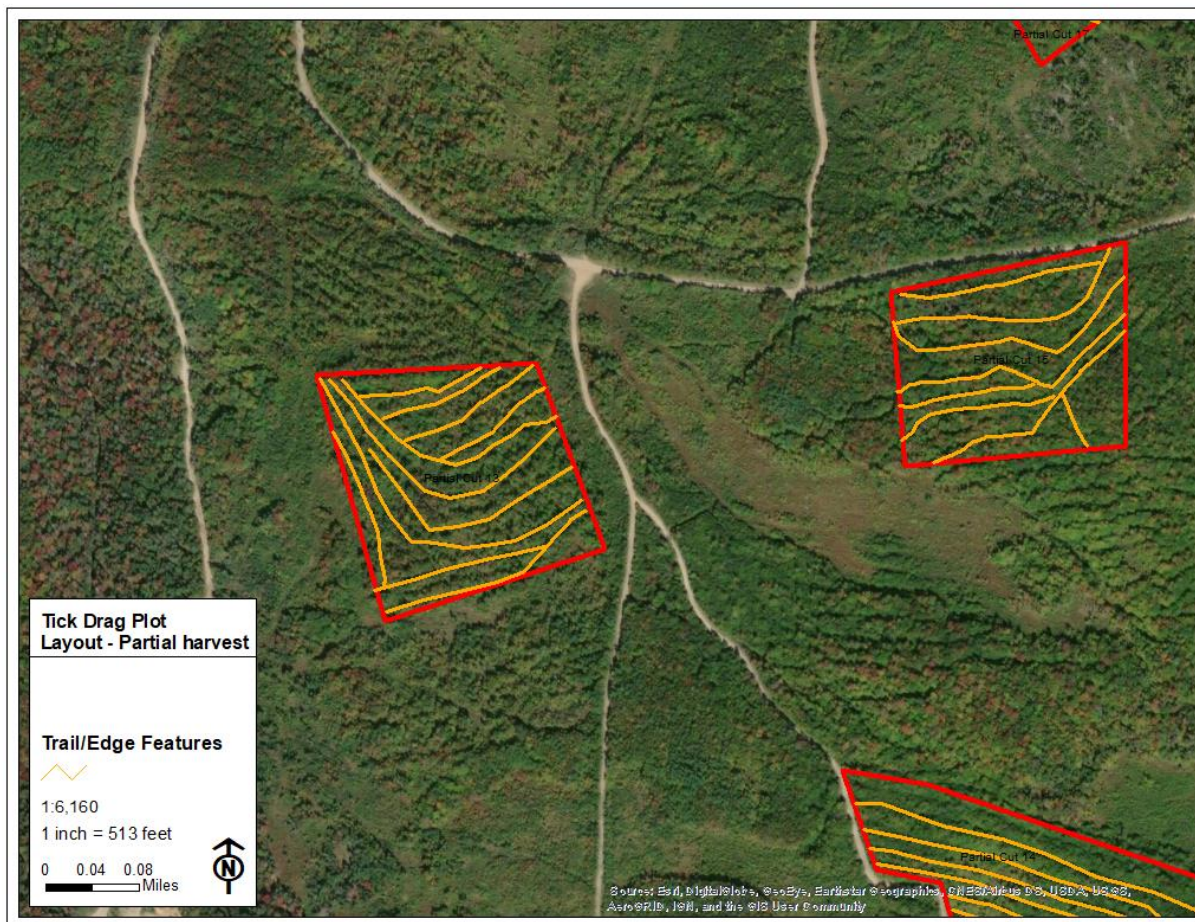


Figure 1.2 Pre-established partial harvest tick dragging plots and high-use transect distribution in Jericho State Park Berlin, NH.

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. 1.1 and 1.2). This sampling approach was adopted to measure overall (random) tick abundance in preferred habitat, and localized abundance in high-use areas within those habitats. It was presumed that random sampling underestimates the relative exposure of moose to larval ticks because use and movement by moose within preferred habitats is non-random. Tick

location and relative abundance should reflect concentrated use of preferred habitat in spring where engorged adult female ticks drop, lay eggs, and larvae hatch and subsequently quest for a host.

Each plot was sampled at least 12 times during the questing season (~mid-September through mid-November); sampling continued until active larval ticks were no longer collected. Plots were sampled bi-weekly with at least 4 transects (2 random, 2 heavy use) measured per visit. The sampling procedure followed the basic flagging technique used by others (Drew and Samuel 1985, Piesman et al. 1986, Ginsberg and Ewing 1989, Aalongdong 1994, Bergeron and Pekins 2014, Addison et al. 2016). A 1 m² cotton cloth was dragged over vegetation to collect questing larvae, and each flag was bagged (plastic ziplock) at the end of each transect. Following an entire count of larvae on each flag, abundance (ticks/m²) was calculated based on transect area (area = transect length (m) x 1 m²).

A subset of plots (4 clear-cut and 4 partial harvest) were monitored continuously with remote dataloggers that measured hourly temperature from mid-August thru 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 abundance data exhibited the typical field-sampling problem of “zero-inflated” data, as ~50% of transects were tick-less (i.e., zero transects); therefore, the data were analyzed using

a hurdle or “two-stage” linear model. The first stage was to conduct a logistic model with a binary form of all the transect data including the zero transects; data were not log-transformed. In the second stage, the zero transect data were removed and only positive transects were analyzed with the linear model. After testing for normality of these data, data were subsequently log-transformed to fit a normal distribution. This analysis was used to determine if larval abundance was different between clear-cuts and partial harvests, and between random and high-use transects within cuts.

Temporal analysis of larval abundance, 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, and plot type; the random effect variable was plot. Data analysis was performed in Program R (ver. 3.4.4, Austria).

Ambient temperature (accuracy +/- 0.5 °C) was expressed and analyzed using basic summary statistics. The average daily temperature was used in conjunction with the abundance data to analyze temporal factors possibly influencing larval abundance within the linear mixed-effects model. A t-test was used to compare temperature between plot types. Analysis was performed in Program R (ver. 3.4.4, Austria).

Results

A total of 589 transects were measured in 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 1.1). Larval questing had initiated at the start of dragging on 15 September 2018. Larvae were collected on 50.5% of all transects combined; proportionally, 57.5% of transects in clear-cuts and 44.3% in partial harvests were positive.

Table 1.1 Field abundance (ticks/m²) of larval ticks collected in 15 September – 10 November 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)
n (transects)	140	138	155	156
Transect length (m)	74 – 321	28 – 322	70 – 322	45 - 322
Mean 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 only				
n (transects)	74	86	66	72
Abundance (se)	0.22 (0.04)	0.25 (0.06)	0.27 (0.23)	0.81 (0.29)
Range	1 – 459	1 – 975	1 – 527	1 – 2554

Larval abundance was calculated as ticks/m² to provide a relative abundance level to compare within and between cut types and transects. The absolute number of larvae collected per transect ranged from 0 – 2,554 larvae and was similar to absolute number of larvae (0 - 2,212) measured in 2008-2009 (Bergeron and Pekins 2014). For combined data, average and maximum larval abundance was greater on high-use than random transects in clear-cuts (0.3 and 2.9x) and partial harvests (3.3 and 3.3x); a similar trend occurred on positive transects only (Table 1.1). Two drags on heavy-use transects in partial harvests (actual counts were 13.23 and 13.44 ticks/m²) elevated the weekly abundance in week 2 (1.25 ticks/m²) and week 8 (0.98 ticks/m²) higher than all other weeks in all other cut and transect types (Table 1.2). These values reflect the

collection of clustered larvae and could be considered outliers relative to average abundance estimation in the other weeks. Interestingly, recalculated abundance without the outliers was similar to other cut and transect types for those weeks (0.10 and 0.05 ticks/m²). However, these outlier values were retained for statistical analysis as they represent a proportionally small yet important characteristic in larvae transmission.

Table 1.2 6-week field abundance (ticks/m²) 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)
n (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
6-week Positive transects only				
n (transects)	53	69	47	52
Abundance (se)	0.27 (0.06)	0.30 (0.08)	0.30 (0.10)	0.74 (0.29)
Range	1 – 459	1 – 975	1 – 527	1 – 2554

The first stage of the two-stage logistic model indicated that abundance on all transects combined was 1.8x times higher ($P < 0.05$) in partial harvests (0.24 ± 0.08 ticks/m²) than clear-cuts (0.13 ± 0.03 ticks/m²) (Fig. 1.3). While not statistically significant ($P = 0.13$), a clear trend in both clear-cuts and partial harvests was that abundance on high-use transects (0.15 ± 0.04 and

0.36 ± 0.13 ticks/m²) was measurably higher than on random transects, (0.12 ± 0.02 and 0.11 ± 0.03 ticks/m²) (Table 1.1, Fig. 1.3).

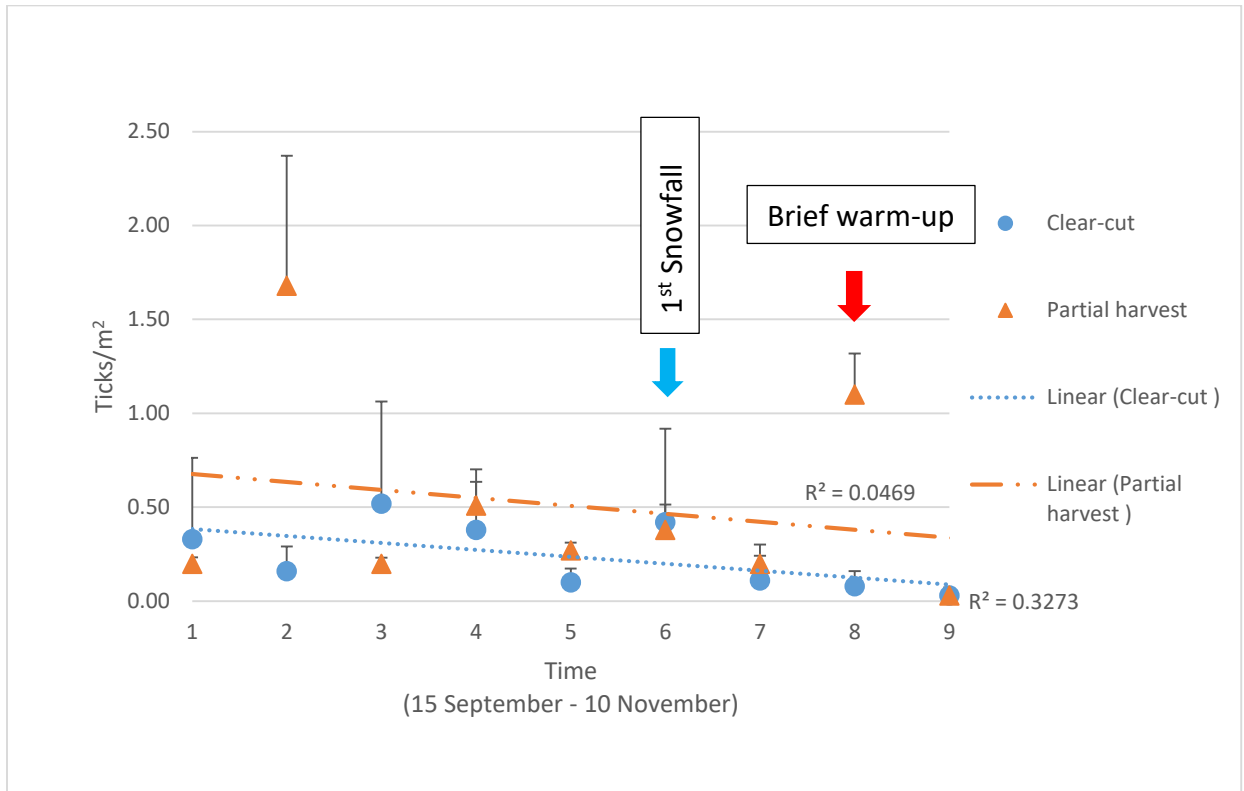


Figure 1.3 Weekly abundance in sampled clear-cut and partial harvests from 15 September – 10 November 2018, Berlin, NH

The second stage model indicated that mean abundance was 2.3x higher ($P = 0.05$) in partial harvests (0.54 ± 0.35 ticks/m²) than clear-cuts (0.24 ± 0.11 ticks/m²) (Table 1.1). In clear-cuts, abundance was similar ($P = 0.47$) on random (0.22 ± 0.04 ticks/m²) and high-use transects (0.25 ± 0.06 ticks/m²). In contrast, abundance was higher ($P < 0.05$) on high-use (0.81 ± 0.29 ticks/m²) than random transects (0.27 ± 0.23 ticks/m²) in partial harvests (Table 1.1).

Because of the obvious decline in abundance from week 6 to week 7 due to a snow event and reduced temperature (except for high-use transects in partial harvests), the logistic regressions were rerun for the 6 weeks prior. The first stage model using the 6-week data indicated that abundance was 1.7x higher ($P = 0.01$) in partial harvests (0.25 ± 0.08 ticks/m²) than clear-cuts (0.15 ± 0.03 ticks/m²) (Table 1.2). Similarly, higher abundance ($P = 0.02$) occurred on high-use transects (0.36 ± 0.15 ticks/m²) than random transects (0.14 ± 0.05 ticks/m²) in partial harvests and in clear-cuts (0.17 ± 0.03 and 0.14 ± 0.03 ticks/m²). Abundance on random transects in both cut types was similar (0.14 ticks/m²) (Table 1.2). Interestingly, the second stage of the model indicated that abundance was 1.9x higher ($P = 0.03$) in partial harvests (0.54 ± 0.16 ticks/m²) than clear-cuts (0.28 ± 0.05 ticks/m²), but transect type had no effect on abundance ($P = 0.90$) (Table 1.2). Absolute abundance on high-use transects was always higher than on random transects in clear-cuts (0.30 and 0.27 ticks/m²) and partial harvests (0.74 and 0.30 ticks/m²) (Table 1.2).

Weekly abundance on plots and transects was calculated over the 9-week measurement period (Table 1.3). Considering absolute larval abundance over time, average weekly abundance in the first 6 weeks was always highest on high-use transects (2x in clear-cuts and 3x in partial harvests) except in week 1 (random – clear-cut). Weekly abundance was > 0.17 ticks/m² in all 6 weeks on high-use transects in partial harvests, but only 3 of 6 weeks in clear-cuts. The most substantial difference was in week 8 (warm-up after snow) when abundance on high-use transects in partial harvests was the second highest measured (0.98 ticks/m²); all other types were < 0.03 ticks/m² (Table 1.3).

Table 1.3 Weekly larval tick abundance (ticks/m²) from 15 September to 10 November 2018, Berlin, NH. Transect type indicated by “Random” and “High-use” within both cut types.

	Clear-cut Random (Ticks/m²)	SE	Clear-cut High-use (Ticks/m²)	SE	Partial Harvest Random (Ticks/m²)	SE	Partial Harvest High- use (Ticks/m²)	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

Weekly abundance on positive transects over the 9-week measurement period was used to assess temporal relationships because the potential infestation rate of moose is presumably correlated with relative abundance of larvae. Because snow abruptly reduced the collection rate (abundance) in week 7, temporal abundance in the previous 6 weeks was also evaluated separately. The first step was to investigate the temporal pattern of abundance with linear and polynomial regression analyses across the 9 weeks, and the second step was to test the slope of the linear relationship in the first 6 weeks to determine if abundance was constant (i.e., slope = 0) prior to the week 7 snow.

Both cut types yielded reasonably significant ($P < 0.10$) relationships across the 9 weeks, but neither the linear or polynomial regressions indicated a strong predictive relationship (i.e., poor R^2 ; range = 0.04 to 0.32) (Fig 1.3). The slope of the 6-week linear regressions in clear-cuts -0.06 (CI range = -0.19 to 0.40) and partial harvests -0.02 (CI range = -0.52 to 1.28) was not

different than 0, or that weekly abundance was stable ($P < 0.05$) for both cut type and transect type (Fig. 1.6).

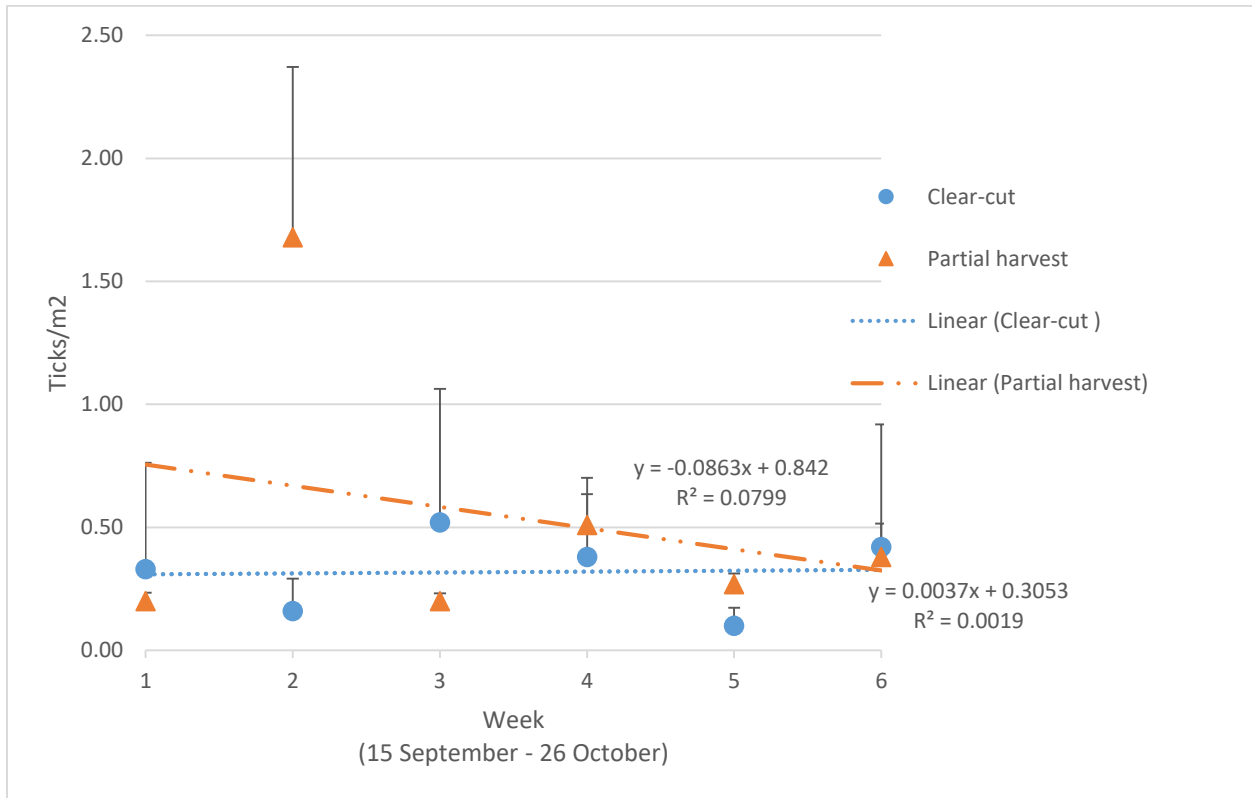


Figure 1.6 6-week abundance in sampled clear-cut and partial harvests from 15 September – 26 October 2018, Berlin, NH

With the onset of cold temperatures and snow in late October (week 7), abundance declined in each plot and transect type. However, a temporary increase in activity and collection occurred on 5 November (week 8) in partial harvests only when ambient temperature rose to 8.5 °C (Fig. 1.3); abundance in clear-cuts did not increase concurrently (Table 1.3). By 10 November (week 9, Fig. 1.3), abundance was determined as functionally zero based on lack of larval

capture and the obvious (observed) inability of larvae to crawl. This decline in abundance was correlated with date in both cut types ($P = 0.002$).

Ambient temperature ranged from -22 to 34 °C in clear-cuts and from -20 to 28 °C in partial harvests from 15 August to 20 November. Daily high temperature was recorded in early afternoon most days after the solar maximum occurred (~ 1300 hr), and the minimal nocturnal temperature occurred in early morning (~ 0500 hr) (Fig 1.5). Diurnal ambient temperature declined to < 0 °C on 1 November which coincided with a snowfall event. Temperature was consistently < 0 °C in November with continuous snow cover of 25–45 cm (Fig. 1.4).

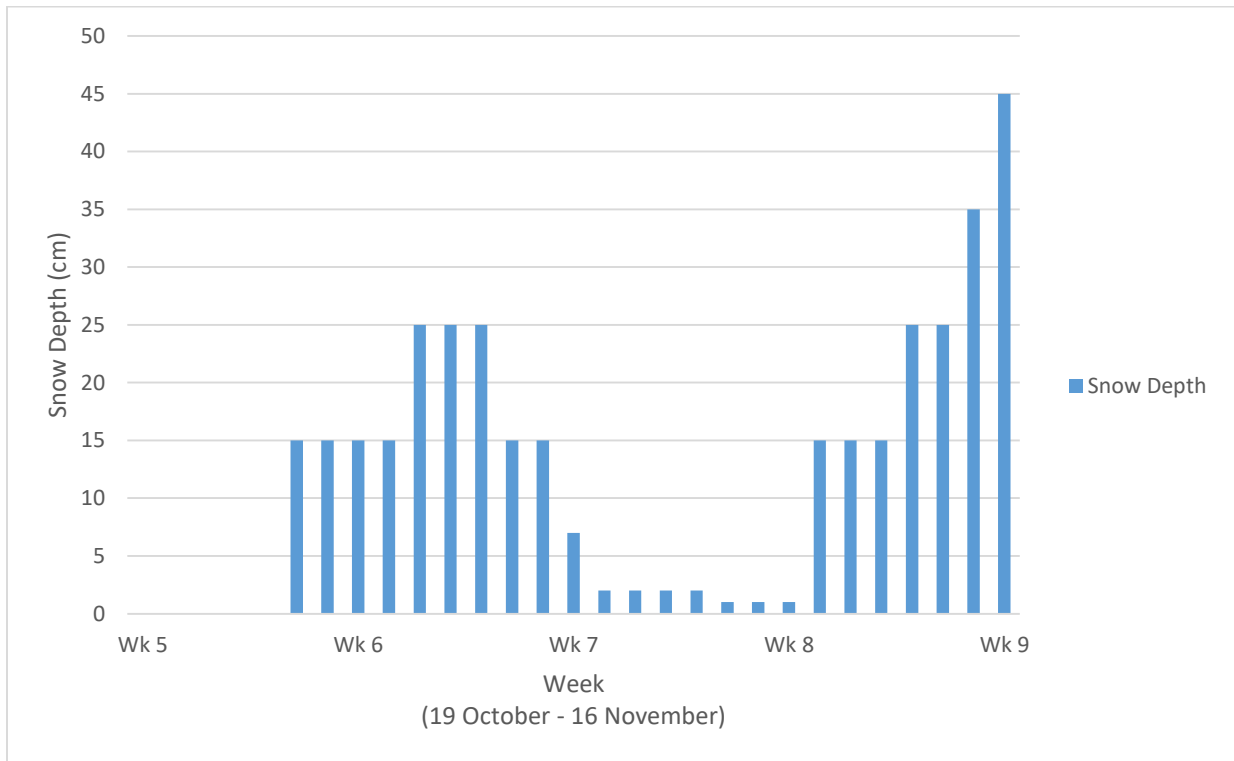


Figure 1.4 Autumn 2018 daily average snow depth in Berlin, NH from 19 October – 16 November.

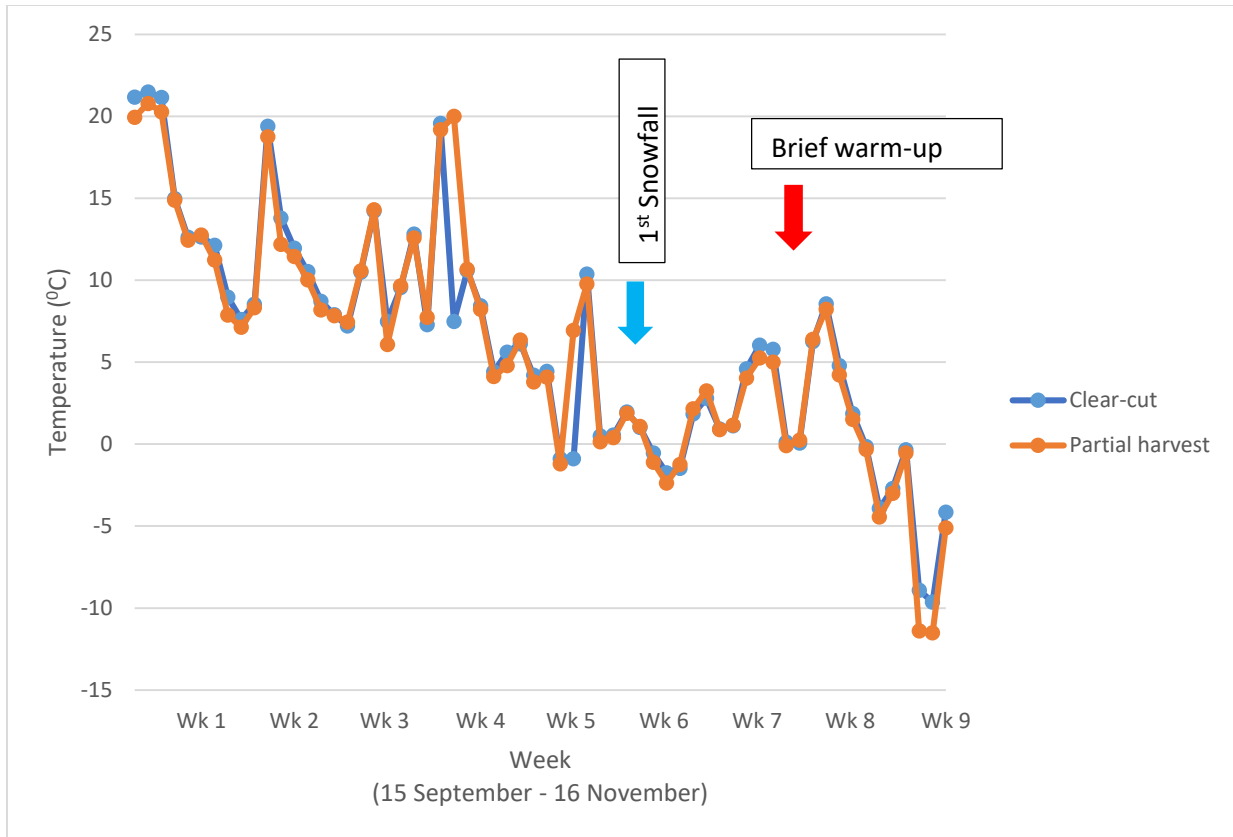


Figure 1.5 Average daily temperatures in clear-cuts and partial harvests from 15 September – 16 November 2018 in Jericho State Park Berlin, NH

Declines in abundance in both cut and transect type from 15 September to 20 November were correlated with date ($P = 0.002$) (Fig. 1.3). No individual effect was found with temperature or snow depth ($P > 0.05$); however, a significant interaction effect ($P = 0.03$) of temperature and snow depth was found indicating their negative combined effect on abundance. A marked decline in larval collection occurred immediately following the first snowfall, although some larvae were collected thereafter. The onset of sustained snow cover and temperature $< 0^{\circ}\text{C}$ coincided with a decline in larval abundance ($P < 0.05$). In conditions of $< 0^{\circ}\text{C}$ and snow cover, collected larvae had limited mobility with appendages curled against the body. The termination of questing was assumed as 10 November based on lack of collection and consistent daily

temperature. The minimal length of the questing period was 56 days based on the sampling period (15 September – 10 November), but this is a conservative estimate because larvae were already questing on 15 September.

Discussion

Winter tick epizootics are typically considered sporadic events with successive years of epizootics undocumented in the northeast until 2014-2018 (Jones et al. 2019). Perhaps not surprisingly, winter tick abundance on the landscape is poorly understood, in part, because epizootics have been infrequent 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 such as host or 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.

The average larval abundances measured on both transect types (0.12 and 0.15 ticks/m²) in clear-cuts and random transects in partial harvests (0.11 ticks/m²; Table 1.1) were not dissimilar to those measured previously in New Hampshire (2-year average = 0.11; Bergeron and Pekins 2014). However, one novel approach and result of this study was that abundance measured on high-use transects was higher than on random transects (Table 1.1). Also, all plots contained ticks unlike in 2008-2009 when ~ 10% of clear-cuts were without ticks (Bergeron and Pekins 2014). The regional study in 2008-2009 did find differences both annually and across regions presumably caused by differences in moose density and weather (Bergeron and Pekins

2014). Average abundance was much lower than in Elk Island National Park in Alberta, Canada (1.36 ticks/m²) in the year preceding a moose die-off (Aalangdong 1994, Samuel 2007), except in week 2 and week 8 in partial harvests (Table 1.2). It is not clear why the Alberta abundance is much higher than that measured here after the spring 2018 epizootic, and why average abundance in New Hampshire is relatively unchanged since 2008-2009 (Bergeron and Pekins 2014). However, maximum abundances were much higher, ranging from 5.52 to 13.45 ticks/m² on high-use transects in partial harvests (Table 1.1).

The sampling scheme was developed to account for non-random distribution of ticks relative to moose movement and foraging behavior because larvae have limited mobility (i.e., < 1.0 m) and are located where the adult female tick drops from a moose (Drew and Samuel 1985, 1986). 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 1.1, Fig. 1.3), both reflecting non-random habitat use by moose. Maximum abundance always occurred on high-use transects in both cut types - 13.45 ticks/m² in partial harvests and 5.52 ticks/m² in clear-cuts. The similarity of larval abundance measured on random transects in this and the previous regional study (Bergeron and Pekins 2014) indicates that random measurements likely underestimate tick abundance, moose-tick encounter rates, and projected infestation rates. It is important to recognize that the earlier study reported a regional abundance, whereas this study was within a focal area of ~70 km² with a moderate-high moose density experiencing winter tick –associated mortality (Jones et al. 2019).

This study measured tick abundance on random and high-use transects in two distinct areas of preferred moose foraging habitat – clear-cuts and partial harvests - that can be used to calculate abundance estimates in each habitat type. The average tick abundance on random

transects was 0.12 and 0.11 ticks/m² in clear-cuts and partial harvests, respectively (Table 1.1), or 1,200 and 1,100 ticks/ha, respectively. Average abundance on high-use transects was 0.15 and 0.36 ticks/m² in clear-cuts and partial harvests, respectively (Table 1.1), or 1,500 and 3,600 ticks/ha. Finer scale movement data from radio-marked animals would further refine the spatial and temporal aspects of habitat use, tick location, estimates of tick abundance, and risk of infestation.

Larvae are poikilothermic, vigor (i.e., movement) is a function of ambient temperature, and at ~5 °C they are less active (Drew and Samuel 1985, 1986, Holmes et al. 2018). Activity stops, appendages curl, and continued exposure at ~0 °C is lethal (Samuel and Welch 1991). However, they are considered hardy and resilient to freezing until the microclimate is semi-permanent; i.e., 3-5 continuous days of snow cover and/or < 0 °C terminate questing (Drew and Samuel 1985). The effect of winter conditions on questing was identified in the mixed linear effects model in that abundance declined under the combined influence of date and weather (Fig. 1.3). Specifically, after the snowfall on 24 October (week 7, Fig. 1.3), overall abundance declined from 0.42 ticks/m² in clear-cuts and 0.38 ticks/m² in partial harvests in week 6, to 0.11 and 0.20 ticks/m² in week 7 (Table 1.2). However, on high-use transects in partial harvests there was almost no change in abundance for the same time period (0.19 to 0.17 ticks/m²) (Table 1.2). 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 indicated resilience at these conditions. Abundance on random transect increased from 0.03 ticks/m² in week 7 to 0.12 ticks/m² in week 8 and from 0.17 to 0.98 ticks/m² on high-use transects (Table 1.2). No similar increase occurred in clear-cuts presumably due to higher exposure to snow and cold. Although a few larvae were still collected in both cut types in snow and < 0 °C in week 9,

they were curled and immobile, characteristics consistent with thermally stressed larvae (Holmes et. al. 2018), and were presumably collected as a result of their claw-like appendages.

The short-term warmup and temporary increase in larval collection in partial harvests indicated that many larvae survived the first snowfall, and prolonged (multi-day) winter weather is necessary to terminate questing. Because the initial snow did not mat vegetation completely to the ground, it is likely that some larvae were protected by insulative layers/gaps within vegetation, specifically in the partial harvests that have more varied vegetative structure than clear-cuts. Given the reduced collection of larvae in weeks 7-9 in clear-cuts, and the lack of larvae in partial harvests in week 9 and that those collected were immobile, the termination date of the questing period was assumed as 10 November, or 56 days (8 weeks) from the initial date of collection (15 September). Because larvae were questing on 15 September, a more reasonable estimate would be 9-10 weeks or 1 September based on start dates in other studies (Drew and Samuel 1985, Aalongdong 1994, Addison et al. 2016).

Preferential habitat use by moose is well documented in northeastern forests (Scarpitti et al. 2005, Wattles and DeStefano 2013, Bergeron et al. 2014), 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 high relative survival of larvae that decline in abundance and survival as canopy cover exceeds 60% (Drew and Samuel 1986a, Aalongdong 1994, Terry 2015). Although a moose-tick encounter rate was not measured, the data provide a proxy for such and indicate that high-use areas harbor higher concentrations of ticks.

Using previous larval abundance estimates (Bergeron and Pekins 2014) in an agent-based model applied to local cut availability and use by radio-collared moose, Healy (2018) predicted calf mortality similar to that measured in the field (Jones et al. 2019). The strong influence of preferential habitat use on infestation of moose was supported by this modeling exercise that restricted moose-tick encounters to cut habitat that was < 20% of the home range of moose. The larval abundances measured here suggest that Healy's predictions were conservative and that proportionally small, yet high-use travel routes and foraging areas within cuts provide the nexus for high infestations on moose.

Three primary factors that influence the occurrence of an epizootic are moose abundance, tick abundance, and length of the questing period. The recent, unprecedented frequency of epizootics in northern New Hampshire (4 in 5 years from 2014-2018) is somewhat of a conundrum given that moose density is ~40% lower than a decade previous. Further, the current regional density (0.4-0.8 moose/km², NHFG 2015) is much lower than that during epizootics on Isle Royale, Michigan (2.3-3.5 moose/km², DelGiudice et al. 1997) and Elk Island National Park, Ontario (Samuel 2004). Although there was no estimate of the local density in the study area, it was clearly higher than the regional estimate. More importantly, despite both moderate moose density and tick abundance in northern New Hampshire, epizootics continue to occur. Others (Dunfey-Ball 2017, Jones et al 2019) have hypothesized that a longer questing period can counter, on a relative scale, tick abundance considered too low to induce an epizootic.

Regarding length of the questing period (i.e., infestation period), both the influence of annual weather patterns and the constant trend in climate change have been correlated with epizootics in New Hampshire. For example, non-epizootic years were characterized by snowfall ~12 November, whereas in epizootic years, snowfall was delayed until ~25 November or later;

the onset of permanent snow/cold by ~15 November reduces the probability of an epizootic to <50% (Dunfey-Ball 2017). A longer questing period would allow for higher infestation in a lower density of moose, and the data indicate that the relative abundance of larvae is spatially concentrated within high-use areas that increase the encounter rate. This combination seems to support a higher frequency of epizootics that keep infestation levels and subsequent tick abundance consistently high. Despite the one-year life cycle of winter ticks, an epizootic surprisingly occurred in 2018 following a non-epizootic year (30% mortality), indirect evidence that under current environmental conditions, an epizootic can occur across a wide range of moose density and tick abundance.

A management challenge is to develop a method to predict the occurrence of an epizootic from accessible and replicated data. States will not have continued access to January (final) infestation levels on captured calves that are related directly to the probability of mortality (Ellingwood et al. 2019). One possible approach is to combine temporal data related to tick abundance, infestation on harvested moose, and weather. An important finding of this study was that tick abundance, hence presumed infestation rate, was constant until a snow event disrupted questing. Further, the similarity in tick abundance measured in clear-cuts nearly a decade apart suggests that tick abundance is relatively stable across a range of moderate moose density. Each state measures tick infestation on harvested moose in October as an annual index and these data might prove useful to predict a final infestation level. For example, by assuming a questing initiation date (e.g., 1 September), a constant daily infestation rate (ticks/day) can be calculated from the infestation measured at harvest and the number of days since the initiation date; applying that daily infestation rate to the harvest infestation until a weather event terminates questing would produce the final infestation estimate. This approach could also be combined

with establishment and subsequent annual dragging of “permanent” plots to track relative, annual tick abundance as an index.

One primary objective was to determine if tick abundance was related to timber harvest method - clear-cut versus partial harvest. Overall abundance in partial harvests was 1.7x higher than in clear-cuts (Table 1.1), and weekly abundance was also consistently higher (Table 1.3 and Fig. 1.3). Further, high-use transects in partial harvests had markedly higher abundance than those in clear-cuts (Table 1.3, Fig 1.3) with maximum abundance following a similar pattern. Abundance was ~1.9 - 3.3x higher than previous estimates in 2008 and 2009 of 0.16 and 0.07 ticks/m² in northern New Hampshire (Bergeron and Pekins 2014). Although both harvest methods create optimal foraging habitat, these differences imply that partial harvests might produce a preferred combination of forage and cover, and that their juxtaposition concentrates spatial and temporal seasonal use by moose, hence tick abundance. Geospatial analysis of moose location data might identify whether moose prefer partial harvest over clear-cuts and/or moose concentrate their use and time in partial harvests.

Interestingly, differences in moose and tick response to these two forest harvest methods might cause differential landscape responses in Maine and New Hampshire. Forest harvest regulations in Maine enacted in the 1989 State Practices Act effectively restricted size of clear-cuts in response to extensive salvage operations associated with a regional outbreak of spruce budworm (*Choristoneura spp.*); ironically, moose expansion in the northeast was related directly to these salvage operations. However, timber removal has increased not declined in Maine since, because the footprint of timber harvest has expanded as partial harvesting has increased > 90% (MFS 2016). Moose density has remained stable in much of Maine despite the similar frequency of epizootics in northern New Hampshire and western Maine (Jones et al. 2019). It is plausible,

if not ironic, that these harvest regulations might have created more optimal moose habitat and higher moose density, while inadvertently concentrating moose activity that increases local tick abundance and exposure to ticks, thereby increasing the probability of an epizootic.

An exception to this pattern is that despite similar infestation levels on moose, fewer epizootics have occurred in northern than western Maine and northern New Hampshire; albeit, calf mortality is typically >30%. Ellingwood et al. (2019) attributed this to higher calf weights in northern Maine that provide a “survival cushion” of endogenous resources in spring. Of concern, however, is that northern Maine has the highest moose density of the three areas, and it is conceivable that a “time lag” is operating in northern Maine given its earlier starting winters (i.e., shorter questing period). Arguably, the advantage of climate change for winter ticks is most evident in south western Maine and northern New Hampshire where the impact on moose survival and productivity seemingly developed over a decade or more (Musante et al. 2010, Bergeron et al. 2013, Jones et al. 2017, 2019). Because moose density, length and start of winter, and timber harvest activity/methods vary within the northeast, it is clear that the moose-winter tick relationship is complex and that predicting an epizootic is an annual challenge within this relatively small geographic region.

Conclusions

1. Tick abundance was higher in partial harvest than clear-cuts.
2. Tick abundance was higher in high-use than random transects in both cut types.
3. Average tick abundance was similar to that measured a decade previous despite lower moose density.

4. Abundance of larvae through time is stable until a weather event ends the questing season.
5. Questing period is highly influenced by ambient temperature and ends with consistent temperatures $< 0^{\circ}\text{C}$ and snow cover.
6. Micro-level ground conditions after days of ambient temperatures $< 0^{\circ}\text{C}$ and snow cover are not always sufficient to kill all larvae. This study documented a brief second questing period due to the insulating effect of air gaps due to snow cover being elevated above the ground surface due to dense vegetation sufficient to suspend snow cover.
7. Partial harvest may create optimal moose habitat that also concentrates moose activity and subsequent tick abundance that induces more frequent epizootics at moderate moose density.

Chapter Two: Population Characteristics of Marked Moose in Northern New Hampshire (2014-2019)

Introduction

At the turn of the century, the moose (*Alces alces*) population in New Hampshire was in steep decline due to loss of habitat from unregulated logging, extensive agriculture/grazing, and over-hunting. The population has since risen dramatically given reforestation and complete protection from hunting for >75 years. A recent contributing factor to this increase was the creation of high quality foraging habitat as a result of a 1970's spruce budworm (*Choristoneura spp.*) outbreak in northern New England. Salvage logging post-outbreak resulted in large-scale creation of regenerating forest that provided an optimal forage base for the remnant moose population in New Hampshire and expansion from Maine. By the 1990s, the population had expanded statewide with the New Hampshire Fish and Game Department reinstating a regulated moose hunt in 1988 (Bontaities et al. 2000).

At its peak, the New Hampshire moose population was estimated at ~8000 animals. With its resurgence, the population brought increased monitoring and study that eventually identified the impact of winter ticks (*Dermacentor albipictus*) as a measureable mortality factor. The first documented epizootic (>50% calf mortality) occurred in 2002 (Musante et al. 2010) and field observations in the Northeast (ME, NH, VT) in 2008 and 2011 (Bergeron et al. 2013), and data from this study (2014-2019; Ellingwood 2018, Jones et al. 2019) have identified the significant regional impact of winter ticks on moose. Since the mid-2000s, the population has slowly declined due to successive years of high calf mortality at a rate beyond the expected retraction of the overall population following expansion. Additionally, yearling and adult cow productivity

has declined due to the metabolic drain of annual infestation (Bergeron et al. 2013, Jones et al. 2017, 2019). Although the occasional epizootic has little long-term impact on a local population, the current trend of frequent and successive epizootics in New Hampshire (5 in 6 years - 2014-2019) is unprecedented and linked directly to the ~30-40% decline in the moose population (Musante et al. 2010, Bergeron and Pekins 2014, Jones et al. 2017, 2019). The density of the northern New Hampshire moose population now ranges from 0.46-0.87 moose/km² (NHFG 2015), about half the peak density.

Calf moose typically experience low mortality after the first month of life except at 8-10 months of age during epizootic years (Musante et al. 2010, Jones et al. 2019); e.g., mortality averaged ~70% in 2014 - 2016 (Jones et al. 2019). Winter ticks are the primary cause of mortality in calf moose in northern New Hampshire (Musante et al. 2010, Jones et al. 2019) and epizootics are projected to become more frequent given weather patterns associated with climate change (Dunfey-Ball 2017, Jones et al. 2017, 2019). Although epizootics tend to occur at a regional scale, Dunfey-Ball (2017) hypothesized that local habitat conditions strongly influence local moose density and calf mortality, and regional mortality reflects the composition and extent of these local conditions. Simulation modeling by Healy et al. (2019) indicated that calf mortality was related to the local proportion of optional foraging habitat (clear-cuts). Furthermore, yearling and adult cows have experienced a related decline in ovulation rate and productivity (Bergeron and Pekins 2014, Jones et al. 2017, Ellingwood 2018). Understanding the variable quantitative relationships among tick abundance, moose abundance, weather, and epizootic events is paramount to managing the moose population of New Hampshire.

Population Dynamics of Moose

Fecundity and mortality rates are typically used to assess population status and direction, and are affected by a wide array of biological and environmental factors. Fecundity is defined as the number of live births per year by reproducing individuals (Schwartz 2007), and subsequent survival of progeny are the two determinants of recruitment rate (Boer 1992). This measure is a sensitive indicator of population status with regard to availability and quality of forage; that is, as populations become food limited, fecundity declines (Verme 1969, Clutton-Brock et al. 1984, Boer 1992). Fecundity in moose is related to maternal age; the yearling phase is followed by high fecundity in prime adults that eventually decline (Markgren 1969). Fecundity is affected by maturation age, twinning rate, and pregnancy rate within a population (Boer 1992).

Delayed sexual maturity or yearling pregnancy is dependent on physiological development and condition of females reflecting habitat quality and adequate nutritional history (Saether and Haagenrud 1983, Boer 1992). Although calf moose ovulate on rare occasion, it is accepted that most are not sexually mature and do not breed (Simkin 1965, Boer 1987, Schwartz and Hundertmark 1993). Pregnant yearlings usually produce a single calf (Sergeant and Pimlott 1959, Simkin 1974, Boer 1992), and can experience a high rate of pregnancy when on a high nutritional plane (Markgren 1969, Franzmann and Schwartz 1985). Other factors such as winter severity, parasites (e.g., winter tick), and body weight impact yearling pregnancy rates (Boer 1992). The threshold body weight for yearling ovulation is 200 kg dressed body weight; reproductive potential rises with increased age and body weight (Adams and Pekins 1995).

Twinning reflects optimal forage quality and quantity (Geist 1974), and is most common in the prime ages of 3-7 years (Boer 1992). Twinning is strongly associated with nutrition, is a

good predictor of high quality habitat (Boer 1992), and varies regionally and temporally.

Twinning rates vary from 22-70% in Alaska (Franzmann and Schwartz 1985), and similarly from 17-63% in Sweden relative to climate and nutrition (Markgren 1982). The twinning rate in New Hampshire was 15% in 2002-2005 (Musante et al. 2010). The annual compounding effect of high infestation of winter ticks is suspected to strongly influence fecundity in New Hampshire (Musante et al 2007, Bergeron et al 2013, Jones et al. 2017, Ellingwood 2018). Although low twinning rates are usually associated with a lack of optimal habitat or winter severity, the study area is considered to have high quality and quantity of optimal habitat and moderate winter conditions for moose (Scarpitti et al. 2007, Bergeron et al. 2013, Dunfey-Ball 2017).

Pregnancy rates across North America are remarkably consistent over a wide variety of habitats and winter severity - averaging 84.2% (Boer 1992); Scandinavian moose respond similarly (Haagenrud and Lordahl 1979). Adult cow moose are most productive when 4 - 8 years old, representing the majority of production in the population. Average fecundity rates below, near, and above carrying capacity (k) are 124.1, 106.1, and 88.0 calves/100 adult females, and 64.5, 41.1, and 17.7 calves/100 yearling females, respectively (Boer 1992). Most adult cows give birth to a single calf, although twinning in expanding populations can be relatively high (Coady 1982). In northern New Hampshire from 2002 -2005, average fecundity was 0.30 for yearlings and 0.94 for adults (Musante et al 2010).

Calf survival is lowest during the early weeks of life with predation the main cause of mortality in the first 30 days (Franzman and Schwartz 1986). In northern New Hampshire, 76% of summer calf mortality occurred within the first 28 days of life (Musante et al. 2010, Jones et al. 2017). Overall, summer calf survival was high, in the first 60 days of life in northern New Hampshire and Maine was 77% and 94%, respectively, from 2014 - 2016 (Jones et al. 2017). A

suspected cause of neonatal mortality is black bears (*Ursus americanus*), and in northern New Hampshire bear density is estimated as 0.38 -0.58 bear/km² (A. Timmins NHFG pers. comm.). Musante et al. (2010) commonly observed black bears around cows with neonatal calves. The relatively high summer survival of calves indicates that predation is probably not a limiting factor of moose abundance in northern New Hampshire (Musante 2006).

Winter Tick Ecology

The winter tick has 3 parasitic stages after attachment to the host moose. Engorged adult females drop from moose at the end of March through early April, after which eggs are deposited in leaf litter (Fig. 2.1) (Patrick and Hair 1975, 1979). Eggs hatch into larvae soon after, forming aggregations in June after which a period of dormancy or quiescence occurs. Fall questing begins in early autumn, typically lasting through early November when weather and ground conditions terminate activity. The questing period is defined by when larvae climb vegetation and wait for a host (i.e., moose) to walk by and attach to their hair and coincides with the moose breeding season when animals are most active (Drew and Samuel 1985). Ticks continue questing until attachment or weather conditions become lethal (e.g., winter snow/freezing temperatures or desiccation) (Drew and Samuel 1985).

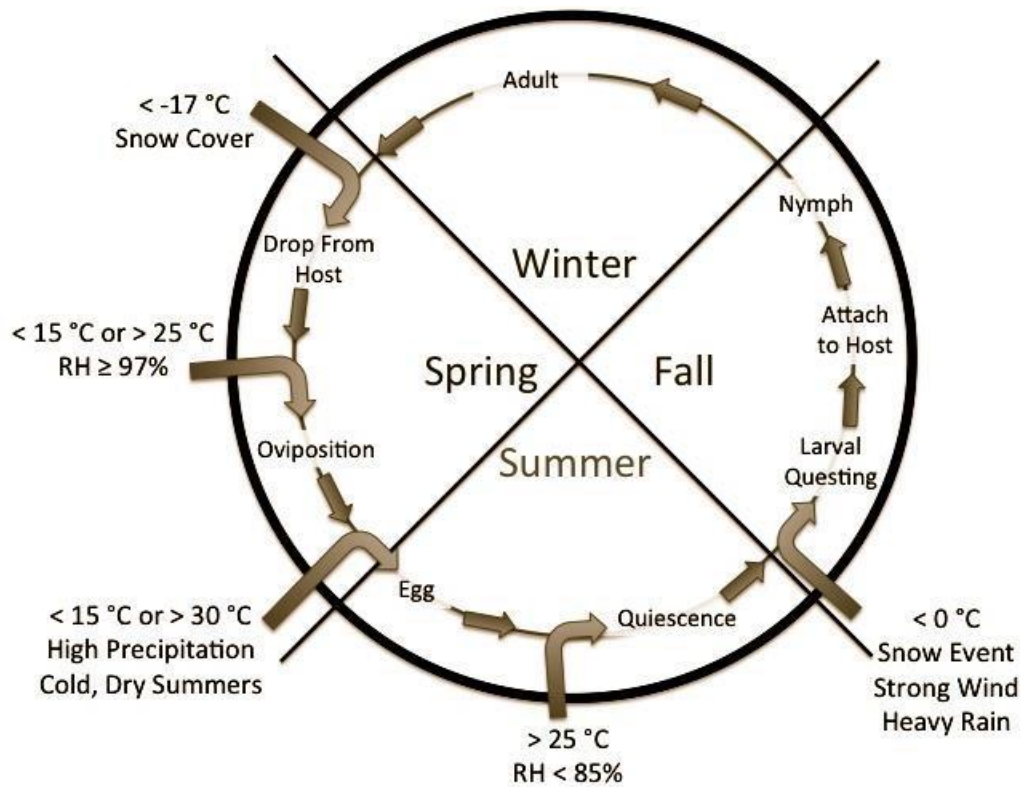


Figure 2.1: Weather conditions that negatively affect the off-host winter tick life stages; conditions decrease abundance and/or decrease larval attachment to host.

Once on a moose, winter ticks have 3 distinct developmental periods (Addison and Mclaughlin 1988). After a larva takes a blood meal, it develops into a nymph in 10-22 days. Nymphs take a blood meal in January-February with peak feeding occurring in mid-February, after which they molt into an adult. By the end of winter (March-April), adult females take a blood meal (the third) and are visible as grayish "grape-sized" ticks engorged with blood. Adult ticks drop from moose mostly in April, beginning in late March and lasting through mid-May; moose are relatively tick-free in summer.

Winter tick abundance is largely influenced by host density, weather, and ground conditions (DelGiudice et al. 1997, Samuel 2004) (Fig. 2.1). Seasonal and daily weather influence relative humidity, ambient temperature, and wind which play critical roles in off-host

tick survival (Drew and Samuel 1985, Aalangdong 1994, Addison et al. 2016, Holmes et al. 2017, Yoder et al. 2017b). Ticks have evolved mechanisms to cope with extremes in temperature and internal water balance, and the winter tick is no different with regard to adaptive physiological and behavioral traits (Holmes et al. 2017). Examples include clustering of larvae, the ability to absorb water vapor with specialized mouth parts, and periods of dormancy to avoid hot, dry weather patterns (Addison et al. 2016, Yoder et al. 2016, Holmes et al. 2017).

Larvae are particularly susceptible to dry, hot conditions causing lethal desiccation in August and September (Addison et al. 2016, Yoder et al. 2016, 2017a, Holmes et al. 2018). Annually, like most ticks, they are negatively impacted by the soil fungus (*Scopulariopsis brevicaulis*) and other microorganisms (Yoder et al. 2017b); however, the relative influence of soil fungi seems insufficient to prevent high abundance in certain conditions.

Spring snow cover presumably has adverse effects on survival and egg-laying of adult females because cold/freezing conditions and frozen litter create poor site suitability for oviposition (Drew and Samuel 1986). Larvae were freeze-intolerant when exposed to ice and inoculative freezing in laboratory studies (Holmes et al. 2017). However, such conditions would be uncommon in New Hampshire, and others (Drew and Samuel 1986, Timmermann and Whitlaw 1992) have documented that survival of engorged females ranges from 55 - 73% after snow melt. Garner and Wilton (1993) found that major die-offs and hair loss were directly related to the mean annual temperature in the prior April. Conversely, long-term climate and weather analysis found little correlation between spring conditions and subsequent regional epizootics (Dunfey-Ball 2017). In a general sense, shorter winters and earlier springs associated with climate change would make unfavorable conditions less common in April.

Aalangdong (1994) found that cold temperatures and low humidity (i.e., dry conditions) in June and July negatively impact egg survival. Although egg production occurs at 15-30 °C, high ambient temperatures and dry conditions increase larval desiccation in *Dermacentor* and other tick species (Knülle 1966, Yoder et al. 2016). These conditions lead to increased rate of water loss in larvae (Holmes et al 2017), yet water deficit can be balanced by absorbing water vapor from air, forming clusters to avoid desiccation, and onset of quiescence (Yoder et al. 2016). The ground conditions in which a female lays eggs likely plays a role in larval water balance and rate of water loss with photoperiod also influential (Yoder et al. 2016). Moreover, Holmes et al. (2017) found that larvae have a wide range of thermal tolerance at short-term exposures, from -18 to 46 °C, but survival declines as duration of exposure increases.

Winter ticks are poikilothermic, reducing metabolic rate and movement at <10 °C, and stopping movement at < 0 °C (Drew 1984, Addison et al 2016); laboratory testing at -18 to 46 °C substantiates this thermal effect (Holmes et. al. 2017). As ambient temperature nears 0 °C, questing begins to slow and cold temperatures coupled with persistent frost or snow are lethal to larvae (Drew and Samuel 1985); these conditions dictate the length of the questing period (Aalangdong 1994, Samuel 2007). Unlike other tick species, winter tick larvae do not descend vegetation during questing and remain exposed to local micro-environmental conditions (Drew and Samuel 1985, McPherson et al. 2000).

Larvae are also sensitive to desiccation during questing. For example, a September drought in 2016 was the presumed cause of substantial decline in infestation of harvested (October) and captured (January) moose that year; subsequent calf mortality in 2017 declined to 30% from 70% in 2016 (Jones et al. 2019). The physiological ability of larvae to absorb water vapor aids in water conservation, but cannot compensate entirely during sustained drought

(Yoder et al. 2016). Further, larvae form clusters that seem to aid individual water balance and insulate from temperature extremes (Yoder et al. 2016); conversely, Holmes et al. (2017) found that clusters had no enhanced temperature tolerance. Because multiple factors interact to influence activity and survival of larvae during questing (McPherson et al. 2000, Dunfey-Ball 2017, Holmes et al. 2017), it is difficult to predict quantitative and temporal availability of larvae on the landscape.

Larvae are localized where adult female ticks drop from moose because the engorged female is immobile (Drew and Samuel 1985, Addison et al. 2016). They maneuver under exposed leaf litter and soon thereafter lay eggs. Addison et al. (2016) found that larval survival was higher in "open" versus "forested"(closed canopy) habitat when larvae were exposed to a moister and cool environment that presumably reduced survival. Most of northern New Hampshire is commercial forest where 1-3% annual timber harvest maintains 15-20% of the area in optimal foraging habitat 4-16 years old (Dunfey-Ball 2017). Moose selectively use this habitat in spring and fall creating a direct connection between tick location and infestation of moose (Healy et al. 2018). Moreover, the larval questing period and moose breeding season overlap both spatially and temporally which enhances the probability of host-parasite interaction and infestation.

Objectives

This chapter contains the summary information associated with 250 radio-collared moose studied in 2014 – 2019 in northern New Hampshire. This information is presented relative to 4 specific objectives:

- 1) measure the productivity of yearling and adult cow moose,

- 2) determine cause and rate of mortality of neonatal moose,
- 3) determine cause and rate of mortality of calf moose, and
- 4) determine cause and annual rate of mortality of yearling and adult cow moose.

Study Area

The study area was in eastern Coos County in northern New Hampshire centered in the town of Milan. Moose density was estimated at 0.46-0.87 moose/km², down from 1.2 moose/km² in 1998 (NHFG 2015). It encompassed Wildlife Management Unit (WMU) C2 and portions of A2, B, and C1 covering ~1,250 km² (Fig. 2.2). It consisted mostly of privately-owned commercial forest harvested on a continual basis. Portions of the study area were high elevation mountain ranges with the Killkenny Range (914-1219 m) bordering to the west and the Mahoosuc Range (914-1219 m) to the south. Year-round access was through a network of 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). This 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, moose

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

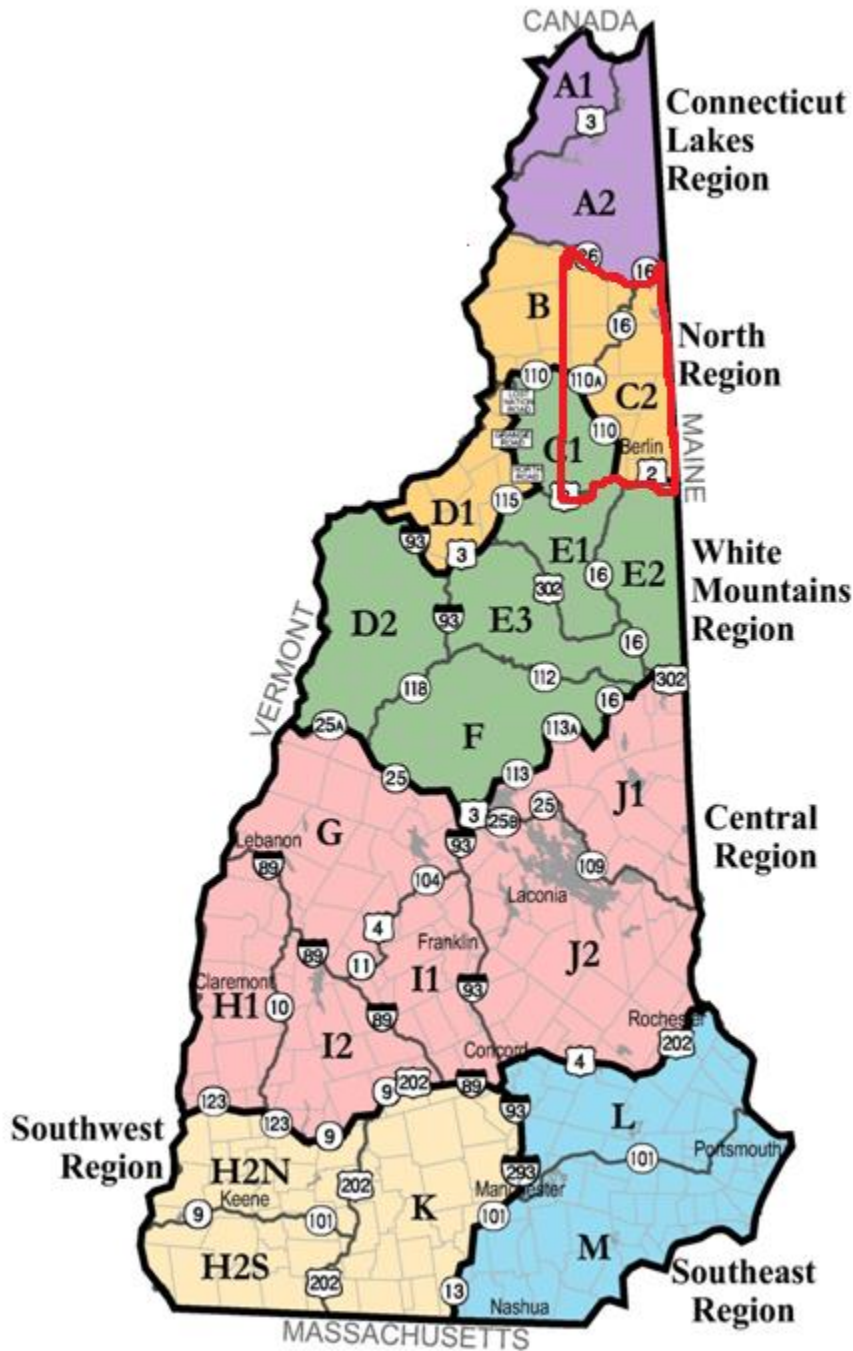


Figure 2.2. Study area of moose research project in the North and White Mountains Region, specifically the eastern half of Wildlife Management Units (WMU) B & C1, and all of WMU C2, in Coos County, New Hampshire.

Methods

Moose Capture

The Berlin Municipal Airport in Milan, NH was the operations base for moose captures that were conducted by commercial wildlife capture teams in January 2014-2018. A fixed-wing flight (e.g., Cessna 155) was used to locate concentrations of moose the week prior to capture. Moose were captured throughout the study area by aerial net-gunning or darting with a 3-person crew consisting of the pilot and 2 animal handlers (moose muggers); a veterinarian was onsite to manage immobilization drugs and respond to injury. University of New Hampshire (UNH) and New Hampshire Fish and Game (NHFG) personnel provided ground support by directing the capture crew to concentrations of moose, providing capture supplies, and processing biological samples. The general strategy was to capture 40-50 moose annually to maintain 30-40 adult cows for long-term monitoring and at least 25 calves to measure current year mortality associated with winter ticks (IACUC #: 151001, Appendix A.).

Measurements at Capture

Weight

Captured calves were harnessed and suspended beneath the helicopter to measure body weight with a 300 kg (+/- 5 kg accuracy) hanging digital scale (Adam Equipment SHS 600a). The same digital scale was used to measure body weight of dead calves by hoisting the carcass with a pulley system suspended from a metal, triangular frame strapped to a tree (Ellingwood et al. 2019). The two weights were used to assess temporal weight loss from January to death.

Tick Abundance

The relative tick load of each moose was assessed with an index by measuring and summing the number of ticks on 4, 10 cm transects on both the shoulder and rump (Sine et al. 2009, Bergeron and Pekins 2014). The sum of those 8 transects is used to compare the relative tick load between individuals and across years.

Physical Condition

A subjective assessment of physical condition of calves was conducted by the capture personnel. Each calf was ranked as either thin, normal, or fat based on palpation, estimation of body fat, and overall physical appearance.

Monitoring

Visual observations were used to measure productivity of yearling and adult cows, the number of calves born per cow, and calf survival through August of the first summer. Radio-collared cows were stalked using ground telemetry 3x weekly in May-July to document the birth rate and survival of calves; thereafter, weekly walk-ins occurred until 15 August. Parturition dates were assigned by backdating from the estimated age of the observed neonate based on its coordination, mobility, wet or dry appearance, and presence of an umbilicus (Larsen et al. 1989). Mortality was assigned after ≥ 3 subsequent walk-ins failed to verify presence of a previous observed calf. Information collected during walk-ins included UTM GPS coordinates, weather, cow and calf behavior, and surrounding habitat characteristics, additional sign included beds, tracks, fecal matter, birthing membranes, and evidence of predation, including black bear (*Ursus americanus*) sightings. Fieldwork was completed by trained technicians (4-5 individuals) working daily from May through August.

Mortality

Mortality events were identified by the radio-collar emitting a "mortality signal" (2x faster pulse rate than normal) which is triggered by no movement for a continuous 5-hour period; the coordinates of that location are also transmitted. Researchers responded to verify mortality and subsequently perform a field necropsy, typically within 24 h. If cause of death was undetermined, biological samples were collected for analysis by the NH Diagnostic Veterinary Laboratory (NHDVL). Each site was examined for signs of predation, human disturbance, scavenging, and any evidence contributing to the clinical evaluation of death (e.g., signs of struggle, disease/injury, bile, blood, vomit, physical injury). The site was GPS-located and photographed to document the general surroundings. The field necropsy followed a customized approach (Jones 2016) developed in cooperation with Dr. Inga Sidor, (NHVDL), and was based on standard procedures for large mammals (Mason and Madden 2007, Munson 2014).

Snow Urine Collection

Snow urine samples were collected every 2 weeks beginning in late January and extending through snowmelt or mortality (March – early April); the goal was to collect 3–6 temporal samples per individual. Samples were collected within 24 h of urination by locating the bedding site and/or tracks in the snow at coordinates transmitted by the GPS radio-collar at 00:00 hr that day; tracks were followed until a sample was identified. Moose with VHF radio-collars were located using ground telemetry techniques (Mech 1983) and back-tracked to collect urine samples. In cases where an adult accompanied the calf, samples were distinguished between the pair by the size of tracks and bed nearest to the sample. Consistent with the methods used by DelGiudice et al. (1988), the most concentrated portion was collected in plastic bags using

rubber gloves to avoid contamination. Samples were subsequently thawed at room temperature and aliquoted into 2 mL cryovials. These aliquots were stored frozen until submission to BiovetUSA (Burnsville, Minnesota) for measurement of urea nitrogen (UN) and urinary creatinine (C) content (mg/dL). These data were expressed as a ratio (UN:C) to correct for the dilution of each sample by snow (DelGiudice et al. 1988); C is proportional to muscle mass and remains near constant in individuals over a given day (DelGiudice and Seal 1988). Analysis included those individuals that were sampled most consistently, while attempting to achieve near equal representation of surviving and dead calves.

Results

Pregnancy rate (2014-2018)

The annual pregnancy rate of adult cows captured and radio-collared in January averaged 73% (n = 65). The annual range was 50-85% with 4 of 5 years at 75-85%; 2018 is considered an outlier (50%) with a sample size of only 6 animals (Table 2.1). Pregnancy rates across North America are consistent over a wide variety of habitats and winter severity, averaging 84% (Boer 1992). Certainly the average rate measured in adults here was lower and contributed to reduced productivity within the population (Jones et al. 2017, Ellingwood 2018). Data available for yearling cows were minimal because that sample consisted of radio-collared female calves that survived 2 years (n = 9); no births were documented in this group. Yearling pregnancy in the study area was 20% in 2002 – 2005 (Musante et al. 2010). Although yearling pregnancy is indicative of relative nutritional status, habitat quality, and reaching a threshold body weight (Franzmann and Schwartz 1985, Boer 1992, Adams and Pekins 1995), the quantity and quality

of habitat were considered high within the study area (Bergeron et al. 2011, Dunfey-Ball 2017) and starvation was never documented with any of the > 250 radio-collared animals.

Table 2.1. Productivity parameters of radio-collared adult cow moose in northern New Hampshire 2014-2019. Sample size in parenthesis. *denotes epizootic year

	% Pregnancy Rate	% Calving Rate	% Twinning Rate	% Successive Calving Rate
2014*	76 (21)	67 (21)	0	N/A
2015*	75 (16)	46 (33)	0	29 (17)
2016*	78 (9)	59 (32)	0	18 (28)
2017	85 (13)	76 (38)	0.03(38)	27 (33)
2018*	50 (6)	58 (36)	0	34 (41)
2019	NA	67 (30)	0	25 (44)
All Years	73 (65)	62 (190)	0.005 (38)	27 (163)

Parturition (2014-2019)

Parturition occurred from 9 May – 20 June (n = 84) (Fig. 2.3). The median parturition date varied annually by only 5 days (16-20 May), and was 20 May in 4 of 6 years (Fig. 2.3). The parturition date in 2002-2005 was similar to this study with a median date of 19 May, indicating that parturition is predictable and consistent across years (Musante et al. 2010). Both studies documented late season calving events (June) that represented late breeding individuals which are expected in any population (Fig. 2.3).

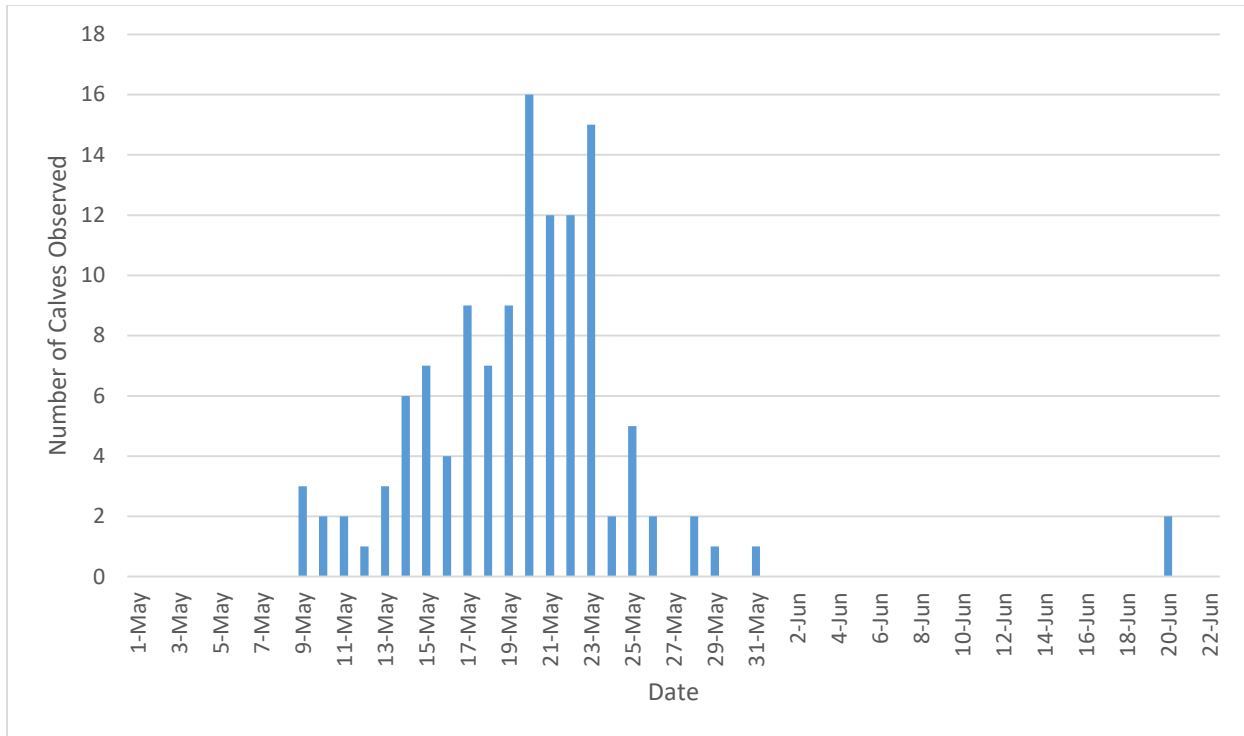


Figure 2.3 Parturition date of radio-marked cows in northern New Hampshire from 2014-2019.

Calving rate (2014-2019)

The annual calving rate of all marked adult cows averaged 62% (n = 190) or ~10-15% less than the pregnancy rate of cows captured in any single year. The annual range was 46-76% with only a single year (2017) >70% (Table 2.1); no yearling cow (surviving female calf) birthed in any year. Only a single set of twins was documented in 6 years; therefore, the fecundity rate was equal to the calving rate. The annual calving rate was always lower than the annual pregnancy rate except in 2018 – further evidence that the pregnancy rate in 2018 should be considered an outlier. Pregnancy, calving, and twinning rates all contribute to the fecundity rate of a population and all were low relative to average rates in healthy populations (Van Ballenberghe and Ballard 2007). The difference between the average pregnancy (73%) and calving rates (62%) likely reflects multiple factors relative to individual cows: e.g., resorption,

still births, compromised calves, and predation prior to field observation. The complete lack of yearling productivity corresponds to the gradual decline in pregnancy rate and dressed body weight from 1998 to 2009 (Adams and Pekins 1995, Musante et al. 2010, Bergeron et al. 2013). The lack of twinning also corresponds with a gradual decline in the corpora lutea count, suggesting subtle decline in physical condition of adult cows (Bergeron et al. 2013).

Successive calving rate (2015-2019)

The annual proportion of adult cows calving in successive years averaged 27%, ranging from 18-34%; a majority never calved successfully in any year (annual n = 17-44; Table 2.1). On an individual basis, 10 cows (23%) calved 2 years in succession and 9 (20%) calved every other year. Two cows (5%) calved 5 years in succession, 1 cow (2%) every year, and 14 failed to calve > 1 year after calving. As noted above, not all calving events may have been documented because the average calving rate (62%) was less than the pregnancy rate (73%). It is possible that field observations failed to find neonatal calves due to still births, or compromised health leading to mortality in 1-2 days. The successive calving rate in 2002-2005 was 75% (Musante et al. 2010), suggesting that the current rate reflects reduced condition in adult cow cohort. The general decline in the New Hampshire moose population reflects reduced productivity characterized by lack of yearling breeding, low twinning rate, and low successive calving rate. These parameters presumably reflect the compromised condition of yearling and adult cows due to the physiological effects of annual infestation of winter ticks (Musante et al. 2010, Bergeron et al. 2013, Jones et al. 2017, 2019), despite occupying optimal habitat (Dunfey-Ball 2017). A working hypothesis is that the combination of the physiological cost of successful production and high winter tick infestation (Musante et al. 2007) compromises the subsequent physiological recovery and compensatory growth, and successful pregnancy of productive cows.

Calf body weight - January captures (2016-2018)

Body weight of calves was measured in 3 years only: 2016-2018 (17, 36, and 44 calves, respectively). The average weight of males and females ranged from 177-185 kg and 165-172 kg, respectively; on average, males were 10-13 kg heavier than females each year (Table 2.2). The highest yearly average for both was in 2017, the year with lowest tick loads (see below). The range of body weights was large, exceeding 100 kg in both sexes across the 3 years and ~30 - >100 kg annually (Table 2.2). This wide range reflects a possible combination of late births, compromised growth, and/or early impact by high infestation of winter ticks. Body weight is a critical factor influencing survival of calves harboring low-moderate winter tick infestations; animals > 174 kg have higher resistance to mortality (Ellingwood et al. 2019). Further, heavier calves (~15 kg) in northern Maine had higher survival than calves with similar infestations in northern New Hampshire and western Maine (Ellingwood et al. 2019). Given that habitat quality in the study area is considered near optimal (Dunfey-Ball 2017), these low calf weights arguably reflect, in part, the carry-over effects of compromised reproductive cows impacted by high annual tick loads (Musante et al. 2010, Jones et al. 2017).

Table 2.2. Summary of body weights (kg) of moose calves captured in January 2016-2018 in northern New Hampshire. *Males were significantly heavier than females each year.

Year	Sex	n	\bar{X}	SD	Range
2016	Female	12	165	18	132 - 195
	Male*	5	177	14	163 - 200
2017	Female	15	172	16	113 - 199
	Male*	21	185	32	109 - 227
2018	Female	19	170	30	91 - 210
	Male*	25	180	17	159 - 231

Physical assessment of calves - January captures (2014-2018)

The subjective assessment of physical condition of calves indicated that most were normal (69%) or thin (29%). Indirectly, this was substantiated by the lower weights measured in northern New Hampshire compared to northern Maine (Ellingwood et al. 2019). Other than 2017 when tick infestation was low (see below), the winter mortality rate of calves average > 60% indicating their compromised condition in epizootic years when tick infestations are high. Because heavier calves have survival advantage at low-moderate infestations (Ellingwood et al. 2019), the preponderance of normal-thin animals suggests that most calves might not realize this advantage during moderate infestations. For example, calf mortality was still 30% even when infestation was comparatively low in 2017; conversely, mortality a decade earlier was minimal other than the epizootic year 2002 (Musante et al. 2010).

Winter tick infestation at capture (2014-2018)

The average infestation estimate on calves was 51 ticks with a median of 45; Adults averaged 33 ticks with a median of 31 (Table 2.3). Average survival of calves associated with the annual winter tick infestations was 39% (range = 23-70%) (Table 2.5). Relative tick infestation (15 of 32) in 2017 was the lowest of any year in adults and calves (Table 2.3, Fig. 2.4), and reflected low tick abundance and higher survival (70%). The late-summer drought in 2016 presumably caused measureable desiccation and reduction of larvae on the landscape, and was followed by early snow cover (late-October) which shortened the questing period by ~1 month, resulting in significantly lower infestation (Ellingwood 2018). Of consequence is that the probability of survival is 50% at an infestation of 37 ticks measured on October-harvested moose (Dunfey-Ball 2017) – these moose have ~4 additional weeks to acquire ticks in a typical autumn

(Table 2.4). Tick infestation level is the most significant factor in determining calf survival, with body weight acting as a balance influencing survival based on the relative tick infestation (Ellingwood et al. 2019).

Table 2.3 Tick abundance on cow and calf moose captured in January in northern New Hampshire (2014-2018). Abundance equals the total count on 8, 10-cm transects, 4 at the shoulder and 4 on the rump. * denotes epizootic year

	n	\bar{X} (SE)	Median	Range
2014*				
Calves	19	64 (9)	53	22-131
Adult cows	23	46 (7)	48	29-169
2015*				
Calves	26	51 (5)	47	10-114
Adult cows	17	39 (4)	35	9-67
2016*				
Calves	32	65 (6)	58	11-190
Adult cows	9	46 (10)	46	2-102
2017				
Calves	37	32 (2)	31	8-63
Adult cows	13	15 (2)	12	7-26
2018*				
Calves	44	43 (4)	38	2-99
Adult cows	6	18 (6)	14	5-44

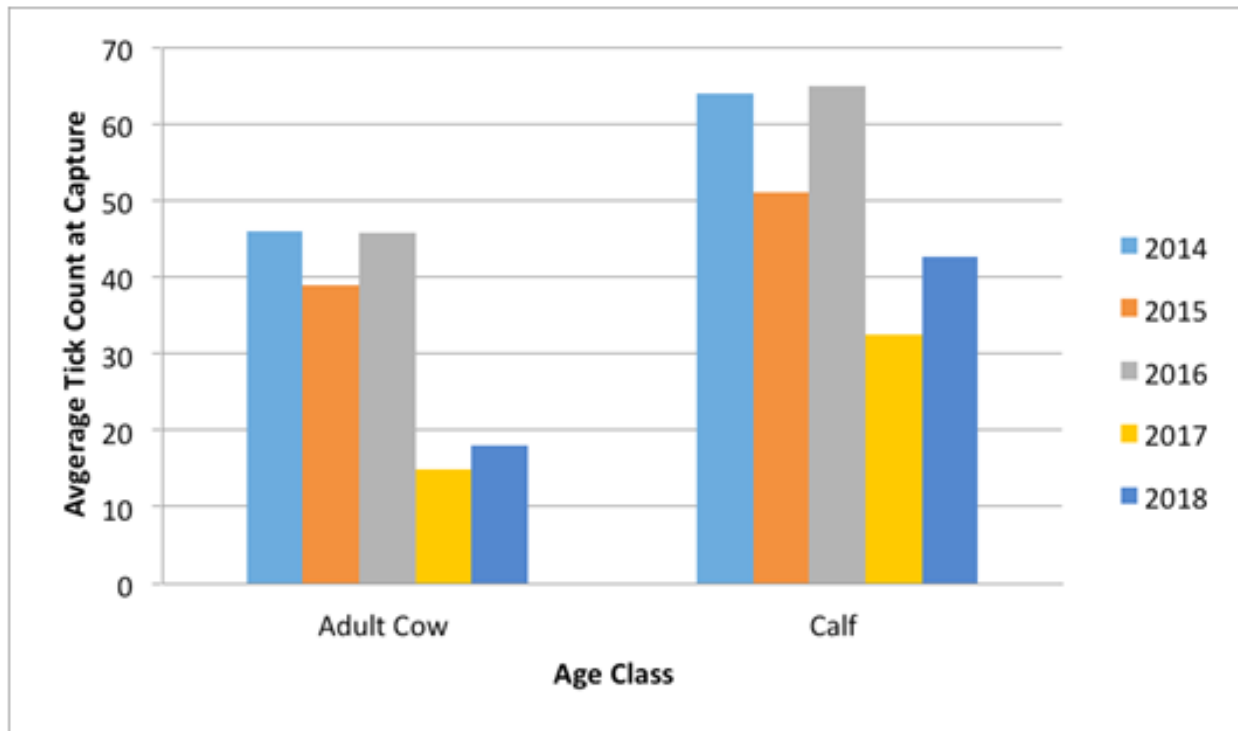


Figure 2.4. Average tick abundance on radio-marked adult cow and calf moose at January captures (2014-2018). Abundance is equal to the total count of ticks along 8, 10 cm transects at the shoulder and rump. An epizootic occurred each year except 2017 where infestation were lowest overall.

Table 2.4. Proportion of moose calves with tick abundance ≥ 37 at January capture, 2014 – 2018. Tick abundance is the combined # of ticks counted along 8, 10 cm transects at the shoulder and rump. Epizootics ($>50\%$ calf mortality) occurred in 2014, 2015, 2016, and 2018. * denotes epizootic year

Year	n	% with ≥ 37 ticks	% calf mortality with ≥ 37 ticks
2014*	19	63	75
2015*	26	58	87
2016*	32	73	63
2017	37	26	54
2018*	44	46	82

Table 2.5. Annual percent calf and adult moose survival in northern NH from 2014-2019. * denotes epizootic years.

Year	Summer (May – Aug.) (0-2 mo.)	Winter (Jan. – April) (8-12 mo.)	Annual Yearling/Adult
2014*	64	38	91
2015*	87	26	78
2016*	78	23	75
2017	80	70	84
2018*	66	39	83
2019	85	NA	86
Total/Avg.	77	39	83

Because states will not have continued access to January (final) infestation levels that are related directly to the probability of mortality (Ellingwood et al. 2019), one possible approach is to attempt prediction of annual epizootics with data about tick abundance, infestation on harvested moose, and weather. Each state measures tick infestation on harvested moose in October as an annual index and these data might prove useful to predict a final infestation level. Combined with the important finding that tick abundance, hence presumed infestation rate, was constant until a snow event disrupted questing (See Chapter 1).

Snow Urine Analysis – UN:C Ratios (2014-2017)

A total of 158 snow urine samples were collected from 38 radio-marked calves (23 winter mortalities and 15 survivors) and cows in the winters of 2014–2017 (Ellingwood et al. 2019). From ~15 January – 14 February, there were no statistical differences between UN:C ratios of

unmarked cows, surviving calves, and calves that died ($P > 0.05$). From ~ 15 Feb – 15 March, the mean UN:C ratio of calves that died and those that survived diverged significantly ($P < 0.05$), whereas the UN:C ratio of cows and surviving calves remained similar. The average UN:C ratio of calves that died increased through the second week of March, peaking at 4.68 ± 2.93 ; the ratio of survivors was lower and relatively stable during this same time period ($\bar{x} = 2.43 \pm 0.74$; Table 2.6). The average ratio of calves that died never returned to levels < 3.5 , and mortality occurred 1–5 weeks after UN:C ratio peaked ($\bar{x} = 3$ weeks).

Table 2.6 Summary of UN:C ratios of snow-urine samples (n) from moose in 2014-2017, New Hampshire, USA. Original UN:C data are presented here with statistical comparisons made after data were log transformed. Dead calves had significantly higher ($P < 0.05$;) UN:C ratios from late February onward. Table 2.6 from Ellingwood et al. 2019 (Table 1.).

Collection Interval	Surviving calves			Dead calves			Unmarked adult cows		
	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD
15-31 Jan.	12	2.17	0.85	13	2.57	1.04	7	1.96	0.60
1-14 Feb.	11	2.50	0.80	19	2.88	0.97	12	2.37	0.87
15-28 Feb.	15	2.99	0.75	18	3.58*	1.19	11	2.56	0.77
1-14 Mar.	14	2.43	0.74	15	4.68*	2.93	9	2.42	0.93
15-31 Mar.	10	2.47	0.53	12	3.66*	0.88	13	2.50	1.01
1-14 Apr.	10	2.18	0.87	9	4.27*	2.37	5	1.90	0.77

While all moose exhibited some degree of undernutrition, the spike observed in the UN:C ratio of dead calves was related directly to the feeding period of adult female winter ticks. In more southern moose populations where winter ticks are of most concern, UN:C ratios from snow urine samples could be used to assess calf condition, identify a potential epizootic

(DelGiudice et al. 1997), and predict mortality rate in the population. Collection and analysis of snow urine samples from calves in the second and third week in March should be adequate to identify the proportion with UN:C ratio > 3.5 and provide a reasonable estimate of the seasonal calf mortality rate.

Calf Survival – winter (2014-2018)

A total of 157 radio-collared calves (86 males and 71 females) were monitored in 2014-2018, 19-44 animals annually (Table 2.7). The annual survival rate averaged 39%, ranging from 23-70%. However, survival was $> 40\%$ in a single year only (2017 - 70%), with mortality averaging 69% the other 4 years (range = 61-77%) calves died as early as February and as late as June most from mid-March through April (Fig. 2.5). Mortality from mid-March through April was concentrated in March and April each year (Fig. 2.5) with $>75\%$. Calf mortality in 2002-2005 was similarly concentrated in this time period (Musante et al. 2010) occurs simultaneously with feeding by adult female ticks - temporal mortality associated with high tick infestations is predictable. Based on evidence from field and laboratory necropsies, 91% of mortality was consistent with, and classified as excessive infestation by winter ticks (Table 2.8). The frequency of epizootics from 2014-2018 (4 of 5) has not been documented previously and is the principal cause of gradual decline in the moose population in northern New Hampshire and western Maine (Jones et al. 2017, 2019).

Table 2.7. Winter (January - April) survival of radio-marked male and female calves in 2014-2018. *denotes epizootic years.

Year	Male Calf		Female Calf		Combined
	n	% Survival	n	% Survival	% Survival
2014*	9	22	10	16	38
2015*	16	22	11	4	26
2016*	17	16	17	7	23
2017	20	40	15	30	70
2018*	24	22	18	17	39
Total/Avg.	86	24	71	15	39

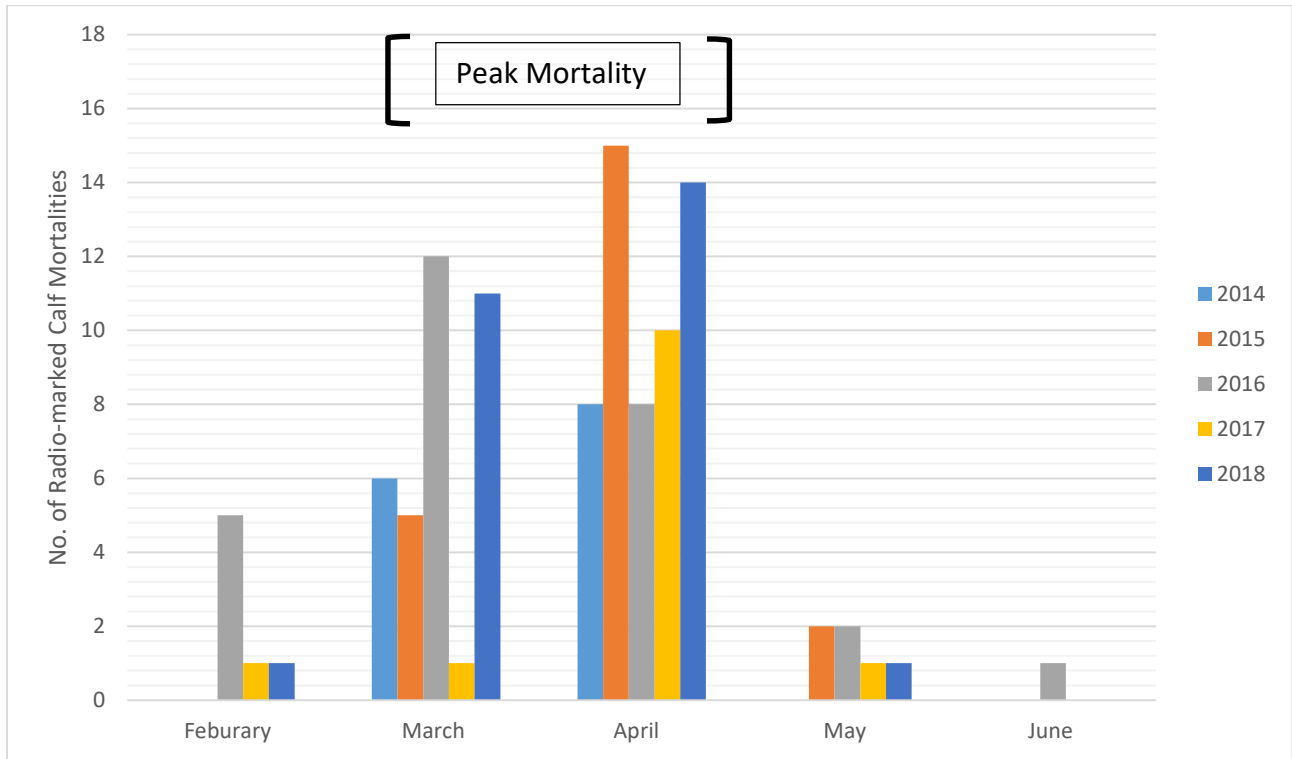


Figure 2.5. Number of radio-marked calf mortalities by month (2014-2018). Mortalities peak during the primary feeding period of adult female winter ticks (March through April).

Table 2.8. Percentage of collar loss and cause of mortality of radio-marked adult and calf moose in northern New Hampshire, 2014–2019.

Parameter	Adult (n)	Calf ^a (n)
Collar Drop/Malfunction^b	16 (10)	17 (21)
Mortality Source		
Capture Myopathy	0	5 (6)
Hunting	8 (4)	0
Vehicle Collision	6 (3)	0
Winter Tick	27 (14)	91 (97)
Brain worm	12 (6)	0
Other Parasite	3 (2)	1 (1)
Accident	6 (3)	1 (1)
Unknown	38 (20)	2 (2)

^a Calves at approximately 8-10 months of age when collared.

^b Loss due to premature collar expansion or unknown technical issue.

Neonate survival - summer (2014-2019)

The average neonate survival rate in summer (through August) was 77%, ranging from 64-87% (Table 2.5). Of this mortality, 64% occurred within 14-days post-birth, and all within 35-days post-birth (Fig 2.6). Cause of death was never documented, although neonate mortality is suspected to reflect still births, compromised health, abandonment, and predation. Predation was never documented although black bears and coyotes (*Canis latrans*) were frequently seen during the calving season. It is possible that dead neonates were scavenged by predators in a relatively short time prior to locating the birth site.

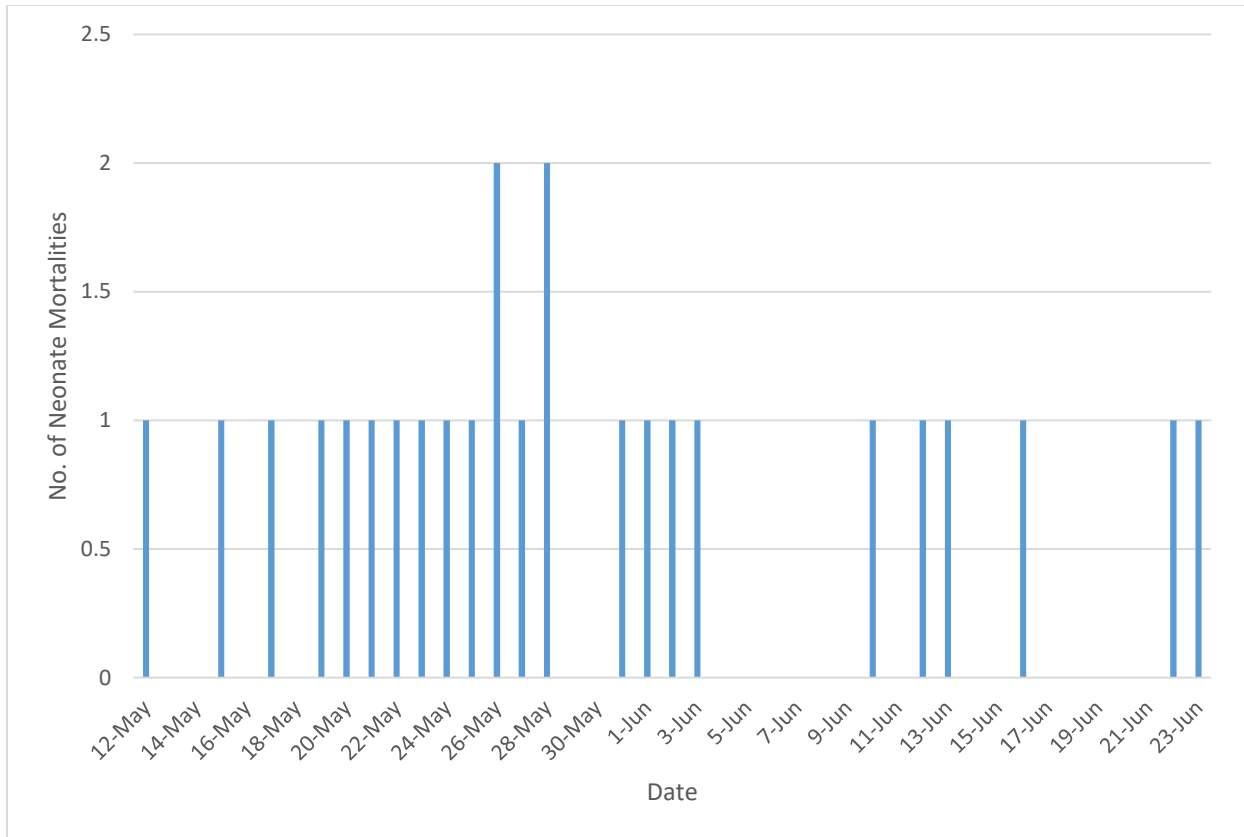


Figure 2.6. Timing of annual neonate moose mortality in northern NH from 2014 – 2019.

Adult Survival (2014-2019)

Annual adult survival was high, averaging 83% over 6 consecutive years (Table 2.5). The 2 leading causes of mortality were brainworm infection (12%) and excessive infestation of winter ticks (27%); a substantial number of mortalities were unexplained (38%) (Table 2.8). Brainworm mortalities occurred in September–February, whereas tick-related mortality occurred in March-April (Fig. 2.7). Four animals (8%) were harvested legally during the fall hunting season, and one illegally. Vehicular collisions were uncommon (6%) and were always adult males, presumably due to their tendency to roam but not related to rutting activity as collisions typically occurred in late summer possibly due to dispersing juvenile males seeking their own

territories prior to the breeding season (Table 2.8). Adult survival (87%) and causes of mortality were similar in 2002-2005 (Musante et al. 2010), although brainworm mortality was < 10%.

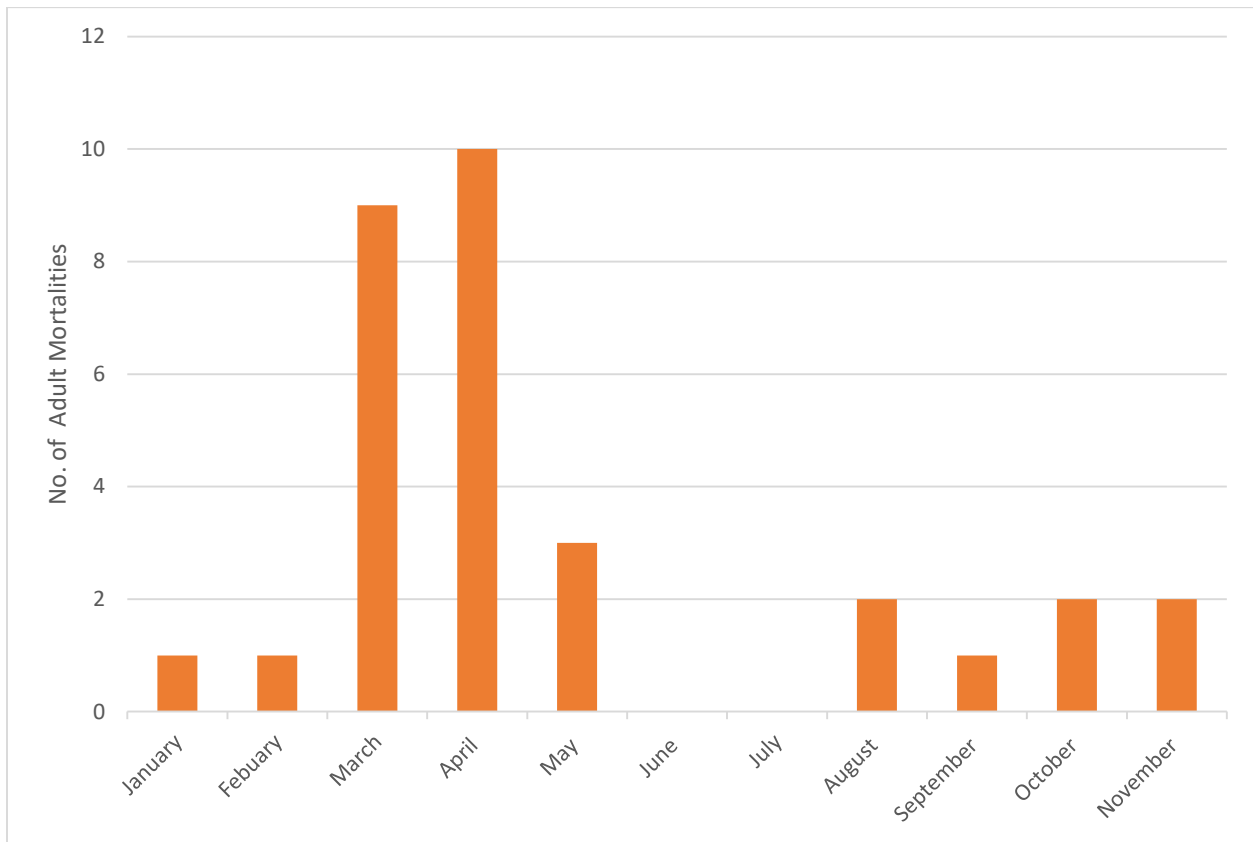


Figure 2.7. Timing of annual adult moose mortality in northern NH from 2014 – 2019.

CONCLUSIONS & MANAGEMENT STRATEGIES

Moose in northern New Hampshire are at the southern extent of their range in eastern North America. The slow, decade-long decline (~40%) of the New Hampshire moose population has been caused by high mortality of calf moose (8-10 months old) and suppressed productivity of adult/yearling cows (Jones et al. 2017, 2019, Ellingwood et al. 2019). These dynamics are related directly to winter tick infestations sufficient to produce epizootic conditions (> 50% calf mortality) in at least 7 of the past 10 years. Specifically, this research has demonstrated the

impact of epizootics with > 60% calf mortality in 5 of the past 6 years (2014-2019), an unprecedented frequency. Neither high calf mortality or reduced productivity are considered a result of malnutrition or severe winter conditions associated with habitat quality, as the study area provides a mix of forest diversity providing a constant supply of quality forage and cover (Bergeron et al. 2011, Dunfey-Ball 2017).

Certain evidence supporting the relationship between population decline and winter ticks includes:

- 1) Calf mortality is concentrated during the March-April feeding period of adult female ticks (Jones et al. 2019).
- 2) The increase of UN:C ratios in snow-urine samples that indicating compromised physiological condition of calves correspond temporally with the feeding period of adult female ticks (Ellingwood et al. 2019).
- 3) The low productivity of adult cows in optimal habitat and moderate winter conditions indicates a physiological influence beyond forage nutrition – importantly, starvation was never documented in the study population. Low productivity was evident in numerous parameters including the moderate pregnancy rate, low birthing rate, low successive birthing rate, low twinning rate, and lack of yearling breeding (Jones et al. 2017) – parameters that were considered normal-high a decade previously (Musante et al. 2010).
- 4) Tick infestation of calves was considered high, conservatively averaging ~ 50,000 ticks annually (Jones et al. 2017, 2019); an infestation of 35,000 ticks is sufficient to kill a calf (Musante et al. 2007). In 2017 when infestation was low, calf mortality dropped from ~70 to 30%, and subsequently, infestation increased and mortality rose to 60% in 2018 (Ellingwood 2018).

- 5) At capture in January, body condition of most calves was assessed as normal-thin, and body weight was low relative to calves in northern Maine (Ellingwood et al. 2019). Calves are in a negative energy balance throughout winter to spring green-up. Heavier calves realize a physiological advantage during low-moderate tick infestations because they have a larger buffer against the temporally concentrated protein and energy loss associated with blood loss and replacement during the feeding period of adult female ticks (Ellingwood et al. 2019). Given high habitat quality, smaller calves presumably reflect the compromised condition of the maternal cow, and/or the effect of larval and nymphal feeding at high infestation levels.
- 6) The birthing rate was consistently lower than the pregnancy rate indicating that a physiological impact likely occurred in late winter-spring when adult female ticks feed. Although adults rarely die from winter tick infestation (Musante et al. 2007), measurable weight loss occurring during the last trimester (March-April) would compromise growth and survival of the fetus and possibly result in stillborn or compromised neonates (Jones et al. 2019).
- 7) Neonate and adult survival were high indicating that maternal cows were on sufficient nutritional plane in summer to successfully raise a calf (Jones et al. 2017, 2019) – not coincidentally, moose are basically tick-free in summer.

Given that winter ticks are implicated in the decline of the New Hampshire moose population, this study investigated other aspects of the moose-winter tick relationship. These included A) assessing the effect of climate change on this relationship (Dunfey-Ball 2017), B) creating an agent-based model to test whether empirical data from the study could replicate the local mortality and relative impact of different infestation levels on calves

(Healey 2018), and C) measuring the relative abundance of winter ticks within openings created by two common forest management practices (Chapter 1).

- A) Winter tick epizootics are generally considered infrequent events, and their occurrence indicates an imbalanced host-parasite relationship resulting from the combination of high host/tick abundance with favorable environmental conditions promoting infestation (Samuel 2004). New Hampshire represents both conditions necessary for an epizootic – high moose density in the recent past and extended autumn weather as a result of climate change. Favorable environmental conditions extended for even 2 weeks in autumn provides for ~25% longer questing period, effectively increasing the infestation of moose. Assuming a balanced relationship exists relative to moose density, tick abundance, and infestation level, an extended questing period would produce higher infestation than otherwise at lower tick abundance. The unprecedented frequency of epizootics occurring in the northeast is perhaps not surprising given the combination of moderate moose density supported by continual forest harvesting (production of optimal habitat) and the positive influence of climate change on winter ticks.
- B) Agent-based modeling using local and regional empirical data (population dynamics, forest habitat, moose density, seasonal habitat use) was used to predict calf mortality under different combinations of weather scenarios, tick abundance, and moose density (Healy 2018). Initial habitat use analysis confirmed that moose selectively use the same optimal foraging habitat (cut openings 4-16 years old) during the drop-off and questing seasons of winter ticks, creating a feedback loop of moose density and tick abundance (Healy et al. 2018). The agent-based models predicted mortality rates similar to those measured. Further, abundance of winter ticks was the key parameter in all models - a

local moose population with more optimal habitat always endured higher mortality (Healey 2018). These findings indicate that field abundance measurements of winter ticks should focus on optimal foraging habitat.

- C) Annual abundance of winter tick larvae on the landscape is difficult to assess. It is influenced directly by the location or habitat use of moose during the drop-off period in April and by summer/fall weather that affect the microclimate on the ground or in vegetation during questing. The selective use of 4-16 year-old cut openings by moose in spring and fall indicates the importance of this habitat type in the winter tick-moose relationship (Healy et al. 2018). Therefore, abundance of larvae was measured in two different cut types (clear-cut and partial harvest) and on two transect types (random and high-use transects) in autumn 2018 (Chapter 1). Abundance was higher in partial harvests and on high-use transects, yet surprisingly, average abundance was not dissimilar to that measured a decade earlier (Bergeron and Pekins 2013), despite ~40% reduction in the regional moose density. This suggests that sufficient annual abundance of winter ticks exist to produce measurable moose mortality in any given year. Higher abundance in partial harvests may reflect optimal juxtaposition of optimal foraging habitat and cover that promotes longer use (time) by moose. Questing ended with onset of temperatures $< 0^{\circ}\text{C}$ and snow cover, but larvae demonstrated resilience for days and during a temporary warm-up. Prior to cold and snow, weekly abundance based on collection rates was stable, indicating that the infestation rate is constant during the questing period. The final infestation level (post-questing period) is related directly to the probability of calf survival (Ellingwood 2018), and theoretically, could be calculated from the infestation rate, October infestation level, and length of the questing period.

That winter ticks are well established is without question, but more importantly are where and at what abundance, and how temporal shifts occur. The regional landscape can be considered a shifting mosaic of optimal habitat (cuts) that largely influences the presence and abundance of moose and ticks. Winter tick abundance on the landscape is ultimately a function of multiple characteristics of the behavior, physiology, and local abundance of moose and winter ticks that are linked to dynamic processes of forest harvesting, weather events, and climate change. Assuming continuation of forest harvest in northern New England that produces near constant 15-20% availability of optimal moose habitat, the near-term occurrence of winter tick epizootics will mostly reflect annual weather events that affect the length of the autumnal questing period. Further, what is the “new” or changing probability of an epizootic in the face of climate change?

A lower moose density should eventually be realized from the continued negative impacts of high calf mortality, low productivity, and delayed maturation of yearlings; however, population decline is relatively slow because adult mortality is not abnormally high (Musante et al. 2010, Jones et al. 2019). Although somewhat counterintuitive, accelerating decline through a more liberalized moose harvest is a possible means to reduce the impact of winter ticks, ostensibly by lowering both moose population density and relative tick abundance (Jones 2017, Ellingwood et al. 2019). Given the availability of optimal habitat, a lower moose density should yield measurably improved health and productivity metrics in the population. Employing such a strategy recognizes parasitism, not habitat, as a primary influence of the population dynamics of New Hampshire moose. Understanding how and when an epizootic occurs is critical to better manage moose in New Hampshire and the region, and multiple measurements including moose density, tick abundance, October infestation level, infestation rate, length of questing period, and

tick abundance will aid in that effort. If purposeful reduction of moose density is a proactive management approach, acquiring reliable and consistent data will be critically important to best assess any harvest management strategy.

Literature Cited

- Aalangdong, O.I. 1994. Winter tick (*Dermacentor albipictus*) ecology and transmission in Elk Island National Park, Alberta. M. S. Thesis. University of Alberta, Edmonton. 174 pp
- Adams, K.P. and Pekins, P. J. 1995. Growth patterns of New England moose: Yearlings as indicators of population status. *Alces*. 31:53-59
- Addison, E. M., and McLaughlin, R. F. 1988. Growth and Development of Winter Tick, *Dermacentor albipictus*, on Moose, *Alces alces*. *J. Parasit.* 74:670–678.
- _____, E. M., McLaughlin, R. F., Addison, P. A., and Smith, J. D. 2016. Recruitment of Winter Ticks (*Dermacentor Albipictus*) in Contrasting Forest Habitats, Ontario, Canada. *Alces*. 52:29–40.
- Bergeron, D. H. 2011. Assessing Relationships of Moose Populations, Winter Ticks, and Forest Regeneration in Northern New Hampshire. M.S. Thesis. University of New Hampshire Durham, NH.
- _____, D. H., Pekins, P. J., and Rines, K. 2013. Temporal Assessment of Physical Characteristics and Reproductive Status of Moose in New Hampshire. *Alces* 49:39–48.
- _____, D. H., and Pekin, P. J. 2014. Evaluating the usefulness of three indices for assessing winter tick abundance in northern New Hampshire. *Alces*. 50:1–15.
- Blyth, C.B. 1995. Dynamics of Ungulate Populations in Elk Island National Park. Master's Thesis. University of Alberta
- Boer, A. H. 1992. Fecundity of North American Moose (*Alces alces*): A Review. *Alces* Supplement. 22: 1421-1423.
- _____, A. N. 1987. Reproductive productivity of moose in New Bruswick. *Alces* 23:49–60.
- Bontaities, K., Gustafson, K. A., and Makin, R. 2000. A Gasaway-type moose survey in New Hampshire using infrared thermal imagery: preliminary results. *Alces* 36: 69-75.
- Clutton-Brock, T. H., Albon, S. D. and Guinness, F. E. 1984. Maternal dominance, breeding success and birth sex ratios in red deer. *Nature*. 308:358–360.
- Coady, J.W. 1982. Moose. Pages 902-922 in J.A. Chapman and G.A. Feldhamer, eds., *Wild Mammals of North America*. The John Hopkins Univ. Press, Baltimore, MD.
- Degraaf, R. M., Yamisaki, M., Leak, W. B., Lanier J. W. 1992. New England Wildlife: Managemnet of forested Habitats. General Technical Report NE-144, Randor, PA: USDA, Forest Service, Northeast Experiment Station.
- DelGuidice, G. D., Mech, L.D., Seal, U.S., and Karns, P.D. 1988. Chemical analyses of deer bladder urine and urine collected from snow. *Wildlife Society Bulletin* 16(3):324-326.
- _____, G. D. and Seal, U.S. 1988. Classifying winter undernutrition in deer via serum and urinary urea nitrogen. *Wildlife Society Bulletin* 16(1): 27-32.

- _____, G. D. and Moen, R. 1997. Simulating nitrogen metabolism and urea nitrogen:creatinine ratios in ruminants. *The Journal of Wildlife Management* 61(3): 881-894.
- Drew, M. L., and Samuel, W. M. 1985a. Factors Affecting Transmission of Larval Winter Ticks, *Dermacentor Albipictus* (Packard), To Moose, *Alces Alces* L., in Alberta, Canada. *Journal of Wildlife Diseases* 21:274–282.
- _____, M. L., and Samuel, W. M. 1985b. Factors Affecting Transmission of Larval Winter Ticks, *Dermacentor Albipictus* (Parkard), to Moose, (*Alces alces*) in Alberta Canada. *Journal of Wildlife Diseases* 21:274–282..
- _____, M. L., and Samuel, W. M. 1986. Reproduction of the winter tick, *Dermacentor albipictus* , under field conditions in Alberta, Canada. *Canadian Journal of Zoology* 64:714–721.
- Dunfey-Ball, K. R. 2017. Moose Density, Habitat, and Winter Tick Epizootics in a Changing Climate. M.S. Thesis. University of New Hampshire Durham, NH
- Ellingwood, D. 2018. Assessing the Impact of Winter Tick Epizootics on Moose Condition and Population Dynamics in northern New Hampshire. M.S. Thesis. University of New Hampshire Durham, NH
- _____, D., Pekins, P. J. and Jones, H. 2019. Using Snow Urine Samples to Assess the Impact of Winter Ticks on moose calf condition and survival. *Acles* 55: 13-21
- Franzmann, A. W., and Schwartz, C. C. 1985. Moose Twinning Rates: A Possible Population Condition Assessment. *The Journal of Wildlife Management* 49:394.
- _____, A. W., and Schwartz C. C. 1986. Black bear predation on moose calves in highly productive versus marginal moose habitats on the Kenai Peninsula, Alaska. *Alces* 22: 139-154.
- Schwartz, C. C. 2007. Reproduction, Natality, and Growth. Pages 141–145 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and Management of the North American Moose*. Smithsonian Institution Press, Washington, D. C., USA
- Garner, D., and Wilton, M. 1993. The potential role of winter tick (*Dermacentor albipictus*) in the dynamics of a south central Ontario moose population. *Alces*. 29.
- Geist, V. 1974. On the evolution of reproductive potential in moose. *Nature Canada*. 101: 527-537
- Ginsberg, H. S., and Ewing, C. P. 1989. Comparison of flagging, walking, trapping and collecting from hosts as sampling methods for Northern Deer Ticks, *Ixodes dammini*, and Lone-Star Ticks, *Amblyomma americanum* (*Acari: Ixodidae*). *Experimental & Applied Acarology* 7:313-322
- Haagenrud, H. and Lordahl, L. 1979. Sex differential in populations of Norwegian moose *Alces alces* (L.). - *Meddr. norsk viltforsk.* 3 (6): 1-14
- Healy, C. L. 2018. Moose habitat use during critical periods in the winter tick lifecycle and

- agent-based modeling of moose-winter tick relationships in northern New Hampshire. M.S. Thesis, University of New Hampshire Durham, NH.
- _____, Pekins, P. J., Kantar, L., Congalton, R. G. and Atallah, S. 2018. Selective habitat use by moose during critical periods in the winter tick life cycle. *Alces* 54: 85-100
- Holmes, C. J., Dobrotka, C. J., Farrow, D. W., Rosendale, A. J., Benoit, J. B., Pekins, P. J. and Yoder, J. A. 2018. Low and high thermal tolerance characteristics for unfed larvae of the winter tick *Dermacentor albipictus* (Acari: Ixodidae) with special reference to moose. *Ticks and Tick-borne Diseases* 9:25–30.
- Jones, H. 2016. Assessment of health, mortality, and population dynamics of moose in northern New Hampshire during successive years of winter tick epizootics. M.S. Thesis. University of New Hampshire, Durham, New Hampshire, USA.
- _____, Pekins, P. J., Kantar, L. E., O’Neil, M., and Ellingwood, D. 2017. Fecundity and Summer Calf Survival of Moose During 3 Successive Years of Winter Tick Epizootics. *Alces* 53:85–98.
- _____, Pekins, P.J., Sidor, I., Ellingwood, D., Lichtenwalner, A. and O’ Neal, M. 2019. Mortality assessment of moose (*Alces alces*) calves during successive years of winter tick (*Dermacentor albipictus*) epizootics in New Hampshire and Maine (USA). *Canadian Journal of Zoology* 97: 22–30
- Knulle, W. 1966. Equilibrium humidities and survival of some tick larvae. *Journal of Medical Entomology*. 2: 335-338.
- Mason, G. L., and Madden, D. J. 2007. Performing the Field Necropsy Examination. *Veterinary Clinics of North America - Food Animal Practice* 23:503–526
- Markgreen, G. 1969. Reproduction of moose in Sweden. *Viltrevy* 6: 129-299
- _____. 1982. Moose populations along a climatic gradient across Sweden. *Statens Naturvardsverk PM 1571: 1-52*
- McLaughlin, R. F., and Addison, E. M. 1986. Tick (*Dermacentor albipictus*)-induced winter hair-loss in captive moose (*Alces alces*). *Journal of Wildlife Diseases* 22:502–510.
- McPherson, M., Shostak, W. and Samuel, W. M. 2000. Climbing simulated vegetation to heights of ungulate hosts by larvae of *Dermacentor albipictus* (Acari: Ixodidae). *Journal of medical entomology* 37:114–120.
- Mech, L.D. 1983. *Handbook of animal radio tracking*. University of Minnesota Press, Minneapolis, MN. 107 pp.
- Mooring, M. S., and Samuel, W. M. 1998. The biological basis of grooming in moose: programmed versus stimulus-driven grooming. *Animal Behaviour*. 56:1561–1570.
- _____, M. S., and Samuel, W. M. 1999. Premature loss of winter hair in free-ranging moose (*Alces alces*) infested with winter ticks (*Dermacentor albipictus*) is correlated with

- grooming rate. *Canadian Journal of Zoology* 77:148–156.
- Maine Forest Service. 2016. *Silvicultural Activities Report including Annual Report on Clearcutting and Precommercial Activities*. Augusta, Maine, USA.
- Munson, L. 2013. *Necropsy of Wild Animals*. University of California, Davis.
- Musante, A. R., Pekins, P. J., and Scarpitti, D. L. 2007. Metabolic impacts of winter tick infestations on calf moose. *Alces* 43:101–110.
- _____, A. R. 2006. Characteristics and Dynamics of a Moose Population in Northern New Hampshire. 162.
- _____, A. R., Pekins, P. J., and Scarpitti, D. L. 2010. Characteristics and dynamics of a regional moose *Alces alces* population in the northeastern United States. *Wildlife Biology* 16:185–204.
- New Hampshire Fish and Game Department. 2015. *New Hampshire Game Management Plan: 2016-2025*. New Hampshire Fish and Game Department, Concord, New Hampshire.
- Oliver, C.D., and Larson, B.C. 1996. *Forest Stand Dynamics: updated edition*. John Wiley & Sons, Inc.
- Patrick, C. D., and Hair, J.A. 1975. Ecological observations on *Dermacentor albipictus*(Packard)ineasternOklahoma (Acarina: Ixodidae). *Journal of Medical Entomology* 12: 393–394.
- _____, and _____.1979.Ovipositionbehaviour and larval longevity of the lone star tick, *Amblyomma americanum* (Acarina: Ixodidae), in different habitats. *Annals of the Entomological Society of America* 72: 308–312
- Piesman, J., Donahue, J. G., Mather, T. N., and Spielman, A. 1986. Transovarially acquired Lyme disease spirochetes (*Borrelia burgdorferi*) in field-collected larval *Ixodes dammini* (*Acari: Ixodidae*). *Journal of Medical Entomology* 23: 219
- Pybus, M. J. 1999. Moose and ticks in Alberta: a die-off in 1998/99. Occasional Paper No. 20. Fisheries and Wildlife Managemetn Division, Edmonton, Alberta, Canada
- Saether, B.-E., and Haagenrud, H. 1983. Life History of the Moose (*Alces alces*): Fecundity Rates in Relation to Age and Carcass Weight. *Journal of Mammalogy* 64:226–232.
- Samuel, W. M. 1991. Grooming by moose (*Alces alces*) infested with the winter tick, *Dermacentor albipictus* (*Acari*): a mechanism for premature loss of winter hair. *Canadian Journal of Zoology* 69: 1255-1260
- _____. 2004. White as a ghost: Winter ticks and moose. *Nature Alberta*. 1:100.
- _____. 2007. Factors affecting epizootics of winter ticks and mortality of moose. *Alces* 43: 39-48

- Scarpitti, D. L., Habeck, C., Musante, A. R., and Pekins, P. J. 2005. Integrating Habitat Use and Population Dynamics of Moose in Northern New Hampshire. *Alces* 41:25–35.
- _____, D. L., Pekins, P. J., and Musante, A. R., 2007. Characteristics of neonatal moose habitat in northern New Hampshire. *Alces* 43:29–38.
- Schwartz, C. C., and Hundertmark, K. J. 1993. Reproductive Characteristics of Alaskan Moose. *The Journal of Wildlife Management* 57:454.
- Sergeant, D., and Pimlott, D. H. 1959. Age determination in moose from sectioned incisor teeth. *Journal of Wildlife Management* 23:315–321.
- Simkin, D. W. 1965. Reproduction and Productivity of Moose in Northwestern Ontario. *Journal of Wildlife Management* 29:740.
- _____. 1974. Reproduction and productivity of moose. *Nat. Can. (Que.)* 101: 517-526
- Sine, M., Morris, K. and Knupp, D. 2009. Assessment of a line transect field method to determine winter tick abundance on moose. *Alces* 45:143–146.
- Timmermann, H. R., and Whitlaw, H. A. 1992. Selective moose harvest in north central Ontario. *Alces*. 28:137-163
- Van Ballenberghe, V., and BALLARD, W. B. 2007. Population dynamics. Pages 223-245 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and Management of the North American Moose*. Smithsonian Institution Press, Washington DC., USA
- Verme, L. J. 1969. Reproductive Patterns of White-Tailed Deer Related to Nutritional Plane. *Journal of Wildlife Management* 33:881.
- Wattles, D. W., and DeStefano, S. 2013. Space Use and Movement of Moose in Massachusetts: Implications for Conservation of Large Mammals in a Fragmented Environment. *Alces* 49:65–81.
- Welch, D. A., Samuel, W. M. and Wilke, C. J. 1991. Suitability of moose, elk, mule deer, and white-tailed deer as hosts for winter ticks (*Dermacentor albipictus*). *Canadian Journal of Zoology* 69:2300–2305.
- Yoder, J. A., Pekins, P. J., Jones, H. F., Nelson, B. W., Lorenz, A. L., and Jajack, A. J. 2016. Water balance attributes for off-host survival in larvae of the winter tick (*Dermacentor albipictus*; Acari: Ixodidae) from wild moose. *International Journal of Acarology* 42:26–33.
- _____, J. A., Pekins, P. J., Lorenz, A. L., Nelson, B. W. 2017a. Larval behaviour of the winter tick, *Dermacentor albipictus* (Acari:Ixodidae): evaluation of CO₂ (dry ice), and short- and long-range attractants by bioassay. *International Journal of Acarology* 43:187–193.
- _____, J. A., Pekins, P. J., Nelson, B. W., Randazzo, C. R., and Siemon, B. P. 2017b. Susceptibility of Winter Tick Larvae and Eggs to Entomopathogenic Fungi - *Beauveria bassiana*, *Beauveria caledonica*, *Metarhizium anisopliae*, and *Scopulariopsis brevicaulis*. *Alces*: 53:41–51.

Appendix

Appendix A: Institutional Animal Care and Use Committee Approval