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DRIVERS OF SPACE USE AND WINTER TICK LOADS OF MOOSE IN MAINE

By

Annie Stupik

B.S. University of Connecticut, 2014

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Wildlife Ecology)

The Graduate School

The University of Maine

August 2024

Advisory Committee:

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DRIVERS OF SPACE USE AND WINTER TICK LOADS OF MOOSE IN MAINE

By Annie Stupik

Thesis Advisors: Dr. Sabrina Morano and Dr. Pauline Kamath

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
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The moose (*Alces alces)* population in the northeastern United States has experienced regional declines in recent years, primarily due to parasitism by winter ticks (*Dermacentor albipictus*). Three factors drive winter tick epizootics: climate change, moose density, and overlap in moose seasonal space use. Previous research has shown that moose density increases with the proportion of optimal habitat (regenerating forest stands) available on the landscape, and average individual tick load is positively correlated with moose density. We used data from GPS-collared moose from 2014–2022 in Maine to explore relationships between moose space use, seasonal overlap, climate, and tick loads on moose.

For Chapter 1, we identified drivers of seasonal moose space use and overlap moose corresponding to the drop-off (spring) and questing (fall) periods of winter ticks. We modeled seasonal home and core range area and seasonal home range overlap, using generalized linear models, and modeled habitat selection of overlap areas using resource selection functions. Fall area increased with precipitation and decreased with later first frost dates. Juveniles had larger fall areas than adults. Spring area decreased with the availability of optimal habitat (forest aged 4-20 years) and snow depth, and it increased with the availability of older forest (aged 21-37 years). Seasonal overlap was positively correlated with the availability of older forest and negatively correlated with snow depth and percent hardwood. Moose selected for optimal habitat within overlap areas compared to the surrounding landscape. Our findings indicate that moose concentrate space use in optimal habitat. Additionally, moose appeared to overlap less in areas with more hardwood, likely due to habitat preferences during the leaf-off season. These results provide insight into demographic and environmental drivers of moose seasonal space use, which play a role in the winter tick system.

In Chapter 2, we modeled tick loads on moose as a function of fall space use, spring-fall home range overlap, and weather variables. To examine the effects of space use and overlap, we made inferences about moose behavior in the period prior to capture based on data from collared individuals after capture. We used generalized linear mixed models to analyze these relationships. Fall precipitation was negatively correlated with tick loads on moose, while late summer drought and snow depth in early spring had positive effects on tick loads. Tick loads were lower on individuals that generally had higher percentages of hardwood in their fall home ranges. Moose with higher seasonal overlap on average had higher tick loads. Our results support the hypothesis that the degree to which moose overlap space use between drop-off and questing seasons may expose individuals to higher tick loads due to re-infection. Additionally, the observed relationship between percent hardwood and tick loads suggests that forest type may affect tick distribution and moose exposure. We recommend that future research focus on winter tick distribution and survival on the landscape at different life stages. Overall, results from this study build upon previous research in the moose-winter-tick system, highlighting the potential importance of space use in parasite transmission.

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CHAPTER 1

DRIVERS OF SEASONAL MOOSE SPACE USE AND OVERLAP DURING WINTER TICK DROP-OFF AND QUESTING PERIODS

1.1 Introduction

Animal movement across the landscape not only influences exposure to limiting factors such as predation and food resources, but also shapes the dynamics of wildlife-parasite interactions. These interactions are changing across taxa and geographic distributions due to the warming climate and land use patterns (Gallana et al. 2013; Cohen et al. 2020; Guo, Bonebrake, and Gibson 2019; Reis et al. 2021). Environmental conditions affect parasite transmission to host animals through both direct effects, such as accelerated phenology of tick species due to a warming climate (Levi et al. 2015), and indirect effects, such as alterations to host animal movement and behavior (Cable et al. 2017; Sih et al. 2018). While changes in host movement may affect wildlife-parasite dynamics through exposure, they also may alter susceptibility to disease through energetic tradeoffs.

The winter tick has recently caused unprecedented mortalities of moose calves in the northeastern United States and Canada (Bergeron, Pekins, and Rines 2013; Jones et al. 2019; Musante, Pekins, and Scarpitti 2010; Pouchet et al. 2024). Like other large herbivores, moose play an important role in the community assembly and structure of the ecosystems they inhabit (Bowyer, Ballenberghe, and Kie 1997). After near extirpation due to habitat loss and unregulated hunting, moose populations in the northeastern United States rebounded in the latter half of the 1900s with landscape changes and harvest regulations (Allen 1870; Ariza 1928; Wattles and DeStefano 2011). Outbreaks of spruce budworm (*Choristoneura fumiferana*) and the subsequent salvage activities of the commercial timber industry created extensive areas of regenerating forest, a preferred habitat for moose (Etheridge et al. 2006; Fisher and Wilkinson 2005; Telfer 1974), from the late-1970s to early 1990s. Recently, however, the regional moose population has begun to decline again, primarily due to parasitism by winter ticks (Bergeron et al. 2013; Blouin et al. 2021*a;* Jones et al. 2017).

Moose space use (i.e., habitat selection, movement, home ranges) is dictated by the same driving factors as other large herbivores, including the search for food, cover, and predator avoidance (Rosenzweig 1981; Mysterud and Ostbye 1999; Lima and Dill 1990). In addition, space use of moose and other ungulates is affected by sex, age, season, and landscape characteristics (Blouin 2021; Osko et al. 2004; Street et al. 2015; Herfindal et al. 2009). Males typically have larger home ranges than females due to mating behavior and differences in energetic demands (Borowik et al. 2021; Allen et al. 2016; Ofstad et al. 2016). Though more variable for females, both sexes have been known to demonstrate greater movement and larger home ranges in the fall season before the onset of midwinter conditions (Stenhouse et al. 1995; Olsson et al. 2011). This pattern is typical for cervids and is likely due to searching for mates in the rut and seasonal changes in forage availability (Harestad and Bunnel 1979; Whitman et al. 2018). In addition to sex and season, individual age factors into how ungulates move and establish home ranges as individuals presumably accrue knowledge of the landscape over time (Malagnino et al. 2021; Herfindal et al. 2009; Allen et al. 2016). Factors associated with seasonality, including snow depth (Melin et al. 2023), timing of spring green-up (Aikens et al. 2020), precipitation (Van Beest et al. 2011), and temperature (Alston et al. 2020), affect ungulate space use in a myriad of ways.

In the northeastern United States, New Brunswick, and southern Quebec, moose density is comparatively higher than in other regions due to lack of predators and abundance of preferred habitat (Wattles and DeStefano 2011; Scarpitti et al. 2005; Bergeron et al. 2011; Kantar and Cumberland 2013). During winter, moose in this region browse primarily on fir (*Abies balsamia*) (Ludewig and Bowyer 1985; Thompson et al. 1995), but are also known to select for other species of softwood, hardwood, or mixed stands, depending on the season (Dimatteo-LePape et al. 2023; Stewart, Komers, and Bender 2010). Fine-scale landscape structure affects habitat use for both sexes across all seasons (Blouin et al. 2021*a*). While space use is highly variable across individuals, overlap between seasons has been consistently documented (Scarpitti et al. 2005; Thompson et al. 1995; Healy et al. 2018; Blouin et al. 2021*b*).

Habitat use in fall and spring has been of particular interest in eastern North America because of its potential for affecting exposure during the corresponding questing and drop-off periods of winter tick (Pekins 2020). Winter ticks seek hosts as larva in autumn, which is known as the questing period. Following attachment, they take two blood meals, the first typically in January to mature into nymphs and the second to grow into adults, before dropping off the host in early spring (Drew and Samuel 1989). Females then lay eggs in the environment which hatch into larva over summer, beginning the cycle again. Using an occupancy modeling framework, Blouin et al. (2021*b*) found that more young forest led to increased use by moose during both the fall questing and the spring drop-off period. Healy et al. (2018) found that fall and spring home ranges overlapped each other as much as 73%. However, no study to date has quantified the degree of fine-scale seasonal overlap to determine whether factors driving seasonal space use also affect seasonal overlap on an individual level.

While winter ticks have been parasitizing moose for centuries, epizootic events – years when calf mortality is greater than 50% – have increased in frequency over the past two decades (Hoy et al. 2021; Bergeron, Pekins, and Rines 2013; Jones, Pekins, and Kantar 2017). The severity of winter tick epizootics in moose is believed to be a function of three factors: environmental conditions for tick larva, moose density, and the overlap of moose seasonal habitat use (Pekins 2020; Samuel 2007). Regarding the first factor, environmental variables such as humidity, snow depth, and temperature affect tick survival and questing behavior in the environment (Yoder et al. 2016; Addison et al. 2016; Pouchet et al. 2024). High moose density is expected to support larger tick populations and increase the probability of transmission (Dunfey-Ball 2017), which is supported by observed positive correlations between moose density and winter tick infection loads estimated via tick counts on individuals (Samuel 2007; Healy et al. 2020; Pouchet et al. 2024). The degree to which moose use overlapping areas on the landscape during the winter tick questing and drop-off periods also can influence tick transmission probability. Moose that demonstrate greater use of the same areas during the tick drop-off and subsequent questing period in a given year may be more likely to re-infect themselves with a high tick load. This higher transmission probability could ultimately increase the frequency and severity of epizootics (Healy et al. 2018; Van Beek 2023; Blouin et al. 2021*b*). While research has shown that moose select for young forest across both the questing and drop-off periods (Blouin et al. 2021*b*; Healy et al. 2018), little is known about other factors that drive overlap in seasonal space use and how it varies among individual moose across time.

The goal of our study was to explore the role of demographic, climatic, and landscape characteristics on moose space use and seasonal overlap during the winter tick questing and drop-off periods. We quantified space use and overlap using data from GPS collared moose in

Maine across 9 years to identify the drivers of variation in moose seasonal space use and overlap, with the latter being of particular interest due to its suggested role in winter tick transmission. Our specific objectives were to 1) estimate seasonal home and core range area and quantify seasonal overlap, 2) examine the effects of demographic and environmental variables (moose age, forest composition, and weather) on home/core range areas and overlap, and 3) identify landcover characteristics within areas of seasonal overlap as compared to the surrounding landscape. We expected that males would have larger range areas due to rutting behavior and greater energetic demands associated with higher mass. We predicted that juveniles would have larger range areas and less seasonal overlap than mature moose due to exploratory movements following natal dispersal. For all moose, we expected that fall range areas would be larger than spring range areas due to seasonal change in forage availability and movement during the breeding season. Additionally, we expected the degree of spring-fall overlap to increase with the amount of regenerating forest available because presumably moose concentrate use in these areas of high-quality forage.

The moose-winter-tick system offers a unique opportunity to examine the role of landscape composition in parasite exposure. By exploring drivers of seasonal overlap, we hoped to contribute to knowledge surrounding moose-winter-tick dynamics and potentially inform management.

1.2 Methods

1.2.1 Study area

The study area encompassed approximately 3,000 mi^2 (8000 km^2) in northern and western Maine, primarily in Wildlife Management Districts (WMDs) 2 and 8 (Figure 1.1). The region is almost entirely forested, composed primarily of mixed hardwood and coniferous stands. The dominant species in the coniferous stands are Balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*); the hardwood stands consist primarily of maple/beech/birch (*Acer, Fagus, Betula* spp.) (McCaskill et al. 2016). Due to active commercial timber harvest throughout the region, the forest age varies from recently cut to relatively mature forest depending on the prescribed rotation (40-80 years old; Seymour and Malcolm 1992). Moose density estimates have varied by location and year, ranging from ~1 to 2.5 moose/km^2 (Jones, Pekins, and Kantar 2017; Kantar and Cumberland 2013). These estimates were collected using aerial surveys on a large spatial scale; more fine scale density on the landscape is difficult to estimate (Moll et al. 2022).

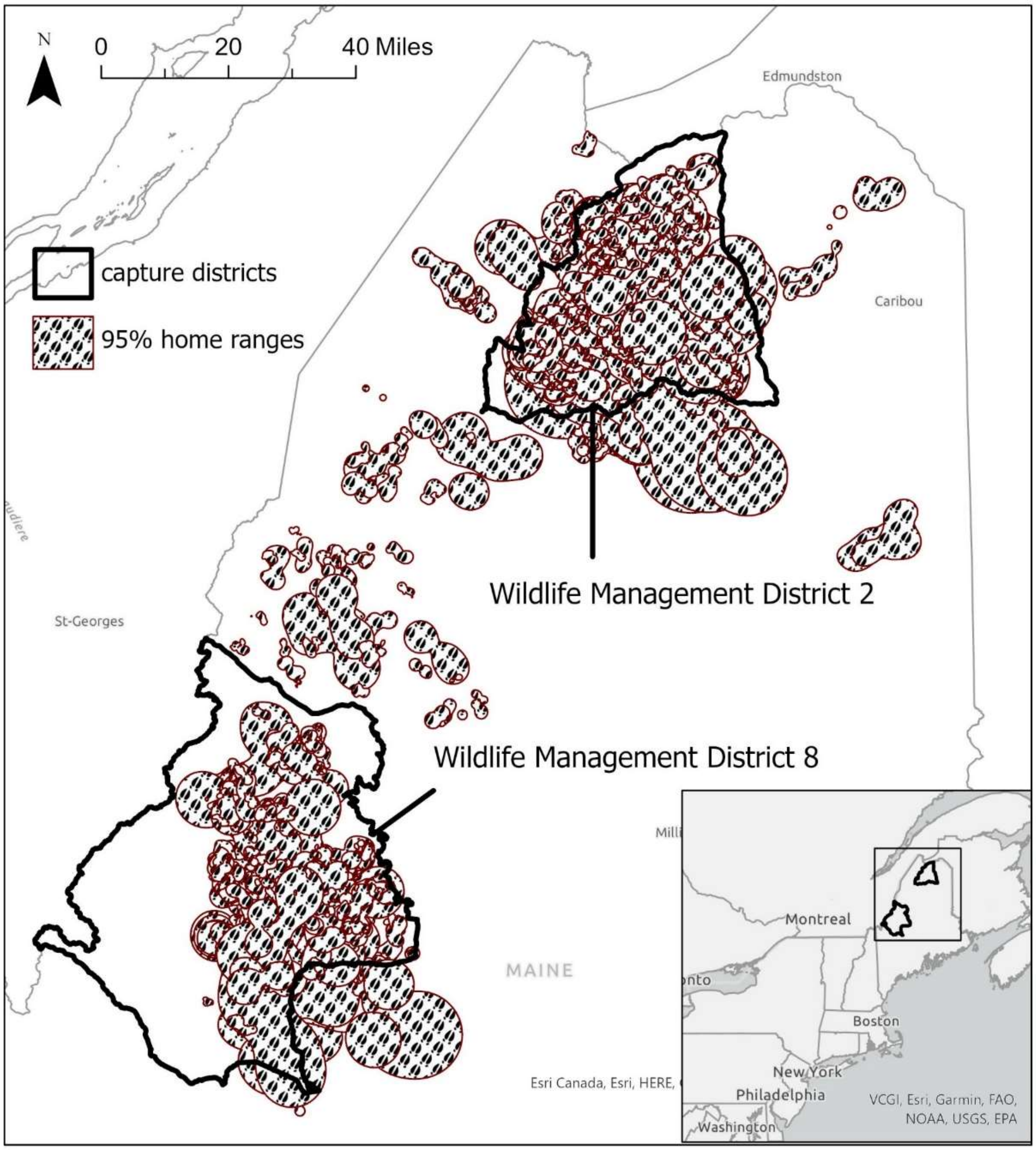

Figure 1.1. *Study area in northern and western Maine. Captures were conducted in Wildlife Management Districts 2 and 8 between 2014 and 2022. Home ranges from 159 female moose used in this study are delineated by the red lines.*

1.2.2 Moose capture and data collection

Since 2014, Maine Department of Inland Fisheries and Wildlife (MDIFW) has been capturing moose annually each January as part of a larger project on calf mortality and winter tick dynamics. Moose (*n* = 727) were captured from a helicopter using a rocket net in Wildlife Management Districts (WMD) 2, 4, and 8. From 2014 to 2020, moose (*n* = 529) were captured in WMDs 2 and 8, and from 2021-2022, moose (*n* = 198) were captured in WMD 4. All animals were captured and handled following protocols established by the Institutional Animal Care and use Committees from the University of New Hampshire (protocol #130805) and the University of Maine (protocol #A2020_12_01). At capture, staff affixed GPS collars (Vectronics-aerospace Vertex Plus Survey Collar [Globalstar], Vectronic-aerospace Survey 2-D Iridium collar). Collars were programmed to transmit GPS locations daily at 5am and 5pm. As moose are active during day and night (Klassen and Rea 2008; Bevins, Schwartz, and Franzmann 1990), we assumed that these two fixes adequately captured a moose's daily activity patterns. Most GPS collars transmitted data from captured individuals for several years. To minimize potential errors in GPS collar locations, we eliminated any fixes that were collected using less than 4 satellites. We also eliminated fixes that were not within the 99% percentile of movement rate to remove a negligible amount of erroneous fixes (99% percentile for spring = 127 meters/hour; 99% percentile for fall = 251 meters/hour).

MDIFW targeted calves and adult females to determine population persistence, with some males and juveniles (2-year-olds) of both sexes also captured. Adult females tend to be a better metric of ungulate population growth (DeCesare et al. 2012), and calves are more susceptible to tick related mortality (Jones et al. 2019; Ellingwood et al. 2020). Calves, or individuals in their first year of life, are notably smaller than adults (Gaillard 2007). Out of the

727 moose captured, 604 were calves. If an individual died following capture, walk-ins on the carcass were conducted when possible and teeth were extracted to retroactively estimate age at capture as either a juvenile (2-year-old) or adult (≥3 years old). For moose that survived through the end of the study, a tooth extraction was not obtained; thus, we considered these individuals to be unknown age (≥2 years old) at the time of capture.

1.2.3 Estimation of space use and overlap

We estimated space use of juvenile, adult, and unknown-aged moose. Because calves can stay with their mothers for up to two years, we did not estimate space use of individuals less than 2 years old (Labonte et al. 1998; Ballard, Whitman, and Reed 1991). However, if an animal collared as a calf (≤1 year old at capture) lived to at least 2 years old, we considered it a juvenile once it reached 2 years of age and included it in our analyses from that point onwards. If an individual was not captured as a calf and no teeth were extracted following capture, we considered the animal to be of unknown age (juvenile or adult) for the first year we estimated its space use. However, once an individual of unknown age at capture was collared for more than one year, we graduated it into the adult age class for subsequent years. If an individual was a calf or juvenile at capture, we also graduated its age class each year. For example, if a given individual was collared as a calf in January of year y, we did not estimate its space use in year y but estimated its space use in year $y + 1$ as a juvenile, and in year $y + 2$ as an adult.

We assigned the spring and fall seasons corresponding to tick drop-off and questing periods, respectively, as identified in previous studies (Healy et al. 2018; Drew and Samuel 1989; Samuel, Mooring, and Aalangdong 2000). In accordance with these periods, we defined spring as March 15 to May 5 (51 days) and fall as September 15 to November 26 (72 days). If a moose lived the entirety of a season with no gaps in collar fix transmission, it would have 102 fixes in the spring and 144 fixes in the fall. However, some collars transmitted less frequently than programmed as they aged. Additionally, many moose died partway through a given season. Thus, to maximize our sample size while still representing several weeks of each season, we only calculated space use for moose that had at least 75% of the maximum potential representation, which was equivalent to ≥76 fixes for spring and ≥108 fixes for fall.

After splitting by spring and fall seasons, we estimated space use using kernel density estimators (KDE), a commonly used method for estimating home ranges. The KDE delineates a probabilistic area based on the animal's utilization distribution (Worton 1989; Powell and Mitchell 2012; Laver and Kelly 2008). Due to our large sample size (*n* = 194 collared moose) and computational demands, we used the traditional KDE instead of the more recently developed autocorrelated KDE (Fleming and Calabrese 2017, Silva et al. 2022). We estimated 95% and 50% fixed kernels to represent a given individual's annual home and core ranges, respectively, which is consistent with the literature (Laver and Kelly 2008; Werdel et al. 2021; Roffler and Gregovich 2018). We used the reference bandwidth as the smoothing parameter and delineated home range and core range isopleths with 95% and 50% contours around the kernel utilization distributions. We removed home and core ranges that intersected Canada due to lack of spatial data for included predictors (see *Landscape data* below). As many moose were collared for multiple years, we calculated seasonal home and core ranges per individual across years when possible. We attempted to account for autocorrelation using individual as a random effect in our models but did not have enough repeated measures to detect an effect. We estimated a total of 757 seasonal home ranges for 190 individual moose and 759 core ranges for 192 individual moose across 9 years.

After separating home ranges by season, we calculated home range area and maximum distance moved between any two fixes within a season and visually compared these two metrics with the home range isopleths to identify outliers. A small subset of our total sample demonstrated apparent displacement. As maximum distance was a more effective metric than home range area for identifying these large movements, possibly indicating dispersal events, we removed home ranges that had a maximum distance greater than 2 times the standard deviation above the mean ($n = 42$ out of 757). We applied this same method to core ranges ($n = 43$ out of 759). Thus, we reported characteristics of 715 home ranges and 716 core ranges, which included both males and females. However, because of sex differences in space use (Ofstad et al. 2016; Ruckstuhl and Neuhaus 2002) and our relatively small sample size for males ($n = 30$ individuals) we excluded males from any subsequent analyses. Using generalized linear models, we modeled home and core range area as a function of the number of fixes per season to ensure that space use area was not biased by the number of fixes per season threshold mentioned above (see Appendix A Figure A.1). The average number of fixes per home range was 74 in the spring and 105 in the fall. We found no evidence that the number of fixes affected home or core range area in either season ($p > 0.2$; see Appendix A Table A.3). To reduce skewness in the data, we log-transformed area for both home and core ranges prior to model estimation. Our final sample size for space use analyses consisted of home and core ranges ($n = 330$ spring, $n = 297$ fall for both home and core ranges) from 159 individual females.

To calculate seasonal overlap between spring and fall, we used the utilization distribution overlap index (UDOI; Fierberg and Kochanny 2005). This method uses the three-dimensional utilization distributions to account for internal heterogeneity of use within the seasonal home ranges. The UDOI represents an index of overlap, where 0 indicates no overlap and 1 indicates

100% overlap. Values greater than 1 occur when highly overlapping utilization distributions are not uniformly distributed. As moose were collared in January, we estimated overlap for individual females (*n* = 111) that had both spring and fall home ranges (95% isopleths) delineated for the same calendar year. Some females were collared for multiple years and contributed more than one year of spring and fall home ranges. In total, our UDOI dataset included 230 seasonal overlap estimates. We examined the relationship between moose age and home range overlap with a subset of the data from known-age individuals but found no significant effect (*p* = 0.4). Thus, we combined all aged individuals (adults, juveniles, and unknown) and did not include age in our seasonal overlap model. To understand how seasonal home range area influenced the degree of overlap, we used generalized linear regression to model overlap as a function of spring and fall home range area. We conducted all home range and overlap estimation in R (CRAN; version 4.2.1) using the ‘amt’ package (Signer et al. 2019, version 0.1.7).

1.2.4 Landscape data

We considered several factors as potentially important for moose space use in eastern North America. While moose are found in many landcover types, previous studies suggest their preferred habitat is regenerating forest at least 4 years after a disturbance event (Peek, Urich, and Mackie 1976; Cumming 1980; Mumma et al. 2021). Across Vermont, New Hampshire, and Maine, forests aged 4 to 16 years post-disturbance have been considered to be optimal moose habitat (Dunfey-Ball 2017; Healy et al. 2018; Blouin 2021). However, our study area within Maine has comparatively poorer soil quality than much of northern Vermont and New Hampshire, potentially causing slower vegetation growth (Ferwerda et al. 1997; Goss and Oliver

2023). To account for this, we expanded the optimal habitat forest age range used in previous studies to forests aged 4 to 20 years post-disturbance. We defined this range based on common tree species height-age curves and the maximum moose browse height of 3 meters (Danell, Huss-Danell, and Bergstrom 1985; Nichols, Cromsigt, and Spong 2015; Meng and Seymour 1992; Carmean, Hahn, and Jacobs 1989).

We used remotely sensed data from the Landscape Change Monitoring System (LCMS, USDA Forest Service 2022) to construct a map of forest age classes. The LCMS contains annual disturbance rasters classified into several vegetation cover change categories; we used the "fast loss" category to identify local disturbance events on the landscape and assign forest age as years since disturbance. To maximize representation of our stand age data set while maintaining a conservative approach, we binned forest age into four classes: <4 years, 4-20 years, 21-37 years, and >37 years. We quantified the percent composition of each forest age class per seasonal home and core range polygon. Because LCMS does not provide information on harvest intensity, we were unable to distinguish between disturbance types (e.g., partial harvest, clearcut, overstory removal). We recognize our approach may overestimate the amount of young forest on our landscape because partial harvesting is the predominant form of management in our study area (Canham, Rogers, and Buchholz 2013).

In addition to forest age, we included forest composition and climate variables in our space use models. We calculated percent hardwood per home/core range using land cover data from the 2019 National Land Cover Dataset (Dewitz 2021) where we considered the deciduous forest category to represent percent composition of hardwood. To estimate spring snow depth, we averaged daily snow depth (mm) in our spring season (March 15 to May 5) across years using data collected from the National Snow and Ice Data Center (NOAA). To estimate fall precipitation, we averaged monthly rasters from September, October, and November to obtain an average fall precipitation raster (mm) for each year (PRISM Climate Group 2013-2022). We used data from Fort Kent and Brassua Dam weather stations from the National Weather Service (NOAA) to estimate Julian day of first fall frost. We extracted Julian day of spring green-up using MODIS Land Cover Dynamics (MCD12Q2 version 6) downloaded from Google Earth Engine (Ganguly et al. 2010; Gorelick et al. 2017; Briones 2021). However, due to high correlation ($R > 0.6$), we used spring snow depth as a proxy for green-up. We extracted snow depth, fall precipitation, and percent hardwood by home/core range polygon. We quantified first fall frost date and spring green-up using the larger scale of the wildlife management district (at capture) due to low spatial variation in these variables (Table 1.1). To quantify how landscape composition variables (percent hardwood and forest age classes) influenced seasonal overlap, we averaged the values across the spring and fall home ranges that were used to calculate a given UDOI.

Table 1.1: *Covariates used in space use analyses, the season and scale at which each variable was quantified, and the source from where the data were obtained.*

Covariate	Season	Scale	Source
Spring snow depth (mm)	Spring	Seasonal home range polygon	Snow Data Assimilation System (SNODAS), National Snow and Ice Data Center (Barrett, 2003)
Spring green-up (Julian day)*	Spring	Wildlife management district	MODIS Land Cover Dynamics (MCD12Q2) version 6 collection, Google Earth Engine (Ganguly et al. 2010, Gorelick et al. 2017, Briones 2021)
Fall precipitation (mm)	Fall	Seasonal home range polygon	PRISM Climate Group (2013-2022; Daly et al. 2008)
First fall frost (Julian day)	Fall	Wildlife management district	Fort Kent and Brassua Dam weather stations, National Oceanic and Atmospheric Administration
Percent hardwood	Spring & fall	Seasonal home range polygon	2019 National Land Cover Dataset (Dewitz, J. 2021)
<4 year old forest	Spring & fall	Percent composition of seasonal home range polygon	Landscape Change Monitoring System (LCMS, USDA Forest Service 2022)
4-20 year old forest	Spring & fall	Percent composition of seasonal home range polygon	Landscape Change Monitoring System (LCMS, USDA Forest Service 2022)
21-37 year old forest	Spring & fall	Percent composition of seasonal home range polygon	Landscape Change Monitoring System (LCMS, USDA Forest Service 2022)

*spring green-up was dropped from all models due to high correlation with spring snow depth

1.2.5 Predictors of seasonal home range area and overlap

To explore drivers of seasonal home range area, we used a two-stage modelling approach. First, we fit linear models to log-transformed home and core range area (response variable) for each variable of interest, separated by season (Table 1.1). We ranked variable importance using AIC model selection on single-term model sets with the ‘AICcmodavg’ R package (Mazerolle 2017). We first considered forest age variables (<4, 4-20, 21-37, and >37 years old), and then added spring snow depth, fall precipitation, percent hardwood, and first fall frost date. We identified important variables as those that ranked above the null model, then used those variables to build our final models for spring and fall home/core range area. In the first stage of model-building, we found high correlation between the >37 forest age class and the 4-20 and 21-37 age classes (Appendix A, Table A.1); therefore, we removed the >37 forest age variable from all models going forward due to this correlation and low rank in AIC models. Second, we fit 4 generalized linear models for each given season and isopleth level (95%/50%) using the variables identified as important. All covariates in the top-ranking models were standardized to compare effect sizes. We treated moose age class as a continuous variable such that 0 = juvenile and 1 = adult. Then, we scaled the variable and assigned unknown aged individuals a value of 0.

We used this same approach to explore variation in overlap for moose that had at least one spring and fall home range (95% isopleth) within the same calendar year, using a linear regression model with UDOI as the response variable. As UDOI was not normally distributed, we applied a square-root transformation to this variable before running the model.

1.2.6 Habitat selection of seasonal home range overlap

After delineating home ranges and quantifying the degree of seasonal overlap, we examined overlap areas for those individuals with non-zero overlap (*n* = 226 out of 230). We delineated the area of overlap using the intersection of the seasonal home ranges. We were interested in both the descriptive statistics of these overlap areas as well as potential selection for landscape characteristics. To estimate the latter, we compared the overlap area to the available surrounding landscape. To define availability, we buffered each overlap area by 5.4km^2, based on the average annual home range size of moose in the region (Dimatteo-LePape et al. 2023). We then compared landscape characteristics in the overlap area to that of the buffer region to determine selection. We quantified the percent cover of forest age classes (<4, 4-20, 21-37) as well as percent hardwood in the used and available habitats and estimated a resource selection function built as a binomial generalized linear model (Manly et al. 2007).

1.3 Results

1.3.1 Seasonal home and core range variation

As several individuals were collared for multiple years, our sample size after data processing (Table 1.2) was 384 spring home ranges (384 core ranges) and 331 fall home ranges (332 core ranges). Across all ages, the average home range area for females was 16 km^2 in the spring and 35 km^2 in the fall, and average core range area was 3 km^2 in the spring and 8 km^2 in the fall (Table 1.3). For males, the average home range area was 22 km^2 in spring and 71 km^2 in fall, and the average core range area was 5 km^2 in the spring and 17 km^2 in the fall. Juvenile males had larger home and core ranges than adult males in both seasons.

Table 1.2. *Sample sizes of moose home and core ranges at each step of our data processing for home and core range analyses. Some individuals contributed more than one year of spring and fall home ranges as they were collared for more than one year. The number of individuals used to calculate home/core ranges is denoted in italics and parentheses following the home/core range sample size.*

	Total estimated	Did not intersect Canada	Split into seasons and sex			After removing those with maximum distance greater than 2 standard deviations from the mean		
Home range (95% isopleth)	767 *(194)*	757 (*192*)	Spring	Female	348 *(147)*	Spring	Female	330 *(145)*
				Male	57 *(30)*		Male	54 *(30)*
			Fall	Female	315 (*136)*	Fall	Female	297 *(131)*
				Male	37 *(22)*		Male	34 *(20)*
Core range (50% isopleth)	767 *(194)*	759 (*192*)	Spring	Female	348 *(147)*	Spring	Female	330 *(145)*
				Male	57 *(30)*		Male	54 *(30)*
			Fall	Female	316 *(136)*	Fall	Female	297 *(131)*
				Male	38 *(23)*		Male	35 *(21)*

***Table 1.3:** Summary of home (95% kernel density estimator isopleth) and core (50% kernel density estimator isopleth) range information for male and female moose in the fall and spring seasons, separated by moose age class, sex, and season.*

Sex	**Season**	**Age**	**Count of unique individuals**		**Count of total ranges estimated**		**Mean area (km^2)**		**Standard deviation (km^2)**		**Minimum and maximum (km^2)**	
			95%	**50%**	**95%**	**50%**	**95%**	**50%**	**95%**	**50%**	**95%**	**50%**
Female	Fall	Adult	101	101	183	183	34.6	8.0	37.9	8.5	4 – 283	0.9 – 59
		Juvenile	51	51	51	51	41.6	9.9	34.3	8.5	9 – 173	2 – 43
		Unknown	63	63	63	63	29.7	7.0	24.8	5.9	4 – 107	0.9 – 28
	Spring	Adult	112	112	219	219	15.3	3.3	15.4	3.5	0.1 – 109	0.02 – 23
		Juvenile	49	49	49	49	15.5	3.3	16.9	4.4	0.3 – 105	0.08 – 28
		Unknown	62	62	62	62	17.6	3.5	18.3	3.7	0.4 – 97	0.04 – 19
Male	Fall	Adult	9	9	14	14	57.8	13.9	44.9	12.1	11 – 180	3 – 48
		Juvenile	20	21	20	21	80.0	18.7	47	10.9	16 – 167	2 – 37
	Spring	Adult	16	16	25	25	14.1	2.9	10.6	2.5	0.3 – 55	0.06 – 13
		Juvenile	29	29	29	29	28.2	5.9	26.3	6.0	0.9 – 114	0.2 – 25

***Table 1.4**: Covariates tested in multi-stage AIC modeling of seasonal home and core range area. We ran four separate analyses for each season and isopleth. The covariates that ranked above the null model in AIC model selection for each seasonal isopleth level were used to build the final four models.*

	Spring		Fall	
	95% KDE	50% KDE	95% KDE	50% KDE
First frost (Julian day)	n/a	n/a	**supported**	**supported**
Fall precipitation	n/a	n/a	**supported**	**supported**
Spring snow depth	**supported**	**supported**	n/a	n/a
<4	not supported	not supported	not supported	not supported
4-20	**supported**	**supported**	not supported	**supported**
21-37	**supported**	**supported**	not supported	not supported
Percent hardwood	not supported	**supported**	not supported	not supported
Age	not supported	not supported	**supported**	**supported**

For each season, variables ranking above the null model were similar between the home and core ranges (Appendix A Table A.2). In the spring, supported variables included average snow depth, percent 4-20 year-old forest, and percent 21-37 year-old forest (Table 1.4). Additionally, percent hardwood was supported for spring core ranges. Spring snow depth was negatively correlated with both home range area ($\beta = -0.08$, $p < 0.1$) and core range area ($\beta = -0.11$, $p < 0.004$) (Figure 1.2). Similarly, percent 4-20 year-old forest had a negative correlation with home range area ($\beta = -0.09$, $p < 0.08$) as well as with core range area ($\beta = -0.06$, $p > 0.1$). In contrast, percent 21-37 year-old forest had a positive effect on spring home range area ($\beta = 0.12$, $p < 0.02$) and core range area ($\beta = 0.07$, $p < 0.07$). Percent hardwood had a positive correlation with spring core range area ($\beta = 0.06$, $p < 0.09$). Adjusted R^2 values for the top spring models were 0.03 for the home range model and 0.05 for the core range model.

In the fall, supported variables for home and core ranges included first frost date, fall precipitation, and moose age (Table 1.4). For fall core ranges, percent 4-20 year-old forest was also supported. Average fall precipitation had the strongest effect, with a significant positive correlation with both home ($\beta = 0.19$, $p = 2e10^{-5}$) and core range areas ($\beta = 0.18$, $p = 2e10^{-6}$) (Figure 1.2). Moose age had a negative correlation with both home ($\beta = -0.07$, $p > 0.1$), and core ranges ($\beta = -0.06$, $p > 0.1$) such that adults had smaller areas than juveniles. First frost date (Julian day) had a negative correlation with home ($\beta = -0.07$, $p > 0.1$) and core ranges ($\beta = -0.07$, $p < 0.1$). Percent 4-20 year-old forest had a significant negative effect ($\beta = -0.09$, $p = 0.02$) on fall core ranges. The adjusted R^2 values for the top fall models were 0.08 for home ranges and 0.09 for core ranges.

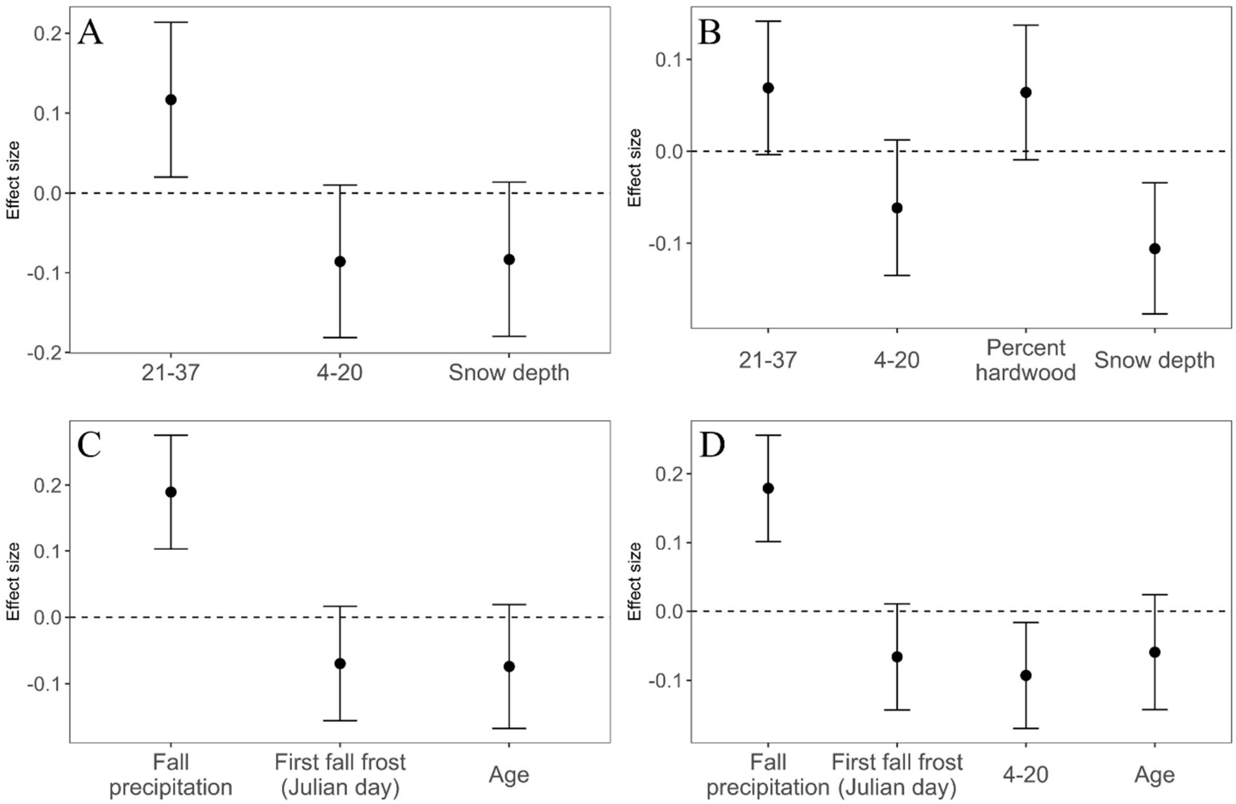

Figure 1.2: *Effect sizes with standard error bars of the z-standardized beta coefficients from the top models for seasonal home (95%) and core (50%) range areas of individual moose. Panels A) and B) depict the model results from spring home and core ranges, respectively, and panels C) and D) depict the model outputs from fall home and core ranges, respectively. We placed age on a continuous scale such that 0 = juvenile and 1 = adult, z-scored the variable, and assigned unknown aged individuals a value of 0 after z-scoring. Juvenile is the intercept-term age.*

1.3.2 Seasonal overlap

Overlap between spring and fall home ranges varied from 0 (no overlap) to 1.04 (100% overlap), with a median of 0.25 and a mean of 0.30. Seasonal home range area affected the degree of overlap in both seasons; area had a positive effect ($\beta = 0.09$, $p = 6e10^{-7}$) in the spring and a negative effect ($\beta = -0.07$, $p = 0.0007$) in the fall (see Appendix A Table A3). Regarding landscape variables, our final model predicting seasonal overlap included percent of 21-37 year-old forest, average fall precipitation, percent hardwood, and average spring snow depth (Figure 1.3, $R^2 = 0.15$). Seasonal overlap significantly decreased with spring snow depth and percent hardwood ($\beta = -0.07$, $\beta = -0.04$ respectively; $p < 0.005$). Percent 21-37 year-old forest had a significant positive correlation with overlap (Figure 1.4; $\beta = 0.04$, $p = 0.007$). While fall precipitation was included in the top model, the effect on overlap was negligible ($\beta = -0.009$, $p > 0.1$).

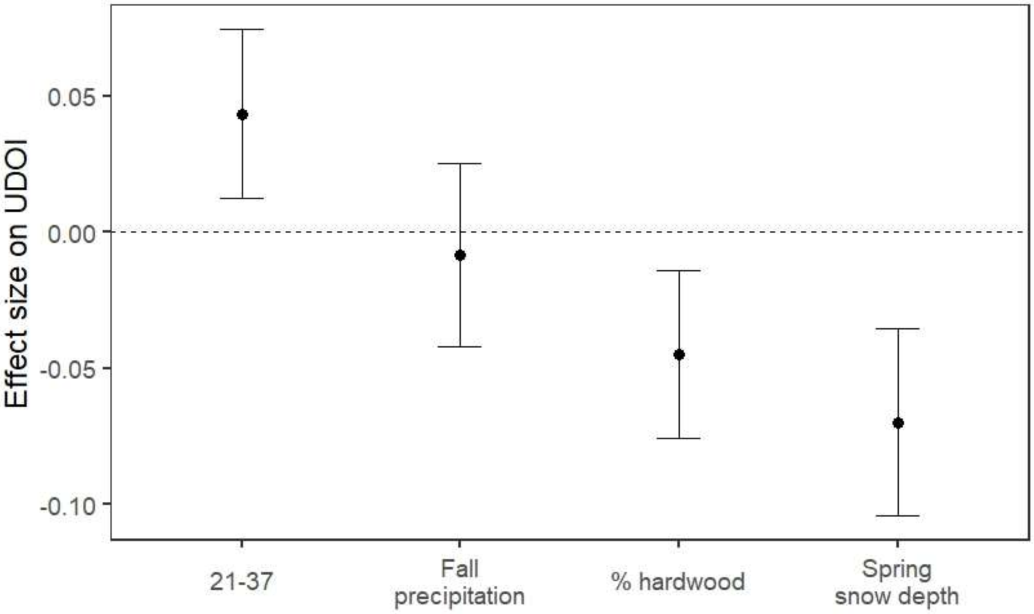

Figure 1.3: *Effect sizes with standard error bars of the z-standardized beta coefficients from the top model for the utilization distribution overlap index (UDOI).*

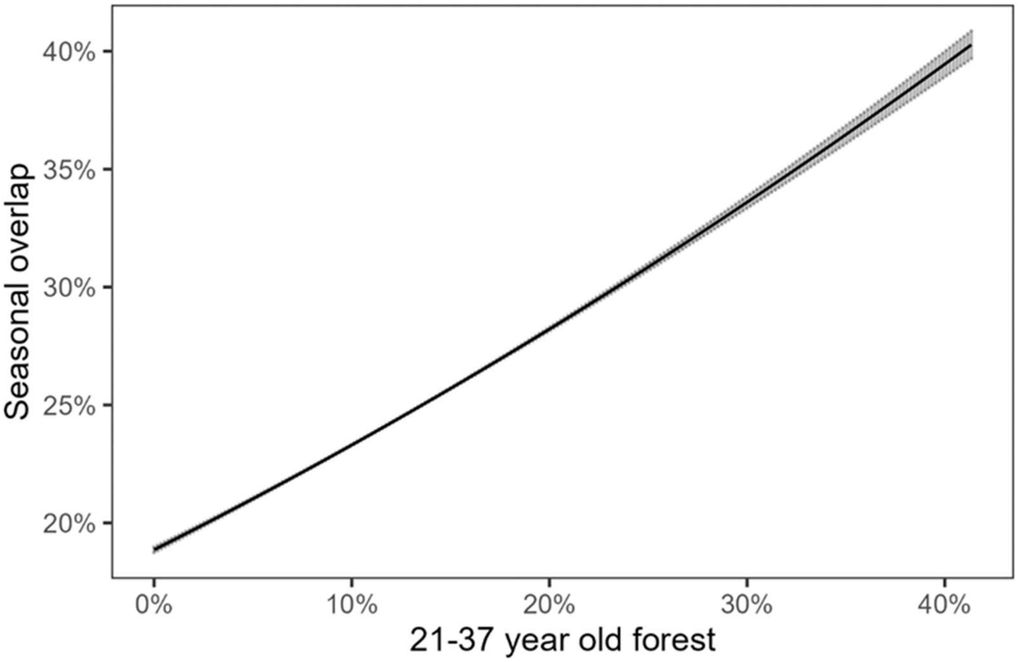

Figure 1.4: *Predicted trend of the effect of percent 21-37 year-old forest on seasonal overlap (UDOI). The lighter gray represents the 95% confidence interval of the trend.*

1.3.3 Habitat selection of seasonal home range overlap

The majority (57%) of the overlap area between spring and fall home ranges consisted of forest aged over 37 years, while 25% was composed of forests aged 4-20 years. The remaining area was distributed among forests 21-37 years old (11%) and forest less than 4 years old (6%). Additionally, hardwood accounted for approximately 19% of the forest composition on average within overlap areas. Resource selection functions comparing overlap areas with the surrounding available landscape revealed that moose showed extremely strong selection for 4-20-year-old forest ($\beta = 0.063$, $p = 9.9e10^{-8}$). Moose did not select for hardwood forest, <4 year-old forest, and 21-37 year-old forest ($p \geq 0.1$).

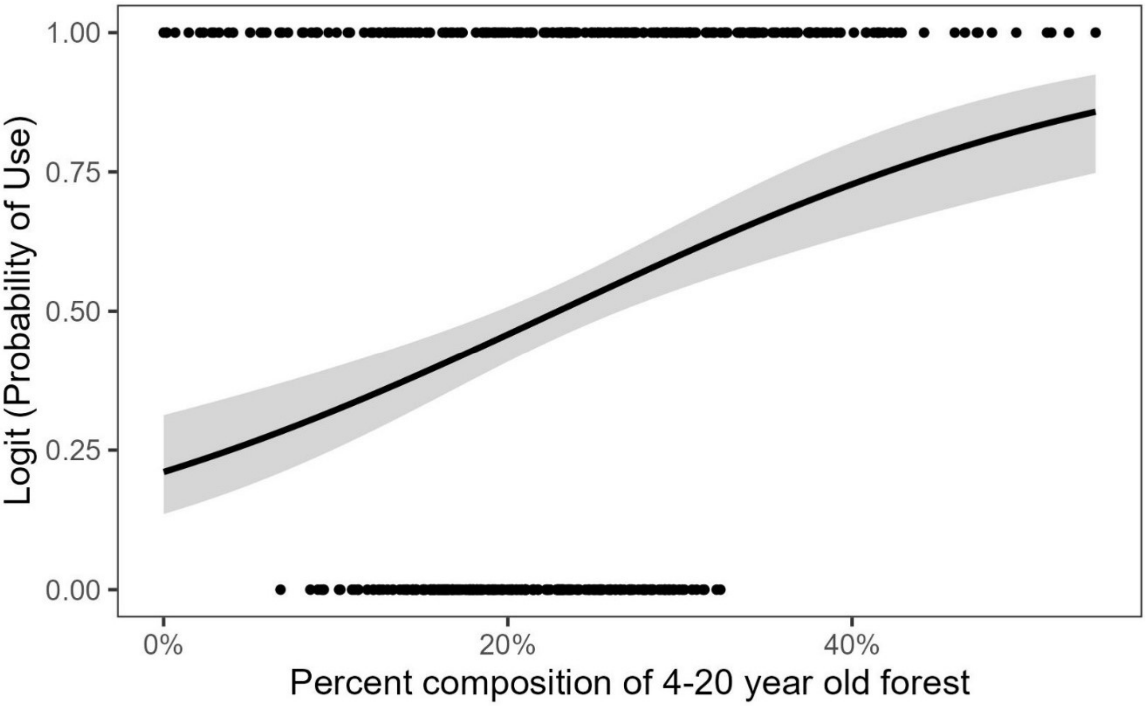

Figure 1.5: *Resource selection function estimates [logit(probability of use)] with standard error as a function of percent composition of 4-20 year-old forest within the seasonal home range overlap area. Points represent used/available data from individual moose.*

1.4 Discussion

Through a study using hundreds of individual moose across several years in Maine, we found that despite high individual variation, moose space use was influenced by several environmental and demographic variables. Overall, home and core ranges were approximately twice as large in the fall than in the spring, and males, especially juveniles, had larger home/core ranges than females. Forest age, snow depth, precipitation, and moose age all affected space use and seasonal overlap, with the strength of effects varying by season and isopleth level (home vs. core range). While higher proportions of older forest across spring and fall home ranges was associated with greater seasonal overlap, moose demonstrated strong selection for young forest within these overlapping areas compared to the surrounding landscape. Previous research has suggested that young forest patches – optimal moose habitat – may be hotspots for winter ticks due to concentrated use by individual or several moose across seasons (Healy et al. 2018; Van Beek 2023). Our findings indicate that in addition to the proportion of young forest, optimal habitat distribution on the landscape affects moose space use. Landscape heterogeneity may play a previously unknown role in moose movement patterns and, consequently, winter tick transmission. Furthermore, this research sheds light on drivers of seasonal overlap in moose. Understanding the dynamics of ungulate space use may be increasingly important to inform management strategies, especially in the face of climate change and parasites.

Our estimates of seasonal home range areas were generally larger than those reported by other studies in the northeastern United States, though our estimates of core range areas were more similar (Scarpitti et al. 2005; Wattles and DeStefano 2013b; Healy et al. 2018). Core ranges represent areas of concentrated use within a given home range, while home ranges typically capture the periphery of an animal's space use (Samuel, Pierce, and Garton 1985; Börger et al. 2006). Average core range area for females was 4 km^2 in the spring and 8 km^2 in the fall, and average home range area was 16 km^2 in the spring and 35 km^2 in the fall. These estimates are similar to those reported in Maine by Healy et al. (2018*b*), who analyzed a subset of this data in a previous study. However, our home range area estimates were larger than those reported in New Hampshire (Scarpitti et al. 2005) and Massachusetts (Wattles and DeStefano 2013*a*). This could be due to differences in methodology; Scarpitti et al. (2005) used the 95% minimum convex polygon to estimate home ranges. Additionally, our sample size for females (n = 330 spring home ranges, 297 fall home ranges) was greater than those reported by Scarpitti et al. (2005) and Wattles and DeStefano (2013*a*). We also used a higher number of locations per season to calculate home ranges. Despite some differences from other studies, we suggest that our estimates of home and core ranges reflect overall trends in standard seasonal differences and individual variation of moose movement.

In this study, we observed seasonal variation in moose home and core range areas, with notable differences between sexes and ages. As expected, male home and core ranges were generally larger than those of females, except for adults in spring. Male ungulates generally have larger home ranges than females due to higher nutritional demands associated with larger body size (Borowik et al. 2021; Allen et al. 2016; Ofstad et al. 2016). Greater home and core range area for males in the fall is also likely associated with increased movement in search of females in estrus (Whitman et al. 2018; Foley et al. 2015; Hundertmark 2007; Borowik et al. 2021). We also observed that juvenile males (2-year-olds) had larger home/core ranges than adult males. In addition to dispersal, younger males are likely outcompeted by older males during the fall rut and move greater distances to find females available for breeding (Cederlund and Sand 1994; Foley et al. 2015; Hundertmark 2007). While larger home and core ranges in fall than spring may be explained by the rut for males, we observed this trend for females as well. One possible explanation for this trend is that moose with heavy winter tick infestations may reduce movement in early spring as a consequence of poor body condition (Jones et al. 2019; Pekins 2020; Rosenblatt et al. 2021). Overall, observed differences between fall and spring space use areas for male and female moose are likely a combination of factors, including breeding status, changes in forage availability caused by seasonal senescence, body condition, and limited movement due to snow in early spring (Seigle-Ferrand et al. 2021; Johnson et al. 2002; Geist 1974; Hundertmark 2007; Morellet et al. 2013; Pekins 2020).

While moose age had no effect on female space use in spring, it did affect space use in fall, when juveniles (2-year-olds) had larger ranges than adults. This is consistent with a study in

Vermont (Blouin et al. 2021*a*), who found that young females had larger home ranges than adult females in the growth season but not in the dormant season. In the period we designated as spring (mid-March to early May), green-up has typically not begun and moose are likely still foraging winter diet species, which aligns more closely with the dormant season from Blouin et al. (2021*a*). This observation of greater home range area in juveniles than adults, while standard for males (Hundertmark 2007; Wattles and DeStefano 2013b; Malagnino et al. 2021), is less consistent for females (Cederlund and Sand 1994; Ofstad et al. 2019). Indeed, several studies have documented the opposite trend, where home range area decreases with moose age (Herfindal et al. 2009; Allen et al. 2016; Froy et al. 2018). Froy et al (2018) suggested older individuals have smaller home ranges due to deteriorating body condition associated with aging. Natural, age-related mortality in moose is expected to occur after approximately 10 years old (Ericsson and Wallin 2001; Montgomery et al. 2013). However, because the mean age of all known-aged adults in this analysis was 5 years old, we suggest that the moose in this study were generally not old enough to experience the detrimental effects of old age. Consequently, we propose that juvenile females had larger home and core ranges due to exploratory movements after leaving their dams in late summer/early fall.

We found that even among moose within the same region and seasons, there was high variation in home and core range area. Some individuals exhibited large movements that appeared to be displacement. While this may be attributed to late dispersal of juveniles and/or males in rut, we also observed this behavior in several adult females across years and both seasons. Several studies have documented largescale movements of both male and female moose (Labonte et al. 1998; Hoffman, Genoways, and Choate 2006). Indeed, seasonal home range area estimates range from less than 1 km^2 to greater than 900 km^2 (Stenhouse et al. 1995; Van Beest et al. 2011; Hundertmark 2007). Some have suggested that large displacement-type movements might be due to individuals searching for areas of lower density to reduce competition (Ballard, Whitman, and Reed 1991; Hundertmark 2007; Hoffman, Genoways, and Choate 2006). Generally, however, high variation of movement and home range area among individuals is common within ungulate populations (Dussault et al. 2005; Healy et al. 2018; Stenhouse et al. 1995; Shakeri, White, and Waite 2021; Ofstad et al. 2016). Differences between individuals often account for much of variance in home range area and movement regardless of demographic attributes (Börger et al. 2006; Van Beest et al. 2011; Melin et al. 2023). Despite the high variation among female moose in our study, our models indicated that demographic and environmental factors accounted for a portion of this variation.

As predicted, forest age influenced space use of female moose in both the spring and fall. Older forest (21-37 year-old) was associated with greater spring home and core range area. Younger forest (4-20 year-old) was associated with smaller home and core ranges in spring, and smaller core ranges in fall. Moose select for early to mid-successional habitat such as young forests because this habitat offers the highest nutritional value (Peek, Urich, and Mackie 1976; Smith et al. 2010). Thus, moose with more older-aged forest in their home range, which encompasses the periphery of an individual's space use, may need to traverse larger areas to meet their forage needs. Similarly, individuals with more young forest, or optimal habitat, available in their core ranges – areas of concentrated use – may need to travel less to find high-quality food resources. While forest age affected core range areas, it was not an important variable for predicting fall home range area. This may be due to availability of food resources with leaf-off as well as the breeding season, as previously discussed (Ofstad 2013; Hundertmark 2007; Seigle-Ferrand et al. 2021; McNab 1963). At the home range level, the search for a mate may take precedence over food resources, while the significance of young forest for forage purposes is reflected at the core range level, where the most reliable food sources are concentrated (Samuel, Pierce, and Garton 1985). Moreover, depending on the timing of senescence, moose may have to travel more to search for food when not using the areas of young forest within the core ranges. Overall, our findings on home/core range area and forest age are consistent with other studies in the region (Healy et al. 2018; Blouin et al. 2021*b*; Dunfey-Ball 2017).

Spring snow depth had a negative effect on both home and core range area for female moose. We documented maximum snow depths of approximately 100 cm within moose spring home and core ranges. Throughout their global range, moose tend to move less in deep snow (except when winter forage plants are covered, see Miquelle et al. 1992), though the strength of this trend varies (Van Beest et al. 2011; Dussault et al. 2005; Melin et al. 2023; Scarpitti et al. 2005). Moose are well-adapted to snow (Telfer and Kelsall 1984), such that one study found that even depths of 100 cm did not impede movement (Melin et al. 2023). However, other studies have shown that snow depths greater than 60 cm significantly restrict movement (Renecker & Schwartz 1998). Due to the abundance of forage and cover available even in winter of our study area, we suggest that moose have smaller home and core ranges in early spring to limit energy expenditure in deep snow (Hundertmark 2007; Van Beest et al. 2011; McNab 1963).

Fall precipitation was a significant driver and positively correlated with both home and core range area in moose. During the time we considered fall (mid-September to late November), precipitation consisted primarily of rain. This result was surprising, as the effect of precipitation on ungulate range area has been found to be variable, with both positive and negative trends documented at different scales (Börger et al. 2006; Van Beest et al. 2011; Rivrud, Loe, and

Mysterud 2010). Additionally, climatic variables such as precipitation are believed to be greater drivers of home range area than core range area (Van Beest et al. 2011; Börger et al. 2006), but we observed an increase in both home and core range area with precipitation. Precipitation can affect space use area directly (i.e., thermal energy loss) and indirectly (i.e., plant growth) (Rivrud, Loe, and Mysterud 2010; Börger et al. 2006). For example, changes in temperature associated with precipitation events could cause individuals to lose thermal energy (Barrett 1981; Parker 1988). While some have suggested this energy loss leads to smaller home ranges, moose may need to compensate for energy loss over longer timespans by increasing overall foraging movements (Barrett 1981; Parker 1988; Rivrud, Loe, and Mysterud 2010). Indeed, moose in Minnesota increased traveling and foraging movements during rain events in spring and summer (Ditmer et al. 2018). Rivrud et al. (2010) observed varying trends between roe deer space use and precipitation according to temporal scale, with a positive effect on summer home ranges. Precipitation could also be functioning as an intermediary for plant productivity and changing life cycles, indirectly driving differences in moose space use (Van Beest et al. 2011; Börger et al. 2006). However, vegetative productivity in our study area decreases during the fall as plants become dormant. Therefore, fall precipitation may be representative of another environmental variable we were unable to capture in this study.

Later first frost dates in the fall were correlated with smaller fall home and core ranges. The first fall frosts dates in this study ranged from September 10 to October 5. In migratory moose populations, the first fall frost can trigger movement to areas with different food resources (Rivrud et al. 2016). A similar behavior could occur in non-migratory moose, by which an earlier fall frost date may prompt an individual to traverse greater distances in search of higher quality forage (Barrett 1981; Parker 1988; Rivrud, Loe, and Mysterud 2010). However, as there are many other variables associated with day of year, the observed effect of first fall frost could also represent some other factor associated with time, such as the rut. Seasonal senescence plays a complex role in ungulate space use and is greatly dependent on scale, as previously mentioned (Herfindal et al. 2009; Seigle-Ferrand et al. 2021). The home and core range scale that we used may have been too coarse to identify fine-scale trends relating to movement following the first frost. Ultimately, the relationships between climate variables and moose space use are complex and cannot be attributed to a single factor.

Like their home and core ranges, female moose exhibited high variability between individuals in spring-fall overlap, from none (0%) to complete seasonal overlap (100%). Using the volume of intersection method between spring and fall home ranges on a subset of these data, Healy et al. (2018) found similar variation in overlap (0 to 73%). Scarpitti et al. (2005) reported a range of 20-34% for spring-fall overlap in New Hampshire moose, with a mean overlap (26%) similar to our estimate (30%). While they did not directly document overlap metrics, Thompson et al. (1995) reported generally high overlap of moose between all seasons in Maine.

Several environmental variables affected the degree of seasonal overlap, as we expected. While fall precipitation was included in the top model, the effect size was negligible and the confidence intervals overlapped zero, likely supporting our suggestion that fall precipitation may reflect other annual environmental variation. Overlap decreased with spring snow depth, potentially due to limited movement in deep snow as previously discussed. Surprisingly, though it was an important predictor in only one of home and core range models, percent hardwood was negatively correlated with seasonal overlap. In mid/late fall and early spring, moose are likely foraging on softwood, consistent with their winter diets during the leaf-off season (Ludewig and Bowyer 1985; Thompson et al. 1995). Therefore, we suggest that moose may avoid areas with more hardwood due to winter forage requirements shared between early spring and late fall habitats.

Differences in the forest variables identified as predicting moose seasonal overlap and selection may be explained by a potential relationship between moose space use and patch heterogeneity. We anticipated that seasonal overlap would increase with the availability of young forest on the landscape due to the high forage quality of these areas year-round (Healy et al. 2018; Van Beek 2023; Blouin et al. 2021*b*). However, contrary to this expectation, we observed greater seasonal overlap in moose space use when there was a higher availability of older-aged forest within the spring and fall home ranges. We also found that moose selected strongly for young forest (4-20 years old) in overlap areas compared to the surrounding landscape. When considered in tandem, these results may reflect an influence of forest age heterogeneity on space use, although assessing this directly was beyond the scope of this study. Moose with an overall lower proportion of young forest available within their home ranges likely concentrate use in the young forest that is available, leading to less overall movement and higher seasonal overlap (Fig 1.6). Previous research (Healy et al. 2018; Van Beek 2023; Blouin et al. 2021*b*) has proposed that young forest patches are hotspots for ticks – dubbed the “tick risk landscape” by Van Beek (2023). We further suggest that young forest, or optimal habitat, patches on the landscape may also affect moose overlap between the winter tick drop-off and questing periods, thereby increasing moose vulnerability to winter ticks. However, winter tick abundance and survival may also vary with environmental conditions when off-host (Pouchet et al. 2024; Pekins 2020; Holmes et al. 2018). More research on tick survival and questing success across a range of forest age and moose habitat types is warranted to understand the complex drivers of moose-winter tick dynamics.

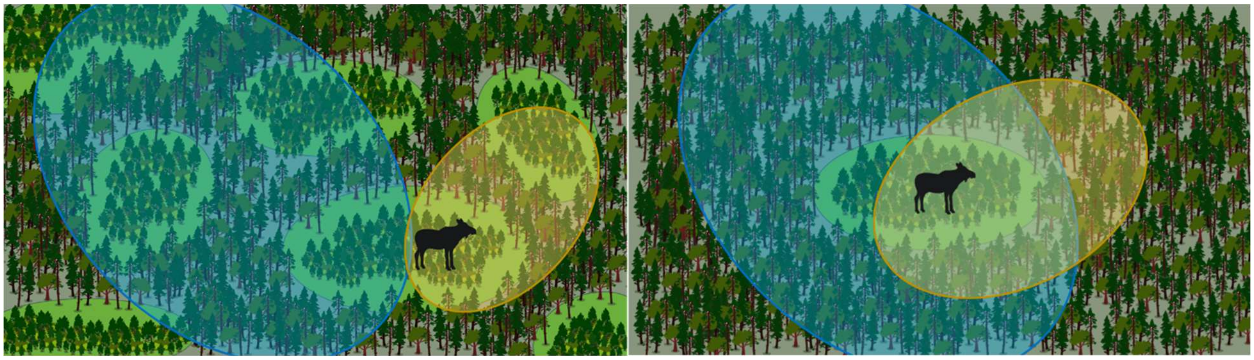

Figure 1.6*: Hypothesized relationship between optimal habitat patch heterogeneity and moose seasonal space use overlap based on the findings of this study. Presumably, a moose that has more optimal habitat (young forest) available on the landscape has less need to concentrate its space use in smaller areas of optimal habitat, and thus has less seasonal overlap.*

While we observed significant trends between moose space use and forest age, we were unable to consider finer scale differences in forest structure. The forest age range that is considered optimal forage for moose varies (Peek, Urich, and Mackie 1976; Cumming 1980; Mumma et al. 2021). Previous studies in the region considered forests aged 4 to 16 years post-disturbance to be optimal moose habitat across Vermont, New Hampshire, and Maine (Dunfey-Ball 2017; Healy et al. 2018; Blouin 2021). We defined young forest as forest aged 4-20 years old, a slightly more conservative estimate than the 4-16 year-old range others have considered optimal moose habitat (Healy et al. 2018; Dunfey-Ball 2017; Peek, Urich, and Mackie 1976; Healy et al. 2020). Furthermore, our method of estimating forest age data was on a scale greater than that required to identify areas of partial harvest, a method commonly used in addition to clearcuts in Maine (Canham, Rogers, and Buchholz 2013). We also had to remove older aged forest (>37 years) from our models due to correlation with other forest age classes. The incorporation of more fine-scale forest variables such as species composition, browse height, and harvest regime would have more accurately represented optimal habitat and their exclusion likely impacted our results.

Considering the complexity of ungulate space use, environmental drivers that we did not capture could have affected variation in home/core range size and overlap. For example, calf presence can impact female home range area in the fall (Van Beest et al. 2011; Cederlund and Sand 1994), but we were unable to include reproductive status in our models. Moreover, population density likely plays a role in individual space use (Hundertmark 2007). Healy et al. (2018) suggested that higher densities lead to increased home range area through intraspecific competition. Alternatively, due to the relatively solitary nature of moose combined with the abundance of high-quality habitat available in our study area, home range area may decrease as density increases (Hundertmark 2007). Indeed, this trend was documented in the mostly solitary roe deer, where home range area of males and females decreased with population density (Kjellander et al. 2004). While individual moose may prefer optimal habitat, this selection is inevitability influenced by how many other animals are using that same patch. The dynamic of these relationships is difficult to disentangle due to challenges in estimating fine-scale density on the landscape (Moll et al. 2022). Thus, we unfortunately were unable to account for moose density in our models and recognize that it may contribute to a significant portion of the observed variation in space use.

1.5 Conclusion

Moose space use has been shown to vary by region, sex, age, season, weather, and landscape characteristics across a broad range of scales (Blouin 2021; Blouin et al. 2021*a*; Osko et al. 2004; Street et al. 2015; Herfindal et al. 2009; Bevanda et al. 2015). Our results are comparable to other studies of moose in the northeastern United States (Scarpitti et al. 2005; Healy et al. 2018; Wattles and DeStefano 2013*b*; Blouin et al. 2021*b*). As many studies on ungulate space use in the past decade have shifted to a movement ecology framework, relatively few have explored variation in home range areas with ecological drivers (Seigle-Ferrand et al. 2021). This study contributes to filling this knowledge gap, providing evidence that precipitation, landscape composition, and individual moose age affect seasonal moose space use. Furthermore, this study is one of the first within the field of ungulate research to explore how overlap between seasons varies on an individual basis. Overall, our observations regarding differing space use in fall and spring support the habitat productivity theory in ungulates, which suggests that individuals maximize forage in areas of high vegetative productivity (Wattles and DeStefano 2013*a*; Seigle-Ferrand et al. 2021; Harestad and Bunnel 1979).

In an era of fragmentation and land use change, landscape composition plays an increasingly important role in animal movement – and the species that parasitize them (White, Forester, and Craft 2018; Bonnell et al. 2018). This study demonstrates that landscape heterogeneity may affect the degree that moose share use across the winter tick drop-off and questing periods, which could have important implications for parasite transmission. We suggest that future research in wildlife parasitology target parasite abundance, survival, and host attachment success across a variety of habitat types within a region. Additionally, we recommend that researchers incorporate landscape heterogeneity at a larger scale as a variable in their models.

CHAPTER 2

EFFECTS OF CLIMATE, FALL HABITAT USE, AND SEASONAL OVERLAP ON WINTER TICK LOADS OF MOOSE

2.1 Introduction

In the era of climate change, shifting parasite distributions and transmission dynamics pose one of many concerns for wildlife populations. Native parasites can be actors in maintaining ecosystem health and equilibrium (Hatcher, Dick, and Dunn 2012; Hudson, Dobson, and Lafferty 2006; Marcogliese 2004). However, the balance of some host-parasite systems is being disrupted by environmental change resulting from anthropogenic activities, such as rising temperatures (Macnab and Barber 2012) and habitat fragmentation (Pérez-Rodríguez et al. 2018; Bitters et al. 2022). The frequency of disturbance to these systems is likely to escalate in coming decades as we confront unprecedented change. While some species face extinction, others will undergo rapid growth and range expansion (Thomas et al. 2004; Pigot et al. 2023).

Changing trends in parasite populations present novel challenges for host species. For example, the northward range expansion of several tick species (Acari: Ixodidae) in North America is associated with an increase in tick-borne diseases (Sonenshine 2018; Baker et al. 2020). In addition to the public health concern, ticks can contribute to declines in wildlife populations, either directly through disease transmission or indirectly through reduction in body condition resulting from high tick burdens (Brown and Brown 2004; Vander Haegen et al. 2018; Moore 2002). While ticks have little to no consequence on fitness for some wildlife species, such as white-footed mice (*Peromyscus leucopus*) (Hersh et al. 2014), heavy tick burdens have been linked to lower survival in other populations such as pheasants (*Phasianus colchicus*) and moose (*Alces alces*) (Hoodless et al. 2003; Musante, Pekins, and Scarpitti 2010). Over the last two decades, winter ticks (*Dermacentor albipictus*) have caused regional population declines of moose in eastern North America (Musante, Pekins, and Scarpitti 2010; Jones, Pekins, and Kantar 2017; Bergeron, Pekins, and Rines 2013).

The winter tick is a single-host species of hard tick in the Ixodidae family. Winter ticks attach to a host as larva in autumn, ingest a blood meal typically in January to mature into nymphs, and take a final blood meal before dropping off the host as adults in early spring (Drew and Samuel 1989). Although they attach to a variety of mammalian species (Sundstrom et al. 2021; Baer-Lehman et al. 2012; Leo et al. 2014; Manville 1978; Calvente et al. 2020), winter ticks exhibit evolutionary traits that indicate a preference for moose as hosts (Samuel 2004; Samuel, Mooring, and Aalangdong 2000). While winter ticks have been parasitizing moose for centuries, epizootic events (years with >50% calf mortality) have increased in frequency over the past two decades (Bergeron, Pekins, and Rines 2013; Jones, Pekins, and Kantar 2017; Pekins 2020; Samuel, Mooring, and Aalangdong 2000). The increased frequency and severity of epizootics has been attributed to climate change, moose density, and moose habitat use (Pekins 2020; Healy et al. 2018; Samuel 2007; Elzinga, Beckford, and Strickland 2023).

Winter ticks are susceptible to various weather events depending on their life cycle stage. For example, mild winters are associated with increased survival of adult winter ticks in the environment (Samuel 2007; Drew and Samuel 1986). Warmer summers led to increased tick loads on moose in Minnesota (Hoy et al. 2021), and warm temperatures across all time periods were positively correlated with winter tick loads on moose in the western United States (DeCesare et al. 2024). Excessive heat in combination with dryness, however, may be detrimental to ticks as low relative humidity causes egg desiccation (Yoder et al. 2016; Pouchet et al. 2024). Indeed, tick recruitment was lower during a hot, dry summer in open areas of forest as opposed to closed canopies in Ontario with the trend reversed during a wetter, cooler summer.

Conditions at different times of year can have a compounding effect on tick recruitment. Pouchet et al. (2024), for example, found that summer drought following an early spring snowmelt led to reduced tick loads on moose. Extreme cold temperatures in combination with snow or ice during questing in the fall can cause mortality of larvae through inoculative freezing (Holmes et al. 2018). Drew and Samuel (1986) reported that snow presence causes mortality of adult winter ticks during drop-off. In the western United States, snowpack in the fall questing period was negatively correlated with winter tick loads on moose, with a weaker negative effect of snow in the spring drop-off (DeCesare et al. 2024). However, Dunfey-Ball (2017) did not observe a relationship between snow persistence in early spring and epizootics the following year in eastern North America. It has been suggested that snow may even have a positive effect on winter tick survival in eastern North America, potentially due to higher humidity as a result of later snowmelt (Pouchet et al. 2024). Additionally, fall precipitation could play a role in questing success of winter ticks; other species of Ixodidae ticks demonstrate reduced questing in periods of heavy rainfall (James et al. 2013). However, no study to date has examined the potential effect of fall precipitation on winter ticks.

In addition to climate effects, forest composition can also influence tick distribution both directly through structural influences on tick survival and indirectly through host behavioral ecology and habitat use. For example, winter tick abundance in partial forest cuts was higher than in clear cuts in New Hampshire (Powers and Pekins 2020), while tick recruitment in open forest patches was higher than closed canopy forest except during dry conditions in Ontario (Addison et al. 2016). In deciduous forests, blacklegged ticks (*Ixodes scapularis*) are influenced by microhabitat features such as the presence of leaf litter (Linske et al. 2019). The castor bean tick (*Ixodes ricinus*) is more abundant in species-rich deciduous stands with shrubs than homogenous pine stands in Europe; however, whether this is an effect of forest composition or host species habitat use is unclear (Tack et al. 2012). More generally, discerning whether the observed tick abundance in a particular area is directly influenced by habitat type or indirectly influenced by host behavior poses challenges and ultimately may depend on study scale (Talbot et al. 2019; Bourdin et al. 2023; Werden et al. 2014).

In addition to climate and forest composition, the extent to which moose overlap in their use of habitat patches during the tick questing and drop-off seasons may affect tick loads (Healy et al. 2018; Blouin et al. 2021*b*). While moose are considered to be generalist herbivores, they generally prefer young regenerating forest due to high nutritional content of forage (Mumma et al. 2021; Peek, Urich, and Mackie 1976; Felton et al. 2020). Given that moose concentrate their time in areas with high-quality forage across both spring and fall, it is presumed that tick density may be disproportionately high in these areas (Healy et al. 2018; Blouin et al. 2021*a*, *b*; Van Beek 2023). In Chapter 1, we documented high variation in seasonal overlap of moose space use across the spring drop-off and fall questing periods, ranging from 0 to 100% overlap. Moose selected strongly for young forest (4-20 years old) within overlap areas compared to the surrounding landscape, but spring-fall overlap generally increased with the availability of older forest on the landscape, suggesting that habitat heterogeneity may play a role in space use. Moreover, seasonal overlap was negatively correlated with the proportion of hardwood on the landscape, though hardwood was not predictive of home or core range size in either season. Moose browse primarily on fir trees during the leaf-off season in Maine (Thompson et al. 1995; Ludewig and Bowyer 1985). Thus, moose may avoid hardwood stands between their shared habitats in early spring and late fall due to winter forage requirements.

Documenting winter ticks off-host is challenging due to larval clustering behavior during the questing season (Samuel 2004; Powers and Pekins 2020). Tick loads on moose have been measured using transect counts on harvested animals (Sine, Morris, and Knupp 2009), but the timing of harvest affects tick loads since moose acquire ticks throughout the fall questing season (Pouchet et al. 2024; Powers and Pekins 2020). Therefore, tick counts on live-captured moose are likely most accurate during winter after fall questing and before spring drop-off. However, capturing live moose is costly, limiting studies to span only a few years (Debow et al. 2021; Jones, Pekins, and Kantar 2017). To improve our understanding of the relationship between climate, moose and ticks, research across several years utilizing tick counts on live moose after the questing period would be beneficial. Additionally, further investigation into moose habitat use during the fall questing period and spring drop-off periods is warranted to better inform this complex dynamic.

The goal of our study was to understand how climate, forest composition, and host space use affect winter tick loads on moose in Maine. To explore these relationships, we used GPS data gathered from collared moose in northern Maine over a 9-year period. First, we examined how weather variables of the previous year affected tick loads measured on moose in January. Second, we explored relationships between moose fall habitat use during the questing period and winter tick loads. Third, we investigated if individuals with a greater propensity for overlap in space use between the spring drop off and fall questing periods had higher winter tick loads. We predicted that summer drought and low precipitation in fall would negatively affect moose tick loads due to desiccation of eggs and larvae. Conversely, we expected that spring snow depth would positively affect tick loads as delayed snowmelt could lead to more humid soil conditions during the tick drop-off and egg-laying periods. Additionally, we anticipated that consecutive days below -15 degrees C would correlate negatively with ticks loads due to potential freezing conditions for adults. Regarding moose habitat use, we expected that individuals with greater mean overlap between the spring drop-off and fall questing periods would have higher tick loads.

In this study, we aimed to address knowledge gaps in the moose-winter-tick system by exploring relationships between habitat use, climate, and winter tick loads. Moose are highly valued by the people of Maine, and we hope our results will guide future research to better understand this system.

2.2 Methods

2.2.1 Study area and data collection

This study was conducted in Maine, primarily the northern half of the state, in parts of Aroostook, Piscatiquis, and Somerset counties. The region is almost entirely forested, dominated by a mixture of softwoods and hardwoods. Commercial timber harvest is active throughout the region. Moose were captured in Wildlife Management Districts (WMDs) 2, 4, and 8 in the winters of 2014 to 2022 (Figure 2.1; see methods from Chapter 1). While captures in WMDs 2 and 8 consisted of a mixture of calves, juveniles, and adults, only calves were captured in WMD 4. At capture, tick load was measured using a standardized transect-count method (Sine, Morris, and Knupp 2009) and GPS collars were deployed (Vectronics-aerospace Vertex Plus Survey Collar [Globalstar], Vectronic-aerospace Survey 2-D Iridium collar). Tick loads were estimated on 701 moose (100 female adults, 310 female calves, and 291 male calves, Figure 2.2) that were captured across the study period. The number of captures varied by year and WMD (n = 212 in WMD 2, n = 198 in WMD 4, and n = 291 in WMD 8, Figure 2.3). We used kernel density estimators to delineate the isopleths of seasonal home (95%) and core (50%) ranges for 159 individual females across 9 years (Worton 1989, Chapter 1). The mean number of fixes per home and core range was 74 in the spring and 105 in the fall. For individuals that had spring and fall home (95%) ranges in the same calendar year (*n* = 111 individuals), we estimated seasonal overlap using the utilization distribution overlap index (Fierberg and Kochanny 2005, Chapter 1).

2.2.2 Climate predictors of tick load

We obtained climate metrics at different scales (WMD and county) depending on the variable. For each year of capture *y*, we measured climate variables of the previous year *y – 1*. We gathered data for average snow depth, average temperature, and number of consecutive days below -15 degrees Celsius (cold days) in early spring (March 1 – April 30) using local weather station data. We used data from the Fort Kent weather station (NOAA) for WMD 2, and from the Brassua Dam weather station for WMDs 4 and 8 (NOAA). To assess drought conditions, we accessed data from the US Drought Monitor (USDA, NDMC, NOAA). We averaged weekly drought indices from July, August, and September for each county, with Aroostook representing WMD 2, Piscatiquis for WMD 4, and Somerset County for WMD 8. Fall precipitation patterns were evaluated from 2013 to 2022 using data from the PRISM Climate Group, as described by Daly et al. (2008). We averaged annual precipitation values from September, October, and November and extracted averages by county. Given our observations of moose space use from Chapter 1, we assumed that individuals generally remained within the same county or WMD in the year preceding capture. Therefore, we considered these climate data suitable for capturing broadscale conditions of the areas occupied by most moose prior to capture.

Some studies suggest that moose age and sex may play a role in tick loads (Bergeron and Pekins 2014; Drew and Samuel 1985). Other studies have included geographic region as a variable, in part to account for regional differences in moose density (Healy et al. 2018; Bergeron and Pekins 2014; Pouchet et al. 2024). However, preliminary examination of data revealed that differences in tick load by age and WMD were inconsistent across years (Figure 2.2). Using a subset of these data, Jones et al. (2019) found no significant difference between tick loads on male and female calves in Maine. Due to this lack of consistency and our interest in broader trends of habitat use and climate variables, we pooled data of both ages and across all three WMDs. We assessed correlation among variables and removed the average early spring temperature due to its high correlation with consecutive cold days in spring (R = -0.7). We used a linear mixed-effect model to analyze the effects of climatic variables on log-transformed tick load, estimated with restricted maximum likelihood estimation. Fall precipitation, spring snow depth, consecutive cold days in spring, and late summer drought were included as predictor variables. We also included year as a random effect in all models to address annual differences in tick loads (Figure 2.3). We ran the analysis using the 'lmerTest' package (Kuznetsova et al. 2017, version 3.1-3) in program R (CRAN; version 4.2.1).

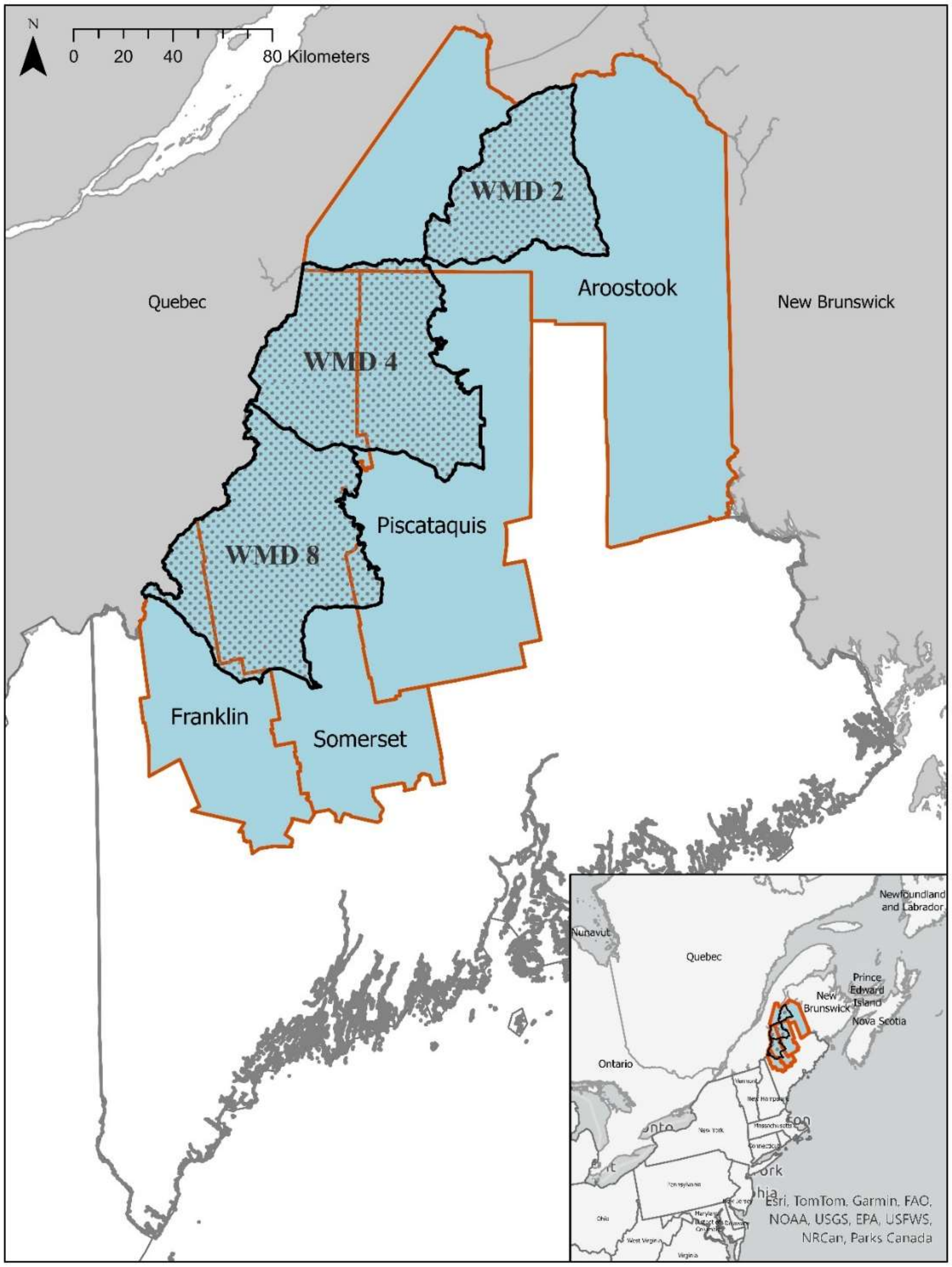

Figure 2.1: *Study area in Maine, USA. A total of 701 moose were captured across 9 years (2013-2022) in Wildlife Management Districts (WMDs) 2, 4, and 8. The capture WMDs were within Piscatiquis, Somerset, Franklin, and Aroostook Counties.*

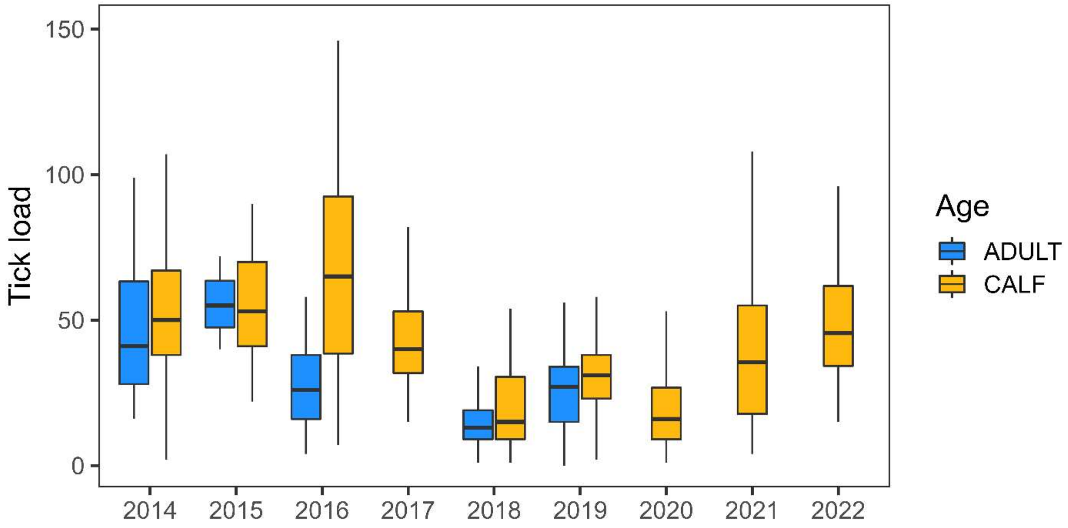

Figure 2.2*: Annual tick counts on adult and calf moose from 2014 to 2022. A total of 601 calves and 101 adults were captured across the study period, with only calves captured in 2017, 2020, 2021, and 2022. Captures were across Wildlife Management Districts (WMD) 2 and 8 from 2014 to 2019, WMDs 2, 4, and 8 in 2020, and WMD 4 in 2021 and 2022.*

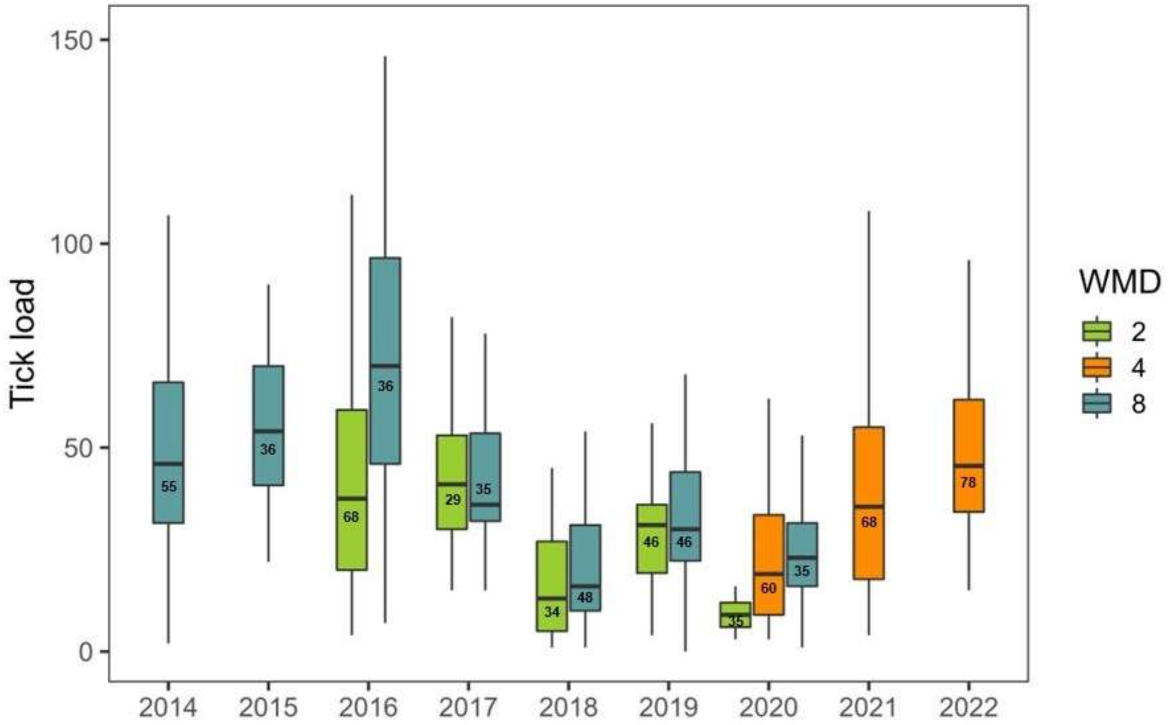

Figure 2.3: *Annual raw tick counts, with sample sizes, on live-captured moose by Wildlife Management District (WMD). 701 moose (601 calves, 100 adults) were captured between the last week of December and the first two weeks of January each year.*

2.2.3 Fall site fidelity and habitat variables

For our second objective, we investigated correlations between potential moose habitat use during the fall questing season and the tick loads measured in the following winter. We were unable to directly measure how fall habitat use related to winter tick loads the following season given that tick loads were measured on captured individuals in January after the questing period. To gain information about movement and potential habitat use prior to capture, we estimated site fidelity across fall home ranges, the latter calculated using 95% kernel density estimators (Worton 1989). We made inferences regarding the individual's whereabouts before capture based on their observed site fidelity after capture, assuming that if an individual consistently displayed high site fidelity in the fall over multiple years, it likely utilized a similar area prior to the tick load measurement in January. Building on the analysis from Chapter 1, we quantified site fidelity for those individuals that had at least two consecutive fall home ranges (n = 134 individual moose) using Bhattacharyya's affinity (BA), which is a measure of general similarity between two utilization distributions (Fieberg and Kochanny 2005; Bhattacharyya 1943). BA provides an index of between 0 and 1, where 0 indicates no overlap and 1 indicates complete overlap or exact similarity between two utilization distributions. We used the 'amt' package (Signer et al. 2019; version 0.1.7) in program R (CRAN; version 4.2.1) to estimate fall home ranges and site fidelity, with the latter estimated using consecutive fall home ranges derived per individual. For instance, for an individual with consecutive fall home ranges across three years, we computed BA between the fall home ranges for years y to $y + 1$, and $y + 1$ to $y + 2$. We produced an index of general fall fidelity by averaging the BA values across these years. We considered an individual to have high fall fidelity if mean BA was ≥ 0.7 (70%) and the standard deviation was ≤ 0.2 (Figure 2.4).

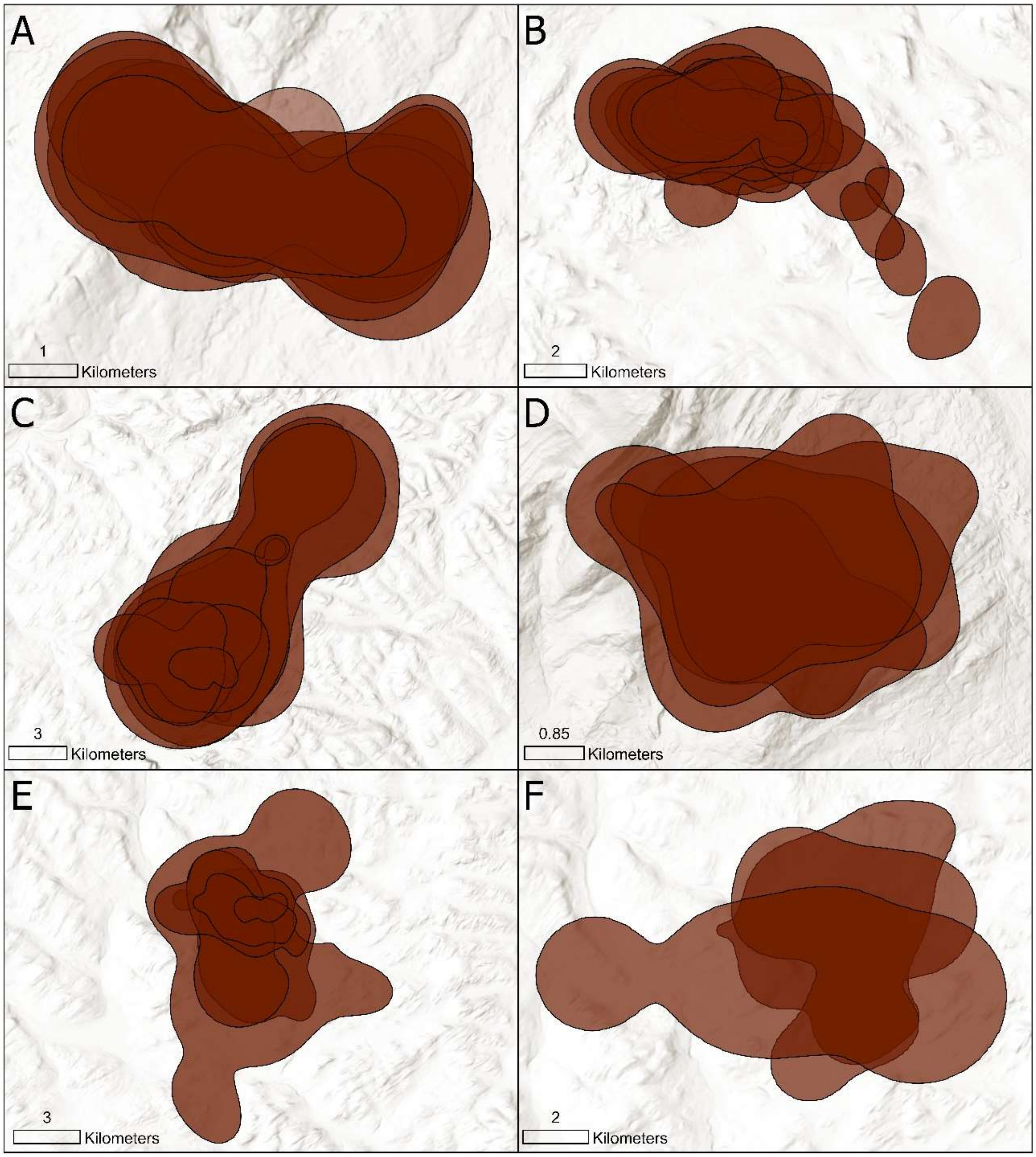

Figure 2.4: *Consecutive 95% kernel density estimated fall home ranges and mean fall fidelity (BA) from 6 representative females: A) 4 home ranges,* $\bar{x}$ *= 0.89; B) 5 home ranges;* $\bar{x}$ *= 0.84; C) 6 home ranges;* $\bar{x}$ *= 0.79; D) 4 home ranges,* $\bar{x}$ *= 0.70; E) 6 home ranges;* $\bar{x}$ *= 0.66; and F) 4 home ranges,* $\bar{x}$ *= 0.61. We used a mean BA (*$\bar{x}$*) of 0.70 as the threshold for high fall fidelity to include in the fall habitat and tick load analysis. Thus, the individuals in panels E and F were not included in the fall habitat analysis.*

For individuals with ticks loads and high subsequent fall fidelity (*n* = 46 females), we estimated the mean fall home range area across years and extracted forest composition variables from all annual fall home ranges used to estimate fidelity. We calculated mean values across fall home ranges per individual for percent hardwood, and percent forests of ages <4, 4-20, 21-37, >37 years old. We modeled log-transformed tick load of these individuals using linear regression, with mean fall home range area and habitat variables used as predictors in single-term models, to explore general trends.

2.2.4 Overlap of seasonal home ranges

To understand if areas with high seasonal overlap of moose could serve as hotspots for winter ticks, we focused on spring-fall overlap as the periods corresponding to winter tick drop-off and questing. Previous research has identified the winter tick drop-off period as approximately March 15 to May 5, and the questing period as September 15 to November 26 (Healy et al. 2018; Drew and Samuel 1989; Samuel, Mooring, and Aalangdong 2000). Seasonal overlap was measured during the questing and drop-off periods using the utilization distribution overlap index (UDOI; Fierberg and Kochanny 2005), calculated using spring and fall 95% kernel density estimators (Worton 1989; Powell and Mitchell 2012) as an index of behavioral tendency for site fidelity across the two seasons. Of the 701 moose that were collared, we estimated seasonal overlap for 111 individual females (see Chapter 1). Due to the variation in overlap demonstrated by individuals, we included only those that had at least two measures of spring-fall overlap (*n* = 65). We averaged the UDOI values across all individuals to obtain mean seasonal overlap for moose. We examined the relationship between tick load, which was measured only once (at capture), and overlap. Like the climatic model, we used a linear mixed-effect model to model log-transformed tick load as a function of mean seasonal overlap with year as a random effect. For both the climatic and seasonal overlap models, we standardized predictor variables to compare effect sizes.

2.3 Results

2.3.1 Climate

After accounting for fixed effects, the random year effect explained approximately 36% of the variation (Appendix B, Table B.1) in tick loads for 701 individual moose (Appendix B, Figure B.2) with year y predicted as a function of climatic variables from $y - 1$. The remaining variance attributed to the combined fixed effects was 13% (marginal $R^2 = 0.13$). Consecutive days below -15°C in early spring (cold days) had a slight positive effect on tick load ($\beta = 0.06$) but this variable was not significant ($p > 0.6$), and confidence intervals overlapped zero (Figure 2.5). Fall precipitation was negatively correlated ($\beta = -0.28$, $p = 0.026$), and late summer drought was positively correlated ($\beta = 0.30$, $p = 0.052$) with tick load. The positive effect of snow depth ($\beta = 0.28$) in early spring was strongly significant ($p = 6.3\text{e-}06$).

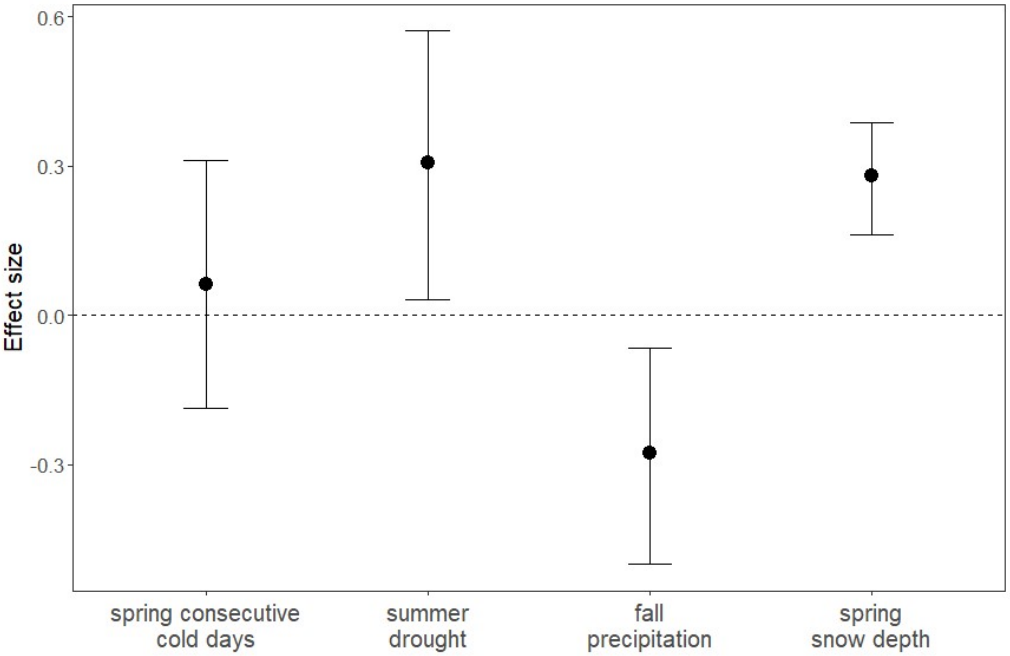

Figure 2.5: *Outputs from the climatic model (n = 701), where the response variable was the log-transformed tick load on moose measured in year y and climatic predictor variables were measured in year y-1. Predictor variables were the number of consecutive days below -15 degrees Celsius, drought index from July and August, precipitation during the winter tick fall questing period (September, October, and November), and snow depth during the winter tick spring drop-off period (March 1 to April 30). All variables were z-scored. Year was included as a random effect.*

2.3.2 Fall habitat use

We explored relationships between fall habitat use during the questing period and subsequent tick loads on captured moose for our second objective. Using individuals with high fall fidelity (≥ 70% BA; $n = 46$), we modeled tick load as a function of fall home range variables averaged across years. We observed positive but non-significant effects of home range area ($\beta = 0.2$, SE = 0.3, $p > 0.4$), 4–20 year old forest ($\beta = 0.01$, SE = 0.02, $p > 0.6$), and 21–37 year old forest ($\beta = 0.02$, SE = 0.02, $p > 0.2$) on tick loads. Forests under 4 years old had a negative effect ($\beta = -0.02$, SE = 0.04, $p > 0.5$), as did forests older than 37 years old ($\beta = -0.01$, SE = 0.01, $p > 0.3$). Percent hardwood had a significant negative effect on moose tick load ($\beta = -0.03$, SE = 0.02, $p = 0.023$; adjusted $R^2 = 0.09$; Figure 2.6).

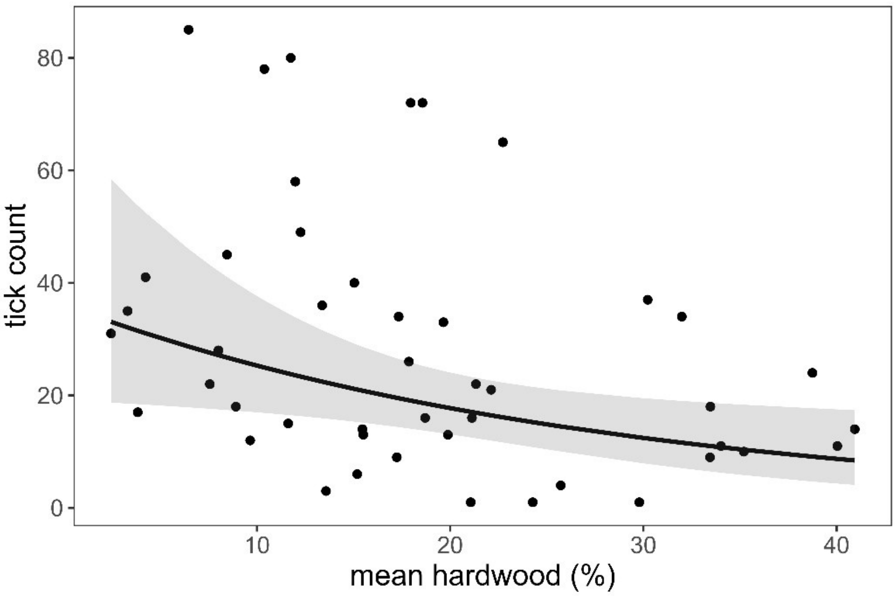

Figure 2.6: *Relationship between winter tick loads on moose at capture and mean percent hardwood of successive fall home ranges in moose with high fall fidelity (n = 46). Predicted trend line from the model is shown with 95% confidence intervals in gray.*

2.3.3 Seasonal overlap during drop-off and questing

In the third analysis, we tested for a relationship between seasonal overlap during the drop-off and questing periods and winter tick loads, using moose that exhibited consistent behavioral tendencies of high overlap across years. We modeled tick loads as a function of mean UDOI with year as a random effect for 65 female moose that had at two years of measured seasonal overlap (Appendix B, Table B.2). There was high variation in mean overlap (UDOI) across individuals, ranging from 0.007 to 0.79 (0.7% to 80%). Mean UDOI was positively correlated with tick load ($\beta = 1.38$, $p = 0.0137$). As in the climatic model, the random year effect explained a high degree of the variance (34%). Mean UDOI explained approximately 0.07% of variance.

2.4 Discussion

Considering anticipated species range shifts in the coming decades, identifying the roles that environmental and climate factors play in host-parasite interactions is crucial. Using data spanning almost a decade, we found that winter ticks burdens on moose were influenced by climate, forest composition of habitat used during the fall questing period, and the degree of seasonal range overlap between the tick drop-off and questing periods. Specifically, late summer drought and snow depth in early spring were positively associated with tick loads, while fall precipitation had the opposite effect. Individuals using areas with greater amounts of hardwood in their fall home ranges also had lower tick loads. Moreover, moose with higher indices of average seasonal overlap had higher tick loads. The relationship we observed between seasonal overlap and winter tick loads suggests that moose using the same areas between the drop-off and questing periods may have higher exposure to winter ticks. This study contributes to existing research in the system, emphasizing the complexity of the winter tick-moose dynamic.

Early spring snow depth was positively correlated with winter tick loads the following year, consistent with our prediction and previous studies. Presumably, the more snow there is on the landscape in early spring, the later some snow cover persists at the end of the season. Later dates of snowmelt may result in higher soil humidity throughout the spring, which is favorable to adult ticks and eggs (Pouchet et al. 2024). In other species of Ixodidae ticks, snow appears to act as an insulator from cold temperatures (Volk et al. 2022; Vollack et al. 2017), though the trend is inconsistent across the literature (Burtis et al. 2016; Linske et al. 2019). While snow may directly affect ticks through survival and recruitment, it also may influence tick loads on moose indirectly through moose behavior. The maximum mean snow depth from March and April in our study area was 70cm, and we recorded daily snow depths exceeding 100 cm (see Chapter 1). In forested regions, snow depths of 70cm or greater can inhibit moose movement and home range areas (Sweanor and Sandegren 1989; Thompson et al. 1995). Thus, deeper snow can restrict moose movement to a smaller area (see Chapter 1), which may lead to higher concentrations of gravid ticks during the drop-off period. Since adult and larvae winter ticks move very little when off-host (Drew and Samuel 1986; Addison et al. 2016), this may lead to greater densities of larvae in those concentrated use areas, during the following fall questing period, which along with higher tick survival can contribute to subsequent higher tick loads on moose in those areas.

Contrary to our prediction, late summer drought was correlated with higher tick loads. We expected the opposite effect, as low relative humidity has previously been found to be associated with reduced survival and recruitment in Ixodidae ticks (Berger et al. 2014; Nieto, Holmes, and Foley 2010), including winter ticks (Yoder et al. 2016; Addison et al. 2016).

Pouchet et al. (2024) found that early spring snow melt followed by dry summer conditions reduced winter ticks loads on moose measured in fall, whereas summer humidity did not have a significant effect as a single term variable (Pouchet et al. 2024). Due to the complexity of interpreting interaction terms, particularly in the absence of a sufficiently large sample size, we did not include interactions in our models. Though we are unsure why we observed a positive effect of summer drought, it could be due to lack of sample representation. We used drought indices from the U.S. Drought Monitor – only two years within our dataset, however, had documented droughts in late summer across our study area. Summer drought conditions were mild to moderate in 2021, moderate to severe in 2020 (U.S. Drought Monitor; Svoboda et al. 2002), and did not occur in the other 7 years of our study period. Therefore, the apparent effect of drought on winter tick loads may reflect another associated variable that we did not capture.

Surprisingly, we observed a negative correlation between fall precipitation and tick loads. We expected precipitation during questing to positively affect tick loads, as high relative humidity is associated with higher winter tick larval recruitment (Addison et al. 2016) and increased larval survival (Yoder et al. 2016). One potential explanation for our observed negative trend is that fall precipitation could affect questing success of winter ticks, as they do not typically descend after climbing vegetation to quest (Drew and Samuel 1985; Samuel and Welch 1991). However, no research to date has examined these relationships directly in winter ticks. Fall precipitation could affect winter tick loads indirectly by influencing moose movement. In Chapter 1, we observed that home range area increased with fall precipitation. Concentration of moose in optimal habitat patches is thought to cause tick "hotspots" on the landscape (Van Beek 2023; Healy et al. 2018; Blouin et al. 2021*b*). If moose have larger home ranges in the fall due to rainfall, they may not spend as much time in tick hotspots and subsequently pick up fewer questing larvae. While we did not find an effect of fall home range area on tick load in highly site fidelic individuals, it could be that movement rates on a finer scale are needed to detect this relationship if it exists.

Our results generally indicate that moose with a higher proportion of hardwood in their fall home ranges have lower tick loads. This may be due to microhabitat differences between forest types, moose habitat preference, or more likely, a combination of both. Forest composition and structure are known to influence abundance of several tick species in complex ways (Werden et al. 2014; Talbot et al. 2019; Bourdin et al. 2023; Linske et al. 2019), though less data exists for winter ticks. In Ontario, winter tick recruitment was higher in open habitats than closed canopy in deciduous forests, except when it was hot and dry (Addison et al. 2016). Another study found that winter tick abundance was highest in partial forest cuts with heavy moose use in New Hampshire, where the forest type was mixed hardwood-softwood (Powers and Pekins 2020). In Maine, moose typically select for softwood stands during leaf-off (Ludewig and Bowyer 1985; Thompson et al. 1995; Dimatteo-LePape et al. 2023). Thus, they may avoid hardwood stands during leaf-off periods such as late fall and early spring, consistent with their dietary preferences. Consequently, individuals that spend more time in areas with a higher proportion of hardwood during the fall questing period could pick up fewer ticks, potentially due to lower adult tick presence or survival in those locations from the previous spring drop-off. Ultimately, winter tick recruitment and abundance are likely shaped by microhabitat characteristics impacting tick survival as well as host use of the landscape (Talbot et al. 2019).

We found that mean overlap between spring and fall space use of moose had a significant positive effect on winter tick loads, as expected. This result is consistent with the notion that moose maximizing space use in the same areas across the drop-off (spring) and questing (fall) periods creates winter tick hotspots on the landscape (Van Beek 2023; Blouin et al. 2021*b*; Healy et al. 2018). It is important to note that our sample size was relatively small (65 individuals) and while we averaged seasonal overlap across at least 3 years for 29 individuals, the remaining 36 had only 2 years of overlap data available. Additionally, tick loads were measured for these individuals only once, and we modeled the tick load estimated at capture based on subsequent years of seasonal overlap. Given the assumptions inherent in this analysis, we advise that our results be interpreted with caution. Nonetheless, these results highlight that moose with greater tendencies to overlap space between the drop-off and questing periods may have a higher probability of tick exposure through re-infection. Additionally, concentrated use in optimal habitat areas (see Chapter 1) could lead to increased moose density in these areas, which is positively correlated with winter tick loads on moose (DeCesare et al. 2024).

There are several factors driving winter ticks loads on moose that were likely overlooked in this study. Despite the observed trends between tick loads, weather, and moose space use, year accounted for three to four times the variance than the other variables. Furthermore, year was confounded with region in our tick load dataset (see Figure 2.3). This indicates that there are other factors fluctuating annually that drive winter tick loads on moose, which is unsurprising given the complex nature of host-parasite dynamics (Hall, Duffy, and Cáceres 2005; Rynkiewicz, Pedersen, and Fenton 2015). Understanding effects of climate and weather on ticks and hosts proves challenging; often studies on tick species produce contrasting results (Talbot et al. 2019; Clow et al. 2017; Werden et al. 2014). Our study area might have been too small or our data too coarse to capture sufficient variation in weather trends, as scale plays a large role in identifying general ecological trends. The apparent effects of weather patterns on winter tick loads may be reflecting other related sources of annual variation (i.e. vegetation phenology) that we did not account for. We recommend that future research prioritize investigating direct effects of habitat and climate variables on winter tick abundance and distribution on the landscape.

Given the difficulty of accurately assessing density at a finer scale for ungulates (Moll et al. 2022; Terletzky and Koons 2016), we opted not to include moose density on the landscape in our models. Density estimates vary within the study area, with WMD 2 likely having the highest moose density (Kantar and Cumberland 2013; Jones, Pekins, and Kantar 2017; Dunfey-Ball 2017; Healy et al. 2018). We acknowledge that moose density on the landscape affects winter tick loads (Pouchet et al. 2024; Pekins 2020; Bergeron and Pekins 2014; DeCesare et al. 2024) and should be considered to better understand the mechanisms of winter tick transmission in moose. We suggest that seasonal overlap, optimal habitat availability, and moose density may have complex interactive effects on moose winter tick loads and tick distribution on the landscape.

2.5 Conclusion

The moose-winter tick system illustrates the complexity of host-parasite systems given landscape composition and forest disturbance. Even when the landscape remains relatively constant across time, changing climate patterns can alter how hosts interact with the landscape and subsequently affect parasite distribution. The scarcity of longer-term datasets poses further challenges on informing these trends. In this study, we analyzed collared moose data spanning 9 years to explore the potential impacts of climate, habitat, and the overlap of moose space use during the winter tick drop-off and questing periods on winter tick loads. Though we observed a relationship between early spring snow and tick loads consistent with previous studies, there was a discrepancy in the effect of late summer drought compared to the findings of Pouchet et al.

(2024). This inconsistency, however, may be attributed to limited variation in our predictor variables. Nonetheless, despite the clear nuances of weather variables, we suggest that fall precipitation may play a previously unrecognized role in winter tick abundance and/or questing success in eastern North America. Further study on this relationship may be warranted to better understand the moose-winter-tick dynamic.

Using inferences made on moose behavior regarding fall site fidelity, we found that individuals exhibiting greater overlap between the spring drop-off and fall questing periods had higher tick loads. Moreover, moose with a higher proportion of hardwood forest in their fall home ranges tended to have lower tick loads. This relationship may be attributed to moose avoidance of hardwood stands during the leaf-off season across the spring drop-off and fall questing periods. Our findings lend support to the hypothesis that concentrated use of habitat across the drop-off and questing seasons may create localized patches of high tick abundance. However, considering that the majority of variance was attributed to annual variation rather than overlap, we suggest that moose habitat use and seasonal overlap may not play as big a role in winter tick loads as other environmental factors more directly affecting winter ticks on the landscape. We recommend that future research on this system encompass a greater study area using tick counts on live moose, incorporating detailed weather variables across many years and seasons. Additionally, more research into finer-scale moose movement and density may help unravel how much these factors drive winter tick loads. While conducting tick counts across multiple years on the same moose by recapturing individuals could provide valuable insights, the practicality of this approach may pose challenges.

Overall, this study presented a unique opportunity to obtain insights into how weather and landscape composition can affect host-parasite transmission both directly, through processes such as egg desiccation, and indirectly through altering host space use. As species range distributions shift in coming years, understanding the nature of these indirect relationships could help inform winter tick management in moose.

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APPENDIX A: CHAPTER 1 SUPPORTING INFORMATION

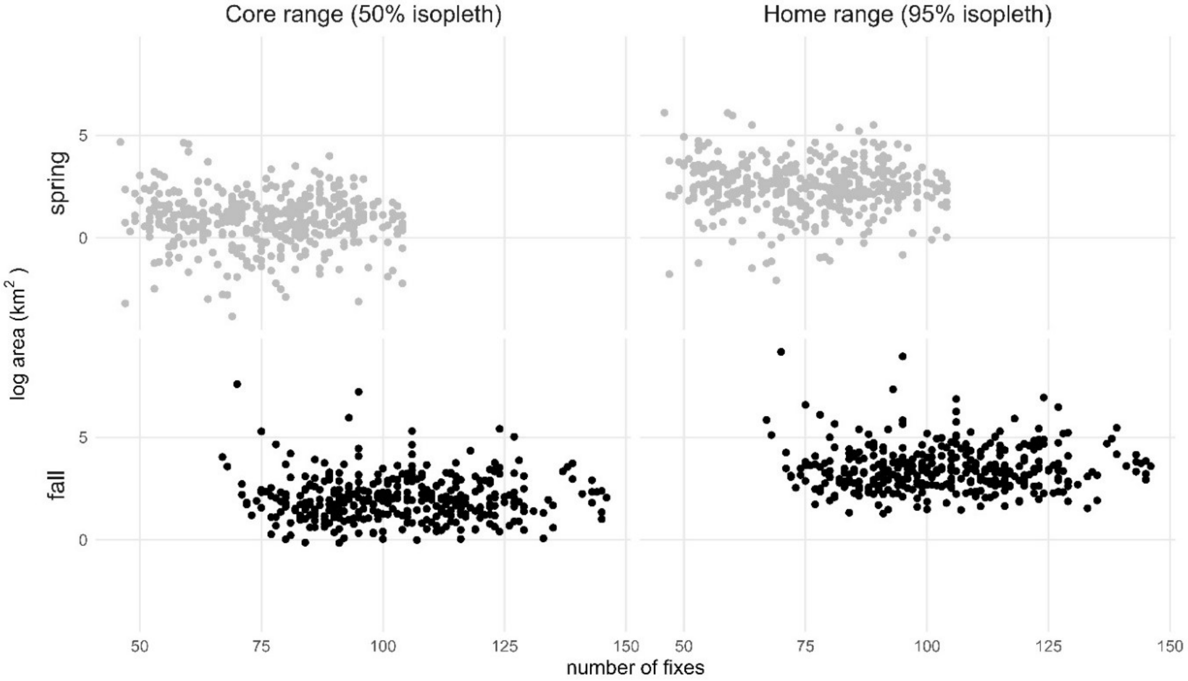

Figure A.1*: Relationship between log area (km^2) of home (95% isopleth) and core (50% isopleth) ranges and the number of fixes used to estimate ranges. We found no evidence that the number of fixes per either season or isopleth level affected home/core range area.*

Table A.1: *Correlation matrices between forest age class variables for spring and fall.*

		under_4_use	betw_4_20_use	betw_21_37_use	over_37_use
fall	under_4_use	1	0.07	-0.17	-0.33
	betw_4_20_use	0.07	1	-0.03	-0.6
	betw_21_37_use	-0.17	-0.03	1	-0.65
	over_37_use	-0.33	-0.62	-0.65	1
		under_4_use	betw_4_20_use	betw_21_37_use	over_37_use
spring	under_4_use	1	0.03	-0.14	-0.37
	betw_4_20_use	0.03	1	-0.05	-0.68
	betw_21_37_use	-0.14	-0.05	1	-0.56
	over_37_use	-0.37	-0.68	-0.56	1

Table A.2: *AIC ranking single-term model sets from home and core range analyses.*

Spring 95% isopleth							
Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
betw_21_37_use	3	862.23	0.00	1.00	0.68	-428.08	0.68
snow_depth	3	865.32	3.09	0.21	0.14	-429.63	0.82
betw_4_20_use	3	866.01	3.77	0.15	0.10	-429.97	0.92
null	2	867.50	5.27	0.07	0.05	-431.73	0.97
percent_hardwood	3	869.29	7.06	0.03	0.02	-431.61	0.99
age_class	4	871.50	9.27	0.01	0.01	-431.69	1.00
Spring 50% isopleth							
Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
snow_depth	3	667.313	0.000	1.000	0.765	-330.620	0.765
betw_21_37_use	3	671.900	4.587	0.101	0.077	-332.913	0.842
percent_hardwood	3	672.108	4.796	0.091	0.070	-333.017	0.911
betw_4_20_use	3	672.165	4.853	0.088	0.068	-333.046	0.979
null	2	675.117	7.804	0.020	0.015	-335.540	0.994
age.class	3	677.076	9.763	0.008	0.006	-335.501	1.000
Fall 95% isopleth							
Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
precip	3	672.76	0.00	1.00	1.00	-333.34	1.00
first_frost	3	689.30	16.54	0.00	0.00	-341.61	1.00
age_class	3	690.31	17.55	0.00	0.00	-342.11	1.00
null	2	692.74	19.98	0.00	0.00	-344.35	1.00
percent_hardwood	3	694.73	21.97	0.00	0.00	-344.33	1.00
Fall 50% isopleth							
Modnames	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
precip	3	606.784	0.000	1.000	0.999	-300.351	0.999
first_frost	3	622.745	15.961	0.000	0.000	-308.331	1.000
age_class	3	623.258	16.474	0.000	0.000	-308.588	1.000
betw_4_20_use	3	625.183	18.399	0.000	0.000	-309.550	1.000
null	2	625.806	19.023	0.000	0.000	-310.883	1.000
percent_hardwood	3	627.182	20.398	0.000	0.000	-310.550	1.000

Table A.3: *Model output of seasonal overlap (UDOI) as a function of log-transformed fall and spring home range areas (UDOI ~ fall home range area + spring home range area).*

Predictors	*Estimate*	*Std. Error*	*Pr(>|t|)*
(intercept)	0.31121	0.07586	5.7e-05
fall home range area	-0.07231	0.02100	0.0007
spring home range area	0.09244	0.01795	5.7e-07

Residual standard error: 0.2378 on 227 degrees of freedom
Multiple R-squared: 0.1275, Adjusted R-squared: 0.1198
F-statistic: 16.59 on 2 and 227 DF, p-value: 1.887e-07

APPENDIX B: CHAPTER 2 SUPPORTING INFORMATION

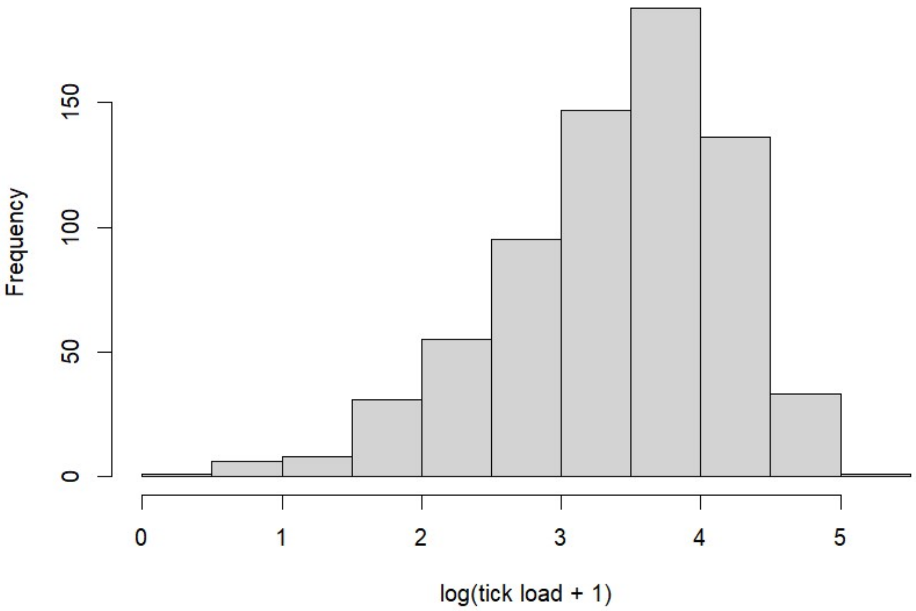

Figure B.1: *Histogram of log-transformed tick counts (n = 701).*

Table B.1: *Outputs from the climatic model (n = 701), where the response variable was tick loads measured in year y and the predictor variables, all measured in year measured in year y – 1, were fall precipitation, consecutive cold days below -15 degrees Celsius, drought index from July and August, and snow depth during the spring winter tick drop-off season. All predictor variables were z-scored and the response variable was log-transformed. Year was included as a random effect.*

Predictors	*Estimate*	*Std. Error*	*df*	*Pr(>|t|)*
(intercept)	3.44	0.17	6	8.5e-07
fall_precip	-0.28	0.12	27	0.026
cold_days	0.06	0.14	9	0.69
summer_drought	0.30	0.15	20	0.052
spr_snowdepth	0.28	0.06	70	6.3e-06
Random Effect (year)				
σ^2	0.45			
$\tau_{00\ year}$	0.26			
ICC	0.36			
N_{year}	9			

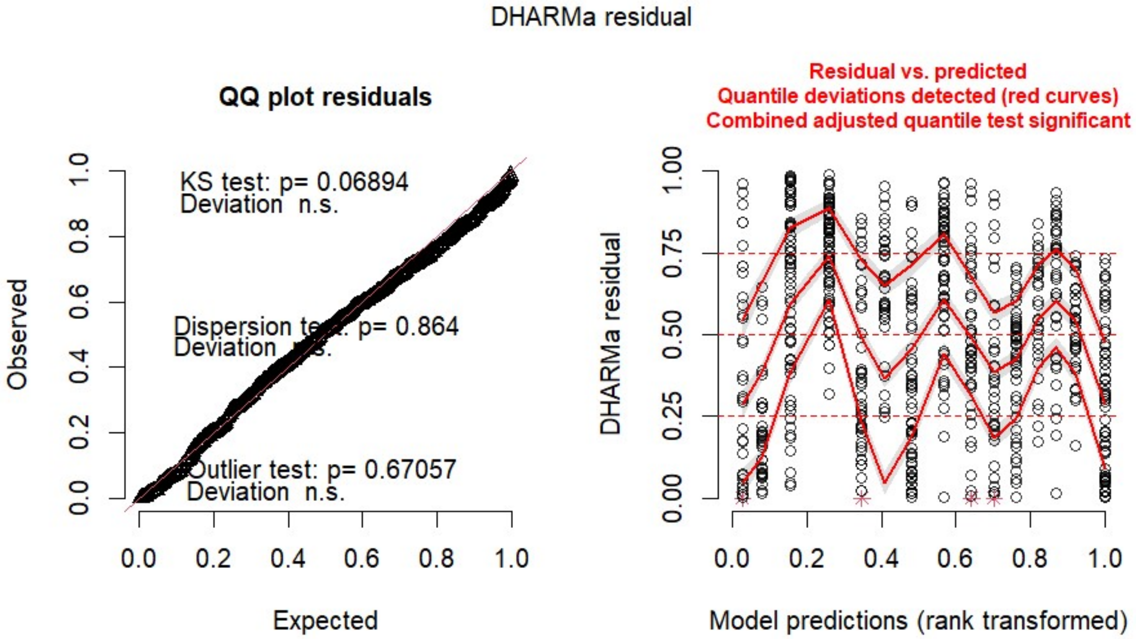

Figure B.2: *Simulated residuals from the additive climate model, plotted using the 'DHARMa' package (Hartig 2022, version 0.4.6) in program R (version 4.2.1).*

Table B.2: *Output from the overlap model (n = 46), where mean seasonal overlap (UDOI) between the winter tick spring drop-off and fall questing periods were averaged across years for individual moose. Mean UDOI was the predictor variable and tick load was the response variable, and year was included as a random effect.*

Predictors	*Estimate*	*Std. Error*	*df*	*Pr(>|t|)*
(intercept)	2.87	0.29	12	5.2E-07
mean_UDOI	1.38	0.54	62	0.0137
Random Effect (year)				
σ^2	0.53			
$\tau_{00\ \text{year}}$	0.28			
ICC	0.34			
N_{year}	6			

BIOGRAPHY OF THE AUTHOR

Annie Stupik was born in Natick, Massachusetts and graduated from Mercy High School in Middletown, Connecticut in 2010. She attended the University of Connecticut, majoring in Natural Resources with a concentration in Fisheries and Wildlife Conservation. For her undergraduate honors thesis, she researched the survival of post-fledgling American kestrels from nest boxes in Connecticut, publishing the findings with her mentors as co-authors (Survival and Movements of Post-fledging American Kestrels Hatched from Nest Boxes, 2015, Northeastern Naturalist 22(1): 20–31). She also worked as an animal educator at a local children's museum while completing her degree. After graduating with her B.S. in 2014, she worked two seasons as a wildlife technician in Wyoming where she worked on small mammal trapping, vegetation surveys, and songbird nest monitoring among other tasks. She then moved to Paraguay to join the Peace Corps as an environmental conservation volunteer, serving in a remote fishing village from 2015 to 2017. Following the Peace Corps, she worked for the Bureau of Wildlife at the New York State Department of Environmental Conservation as a technician for two years. She is currently a member of the Wildlife Society. In June of 2024, Annie began working for the New York State Department of Environmental Conservation as a wildlife biologist. Annie is a candidate for the Master of Science degree in Wildlife Ecology from The University of Maine in August 2024.