SELECTIVE HABITAT USE BY MOOSE DURING CRITICAL PERIODS IN THE WINTER TICK LIFE CYCLE

Christine Healy[1], Peter J. Pekins[1], Lee Kantar[2], Russell G. Congalton[1], and Shadi Atallah[1]

[1]Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH, 03824, USA; [2]Maine Department of Inland Fisheries and Wildlife, Research and Assessment Section: Bangor, Maine, 04401, USA.

ABSTRACT: High calf mortality attributed to winter tick (*Dermacentor albipictus*) parasitism occurs in moose (*Alces alces*) populations along their southern range in the northeastern United States. We analyzed habitat use of cow and calf moose during the critical drop-off and questing periods in the winter tick life cycle to determine a potential relationship between tick density and habitat. We measured habitat use using geospatial analyses of locational data from > 200 radio-marked animals at 3 sites in New Hampshire and Maine. Moose selected for optimal habitat, defined as 4–16 year-old forest openings, regardless of season or site; this was the only land cover type used more than available (1.1–2.1X availability in home range, 1.2–3.1X availability in core range). Further, the proportional availability of optimal habitat within overlapping portions of seasonal home and core ranges exceeded the absolute proportion of optimal habitat within any one range. Temporal use of optimal habitat, which is available in relatively low proportion (15–20%) across the landscape, likely exceeds the geospatial estimates of use because moose spend 30–40% of daily activity foraging. We conclude that disproportionally abundant densities of winter ticks exist in this preferred cover type because of its selective use during the drop-off and questing periods of winter ticks.

ALCES VOL. 54: 85–100 (2018)

Key words: *Alces alces*, *Dermacentor albipictus*, GIS, home range, Maine, New Hampshire, optimal habitat, questing.

Moose (*Alces alces*) populations in portions of the northeastern United States have recently experienced high mortality of 10–12 months-old calves. In 3 (2014–2016) of the past 5 years, mortality has exceeded 70% in northern New Hampshire and western Maine (Jones et al. 2017). The preponderance of this mortality is attributed to blood loss from excessively high loads of winter ticks (*Dermacentor albipictus*) (Jones et al. 2018). Winter tick epizootics (mortality > 50%) occurred periodically in Canadian provinces during the late 20th century (Samuel 2004, Samuel 2007); however, their frequency has increased in the northeastern United States in the last 15 years (Bergeron et al. 2013; Jones et al. 2017, 2018). High local moose density (Samuel 2004) and climate change resulting in later onset of winter snow (Musante et al. 2010, Bergeron and Pekins 2014, Dunfey-Ball 2017) are considered the primary reasons for the upsurge in winter tick parasitism.

Winter ticks range south of 60° N latitude throughout much of North America (Gregson 1956). They are monoxenous parasites found on a variety of vertebrate species, but are most commonly associated with ungulates, specifically moose, elk (*Cervus canadensis*), and white-tailed deer (*Odocoileus virginianus*) (Samuel et al. 2000). The life cycle of winter tick metamorphoses (3 stages - larvae, nymph, and adult) is consistent across their range (Lankester and Samuel 1998). Winter tick larvae ascend vegetation in early autumn and congregate at roughly shoulder height of large ungulates (McPherson et al. 2000, Samuel 2004). Clusters of ticks seek hosts from mid-September to the first permanent snowfall, and engorged adults drop from their hosts from mid- to late-March through April. Because adult female winter ticks, eggs, and larvae are relatively immobile, it is presumed that where adult females detach from their host in spring is where larvae quest the following fall.

Although moose are considered a generalist species, Peek (1997) argues that moose are "selective generalists" because they occupy early successional habitat more than proportionally available. Core ranges of moose in Sweden included cut areas with ~10% availability, twice that across the landscape (Cederlund and Okarma 1988), and moose in the Yukon consistently preferred shrub cover types over everything but conifers in all seasons (McCulley et al. 2017). Peek et al. (1976) described high quality habitat in Minnesota as sites consisting of 40–50% early successional vegetation < 20 years old, but considered 1% annual rate of forest removal as very good moose habitat.

The proportion of available optimal habitat (4–16 year-old cut areas) impacts moose movement across a landscape. They exhibit high fidelity to seasonal ranges between consecutive years (Gasaway et al. 1980, Cederlund et al. 1987, Cederlund and Sand 1994) and access to sufficient quality forage minimizes movement (Timmerman and McNicol 1988); therefore, small home ranges are considered an indicator of good habitat for non-migratory moose populations (Scarpitti 2006). Ranges are also affected by other factors including sex and age, so large ranges do not necessarily point to poor habitat composition. Males typically use larger ranges than females, particularly during the rut when access to potential mates is more important than forage (Goddard 1970, Cederlund and Sand 1994). Females are generally not as active and continue to prioritize feeding with their calves throughout autumn. Males tend to have more exclusive, less social home ranges than females that often overlap with other females (Cederlund et al. 1987). Additionally, yearlings and 2 year-old moose are known to disperse, often long distances, from their natal home range (Roussel et al. 1975, Lynch and Morgantini 1984).

Many studies have compared moose movement and habitat use during approximate calendar seasons or biologically significant periods (e.g., calving, breeding, winter) (Cederlund et al. 1987, Cederlund and Okarma 1988, Cederlund and Sand 1994, Thompson et al. 1995, Scarpitti 2006, Wattles and DeStefano 2013, Andreozzi et al. 2016, McCulley et al. 2017). Terry (2015) analyzed movement paths of moose during the drop-off and questing periods of winter ticks, but did not delineate home and core ranges. No study has specifically investigated home range and habitat use during the critical questing and drop-off stages in the winter tick cycle, which generally spans the cusp of multiple seasons typically described in the literature. Given the sedentary nature of winter ticks, their off-host location in summer and fall is dependent on moose location during specific weeks in late winter and spring when adult female ticks drop from moose. Determining moose movement and habitat use during these weeks and in autumn when winter ticks quest for a host at the same location is critical to understanding the spatial ecology of winter tick epizootics.

The New Hampshire Fish and Game Department (NHFG) in collaboration with the University of New Hampshire (UNH) and the Maine Department of Inland Fisheries and Wildlife (MDIFW) began outfitting moose with VHF and GPS radio-collars in 2014 to monitor productivity and mortality in northern New Hampshire and western and northern Maine. These sites exhibit a range in moose density and seasonal weather, with the site in northern Maine typically experiencing earlier snow cover. Timber harvesting is widespread at all sites, and is the primary means by which optimal moose habitat is created. After the institution of the State Practices Act in 1989 which restricted commercial clearcutting, partial harvesting became the most common logging strategy in Maine, making up > 90% of all statewide harvest in recent years (MFS 2016); in New Hampshire clearcutting remains common.

The objective of this study was to compare home/core ranges and seasonal habitat use by female moose during the two significant periods in the winter tick life cycle, at 3 sites in New Hampshire and Maine where onset of snow cover can vary by 2–4 weeks and moose density is considered moderate-high. Only females were considered because their locations are representative of calves, the cohort at greatest risk of winter tick-related mortality. It was hypothesized that moose would preferentially include optimal habitat within their home and core ranges during the questing and drop-off periods.

STUDY AREA

New Hampshire

The study area (Berlin) is located within Coos County and includes sections of Wildlife Management Units (WMU) B, C1, and C2 in the towns of Berlin, Milan, Dummer, Success, Cambridge, Millsfield, Stark, and Second College Grant (Fig. 1). The landscape is bisected by the Androscoggin River and is relatively mountainous, bordered to the west by the Kilkenny Range and the south by the Mahoosuc Range. Landcover is predominately commercial forest in which deciduous areas are dominated by yellow (*Betula alleghaniensis*) and paper birch (*B. papyrifera*), American beech (*Fagus grandifolia*), and sugar maple (*Acer saccharum*), with softwood stands that include black spruce (*Picea mariana*), red spruce (*P. rubens*), balsam fir (*Abies balsamea*), and white cedar (*Thuja occidentalis*) (DeGraaf et al. 1992). Logging operations remove 1–3% of timber annually, and optimal moose habitat increased 2.5X between 2001 and 2015 to equal > 17% of forest cover (Dunfey-Ball 2017). Habitat quality is considered good and not a limiting factor to the local moose population (Bergeron et al. 2011, Dunfey-Ball 2017). The average date of first snowfall is 14 November, with permanent snow typically beginning on 25 December (Dunfey-Ball 2017).

The site is part of the NHFG North Region and was the location of a comprehensive study of moose population dynamics in 2001–2005 when density was estimated to be ~0.8 moose/km^2 (Musante et al. 2010). The most recent population estimate is ~0.6 moose/km^2, and from 2014–2018, > 200 moose have been fit with radio-collars as part of a productivity and calf mortality study. Winter tick-related calf mortality was 62%, 74%, 77%, and 30% in 2014, 2015, 2016, and 2017, respectively (Jones et al. 2018, P. J. Pekins, UNH, unpublished data).

Maine

The site in western Maine (Jackman) occupies portions of Somerset and Piscataquis Counties in Wildlife Management District (WMD) 8, surrounding the towns of Greenville and Jackman (Fig. 2). The eastern boundary is Moosehead Lake and the

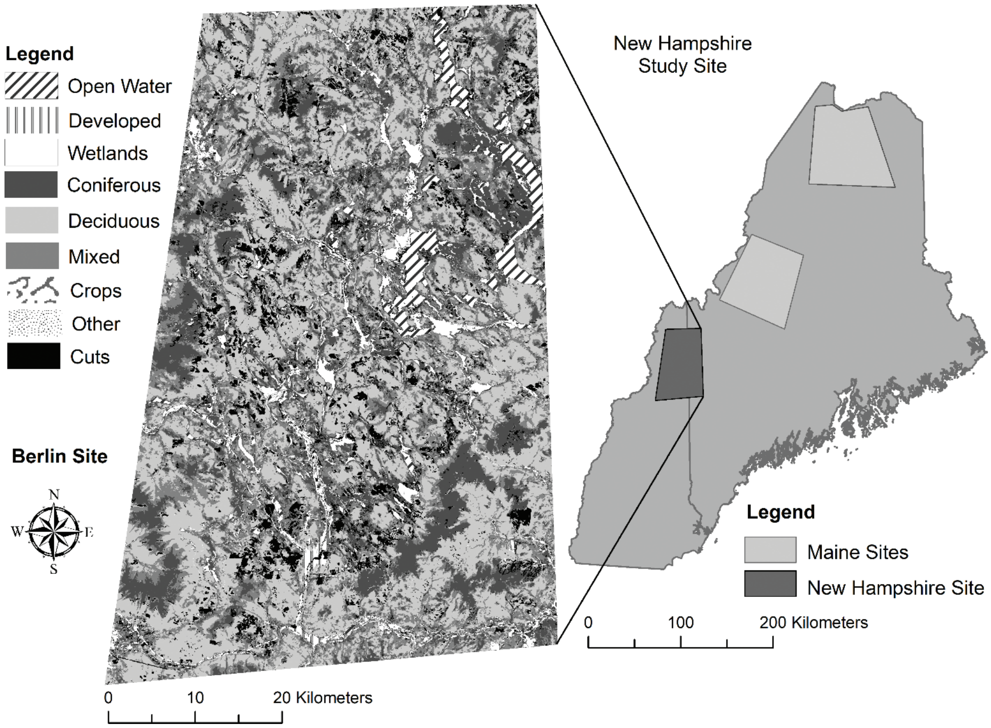

Fig. 1. The Berlin study site expanded from the regional map, displayed with reclassified NLCD habitat classifications.

Maine-Quebec line borders the west; Golden Road and Route 27 are the northern and southern borders. The site is considered primarily a maple-beech-birch hardwood forest of red maple (*Acer rubrum*), sugar maple, yellow birch, and American beech, with balsam fir as the dominant softwood; portions of the site also include northern white-cedar and red spruce (McCaskill et al. 2016). Though clear-cutting has declined in Maine due to regulatory change (MFS 1999), and is largely replaced by partial harvesting across a larger footprint, ~32% of statewide clear-cutting activity (14,531 total acres) in 2015 and 2016 occurred in Somerset and Piscataquis Counties (MFS 2015, 2016). Overall, optimal habitat has continuously been > 17% of forest cover since the early 2000s, and Maine forestland is considered excellent moose habitat (Dunfey-Ball 2017). Average dates of first and permanent snow are similar to those at the New Hampshire site.

Aerial surveys in 2013 estimated the average moose density as ~1.7 moose/km^2 (Kantar and Cumberland 2013); more recent estimates indicate a decline to 0.97–1.35 moose/km^2 (Jones et al. 2017). In 2014 – 2018 > 200 moose were GPS radio-collared as part of the collaborative study with New Hampshire. Calf mortality attributed to winter tick parasitism was 73%, 60%, 72%, and 53% in 2014, 2015, 2016, and 2017, respectively (Jones et al. 2018, L. E. Kantar, MDIFW, unpublished data).

The site in northern Maine (Aroostook) is located in Aroostook County within WMD 2 (Fig. 2). It includes the towns of Wheelock Mill and Winterville and is bordered by the Allagash River to the west. The eastern boundary is Route 11, and the southern boundary is American Realty Road.

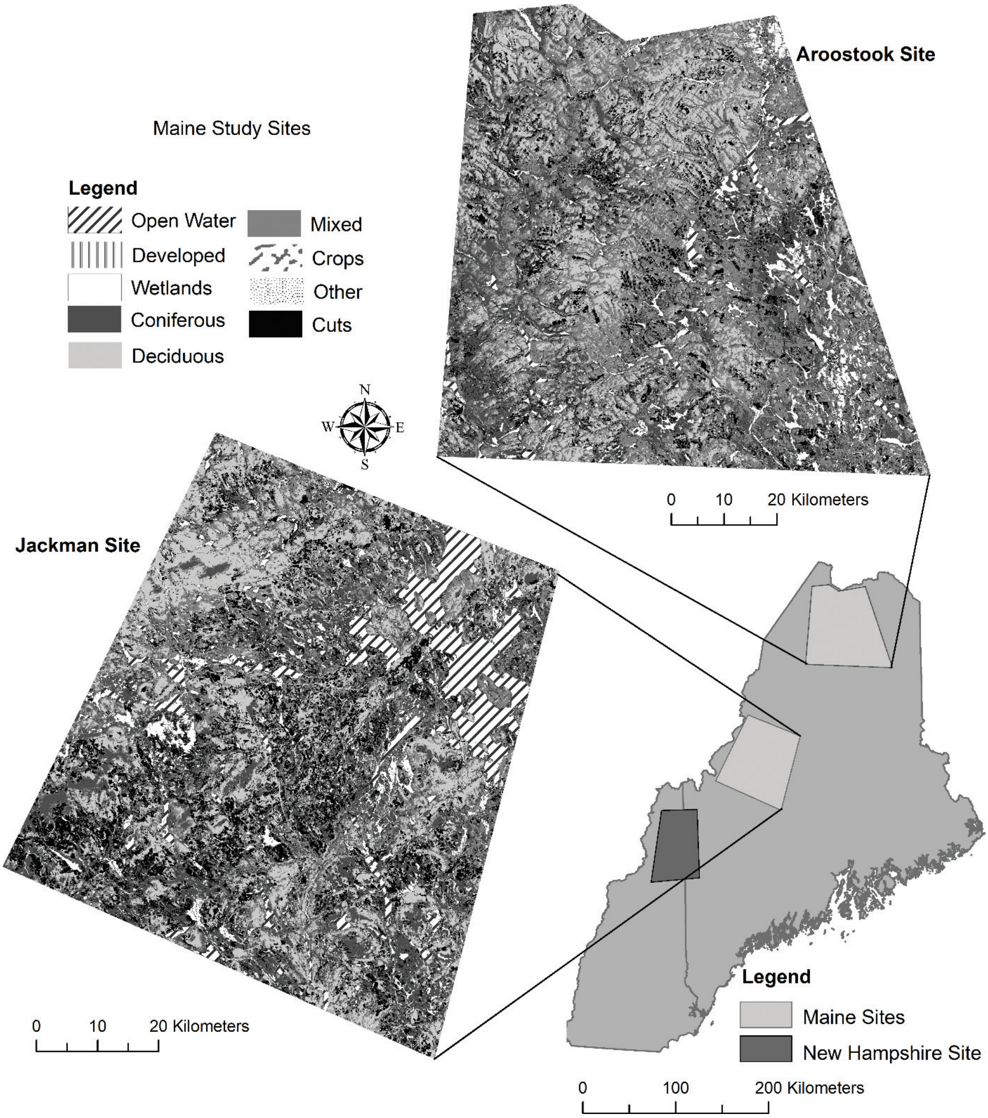

Fig. 2. The Jackman and Aroostook study sites explanded from the regional map, displayed with reclassified NLCD habitat classifications.

Spruce-fir and maple-beech-birch forest types categorize the site, with softwood stands dominated by balsam fir, northern white cedar, red spruce, and black spruce (McCaskill et al. 2016). About 1/3 of annual statewide clearcutting occurs in Aroostook County, with a total of 14,863 acres harvested in 2015 and 2016 combined (MFS 2015, 2016). Proportional availability of optimal habitat for moose was not available for this site, although it is considered excellent moose habitat (Andreozzi et al. 2016). Snow typically begins earlier at this site than at the other sites, and is thought to possibly limit the questing period and frequency of winter tick epizootics (Ellingwood 2018).

Moose density was estimated as 3.0–3.1 moose/km^2 during 2013 aerial surveys (Kantar and Cumberland 2013), and has since been adjusted to ~2.5 moose/km^2 in more recent surveys (Dunfey-Ball 2017, L. E. Kantar, MDIFW, unpublished data). This site was established in 2016 with > 120 GPS radio-collars deployed in 2016–2018. Winter tick-related calf mortality was 52% and 24% in 2016 and 2017, respectively (Jones et al. 2018, L. E. Kantar, MDIFW, unpublished data).

METHODS

Landcover

National Land Cover Data (NLCD 2011) were used to estimate habitat composition at the 3 study sites (Berlin, Jackman, and Aroostook). Land cover categories of emergent and woody wetlands were combined to represent "general wetlands". NLCD layers for New Hampshire and Maine were projected in UTM 19 N coordinates, and were clipped to polygons that had been digitized in ArcMap 10.3.1 (ESRI Redlands, CA) around locations of GPS transmissions in each site. The imagery dates ensured that new cuts (< 4 years since disturbance) were not included in the analysis.

Because the classification scheme categorizes early successional habitat as shrubland, herbaceous, and barren, these cover types were reclassified as "cuts" and considered optimal habitat. This approach likely underestimates optimal habitat for moose, as 16 year-old forest likely displays reflective properties more similar to mature forest than areas of recent disturbance. Additionally, partial cutting has proven more difficult to discern than larger clearcuts in Landsat imagery, as cut openings may be too small to be perceived as anything but noise at 30 × 30 m resolution. Change detection studies utilizing Landsat images to map forest disturbance have reported greater classification accuracy when the disturbance was clearcutting rather than partial harvesting (Wilson and Sader 2002: clearcuts = 79–96% accurate, partial cuts = 55–80% accurate; Jarron et al. 2017: clearcuts = 84% accurate, partial cuts = 64% accurate). The difficulty in identifying partial cuts is attributed to a more subtle and gradual change in spectral reflectance than evident with clearcuts (Jarron et al. 2017). Although this may yield a conservative estimate where partial harvesting is the predominant method of harvest, it was assumed that patterns of habitat use and selection would be evident.

The landcover composition at Berlin (3,405 km^2) was 82% forest comprised of deciduous (36%), mixed (27%), and coniferous (19%) types. Cuts represented ~9% of the landscape, and the remaining was wetlands (5%), open water (3%), and development (2%) (Fig. 1).

The Jackman site (5,535 km^2) was 65% forest cover: 23% coniferous and 21% deciduous and mixed forest each. Cuts were 19% and more prevalent than in Berlin or Aroostook; wetlands and open water (due to the inclusion of a portion of Moosehead Lake) were 8% (Fig. 2).

Aroostook (6,360 km^2) forest cover was mixed forest (38%), coniferous (22%), and deciduous (17%). Cuts were 11% with wetlands (8%), open water (2%), and cropland (1%) the remainder (Fig. 2).

Range size

Two seasons were defined to account for when 1) adult female ticks drop from moose in spring, and 2) larval ticks quest for a host in autumn: drop-off (15 March – 5 May) and questing (15 September – 26 November). GPS transmissions from adult cow moose logged to GPS Plus X (Vectronic Aerospace GmbH) during drop-off (2014–2017) and questing (2014–2016) were exported to Microsoft Excel to summarize the number of locations per animal; radio-collars were programmed to transmit locations twice daily. Radio-collars that logged ≥ 50 locations during a season were used to calculate home and core ranges of individuals using kernel density estimation; a sample size of 50 is recommended with the kernel density method (Seaman et al. 1999). In 2014–2017, 49 animals in Berlin and 124 in Jackman contributed to the dataset during drop-off; 7 animals in Berlin and 75 in Jackman were used during questing (2014–2016). In 2016–2017 in Aroostook, 83 animals were used in the drop-off period and 26 were used during questing (2016 only). Certain moose were used in multiple seasons.

The fixed kernel density method produces a more accurate measure of landscape use than other techniques such as minimum-convex polygons (Worton 1995, Seaman et al. 1999). The smoothing factor chosen was least-squares cross-validation (LSCV) as it results in the least bias when sample sizes are sufficient (Seaman et al. 1999). Contours generated in this analysis highlight the areas in which an animal would theoretically be located a certain proportion of the time (Worton 1995). Home and core ranges were defined as the 95% and 50% probability densities since these are the most commonly reported in the literature (Worton 1995, Seaman et al. 1999, McCulley et al. 2017). Ranges were calculated in the Geospatial Modelling Environment v. 0.7.4.0 (Beyer 2015) for each moose and imported to ArcMap.

Area (km^2) of home and core ranges was calculated using spatial statistics in ArcMap 10.3.1. Because kernel density estimation produces non-parametric results (Seaman et al. 1999), the comparison of mean ranges by season between sites was completed in R Studio 0.99.903 using the Kruskal-Wallis test which does not assume normality of data. The ranges of calves during drop-off were combined with the adult cow age class, as calf ranges are presumed similar to their mother's range (Ballard et al. 1991); no questing period was available for calves captured in January. Where results were significant for multiple variables ($P < 0.05$), Dunn's test using Bonferroni adjustments (R package PMCMR) was used to determine which variables accounted for that significance.

Habitat use

The NLCD layer for each site was clipped to and unioned with each home and core range polygon that fell within its boundary to measure the proportional availability of land cover types in ArcMap. The composition of core ranges was important because core range presumably reflects the area and habitats used most, whereas home range is a larger area that reflects less selective use. Comparing the composition of both ranges indicates if moose selected core ranges with specific habitat types less available within the home range. The Kruskal-Wallis test was used to compare the importance of each habitat type between seasons for adult cows and the composition of home and core ranges within each site. Because of a difference in proportional availability, significance testing between sites was not completed for habitat composition within home and core ranges.

Range overlap

This analysis included adult cows and calves that survived successive drop-off and questing periods in 2014, 2015, and 2016 in Berlin and Jackman, and 2016 in Aroostook. A total of 7 moose from Berlin, 76 moose from Jackman, and 26 moose from Aroostook fit this criterion. Home and core ranges for each moose measured during drop-off and questing of the same year were intersected using ArcMap 10.3.1 to determine where overlap occurred between seasons. The area of overlap was then divided by the total area covered by the drop-off and questing ranges to determine the proportion of habitat consistently used in both seasons. Non-parametric Kruskal-Wallis tests were performed in R Studio to determine if proportional overlap of home and core ranges differed by site. Where differences were significant

($P < 0.05$), Dunn's test was used to distinguish between sites.

National Landcover Data was clipped to each overlap to determine the proportion of optimal habitat consistently used between seasons. Spatial statistics within ArcMap were used to calculate the area of cuts within the overlaps, which was divided by the total area of the overlaps for both home and core ranges. Non-parametric Kruskal-Wallis tests were performed in R Studio to determine if the proportion of cuts within overlaps of home and core ranges differed by site. Where differences were significant ($P < 0.05$), Dunn's test was used to distinguish between sites.

RESULTS

Range size

Questing ranges were consistently larger than drop-off ranges, with the single exception of the core range at Berlin. Core ranges comprised 18–25% of home ranges regardless of season or site. Home ($P = 0.39$) and core range ($P = 0.82$) size during drop-off was similar at all sites, ranging from 9.9–15.0 and 2.1–2.7 km^2, respectively. Conversely, size of home ($P = 0.02$) and core ranges ($P = 0.03$) was different during questing; Aroostook was larger than Berlin (>2.5X larger) (Table 1). Individual variation in home and core range was high, ~4–5 fold.

Habitat use

Although available within each site, open water, developed, cropland, and "other" habitat types combined was < 2% of drop-off and questing ranges, and considered insignificant in the analysis. The proportional use of habitat types within home ranges was similar each season ($P > 0.05$). In core ranges during drop-off, deciduous forest was used more in Aroostook and Jackman ($P = 0.02, 0.05$), and coniferous forest was used more in Aroostook ($P = 0.03$). Cuts were the only habitat type consistently used more than available, regardless of site or season. Cuts were used 1.1–2.1X their availability within home ranges, and 1.2–3.1X their availability within core ranges (Fig. 3). Deciduous and coniferous forest types were used less than available at Berlin and Jackman; mixed forest was used equal to or above its availability.

Few differences were found between home and core ranges within a site during

Table 1. Home range (HR) and core range (CR) recorded for moose during the questing and drop-off periods at each site in New Hampshire and Maine, USA. Data for Berlin (New Hampshire) and Jackman (Maine) were collected between 2014–2017 and for Aroostook (Maine) in 2016–2017. Where *P* values were significant, the results of Dunn's test indicating which sites were significantly different is listed, with sites abbreviated by first initial (A = Aroostook, B = Berlin, J = Jackman).

Seasonal Range	Aroostook			Berlin			Jackman			*P*
	n	Mean ± SE (km^2)	range (km^2)	n	Mean ± SE (km^2)	range (km^2)	n	Mean ± SE (km^2)	range (km^2)	
Home Range										
Drop-off	83	15.0 ± 2.0	0.3–117.6	49	13.0 ± 2.0	0.5–70.9	124	9.6 ± 0.7	0.2–43.9	0.39
Questing	26	34.1 ± 7.0	4.2–171.2	7	11.8 ± 2.6	3.7–23.2	75	23.2 ± 3.0	3.5–151.2	0.02 (A-B = 0.04)
Core Range										
Drop-off	83	2.7 ± 0.3	0.1–14.0	49	2.6 ± 0.4	0.1–11.6	124	2.1 ± 0.2	0.1–7.1	0.82
Questing	26	7.4 ± 1.2	1.1–22.7	7	2.9 ± 0.8	0.8–6.6	75	5.7 ± 0.8	0.9–43.9	0.03 (A-B = 0.04)

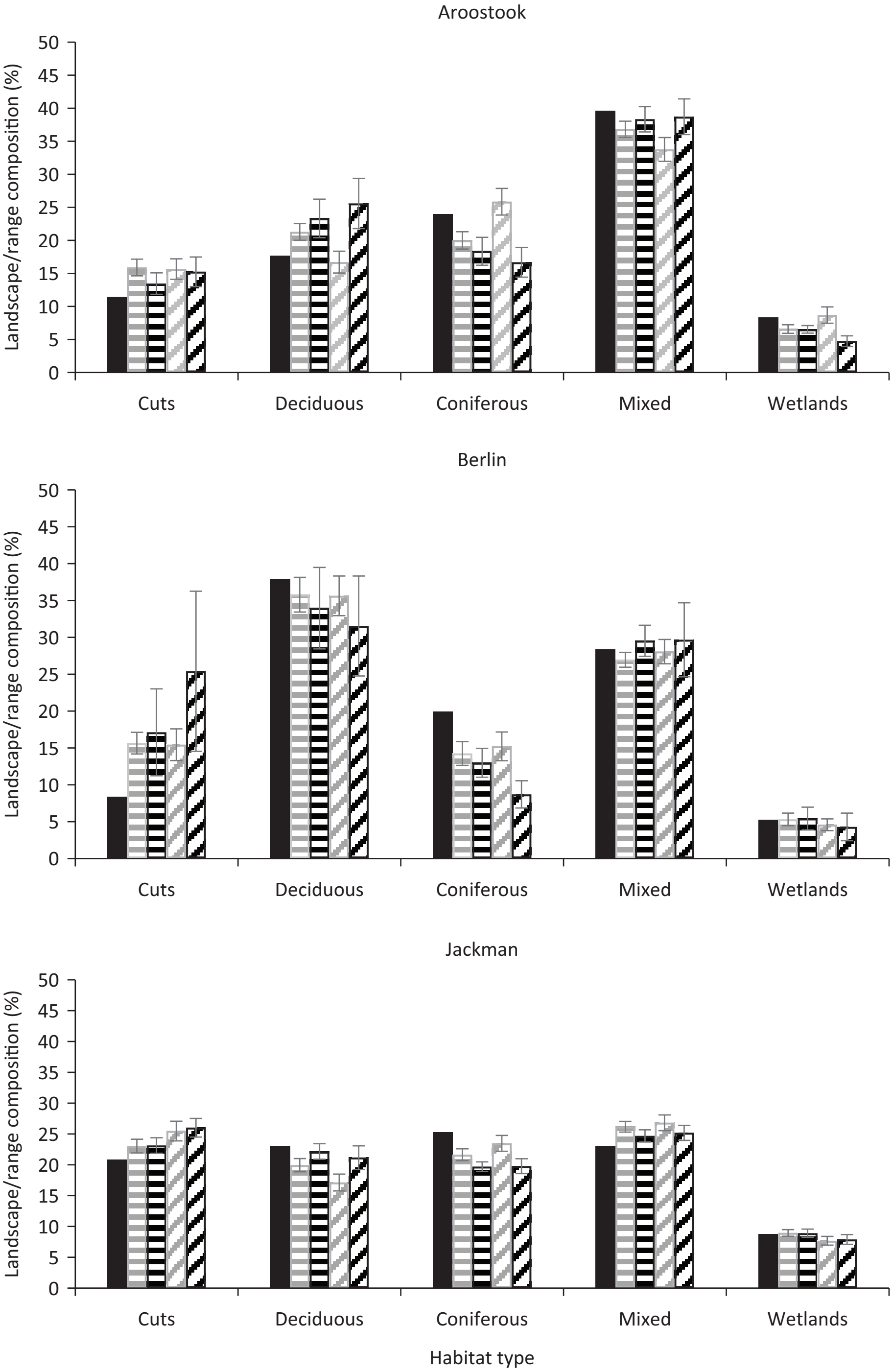

Fig. 3. Adult use of each of the 5 major habitat types. Solid black bars show landscape availability specific to each site. Horizontal stripes indicate use of habitats within home ranges, while diagonal stripes show core ranges. Light grey bars correspond to the drop-off period and patterned black bars are questing. Error bars represent standard error.

the same season. Exceptions in core ranges during drop-off included less use of mixed forest in Aroostook (*P* = 0.03), deciduous forest in Aroostook and Jackman (*P* = 0.02, 0.01), and wetlands in Jackman (*P* = 0.10). Moose at all sites displayed 2–8% higher selection of optimal habitat within core ranges during questing, whereas use of optimal habitat was similar (within 2%) for home and core ranges during drop-off.

Range overlap

Overall, 97% of moose had overlapping home ranges and 66% had overlapping core ranges. The proportion of home and core range overlaps varied from 0–73% and 0–43%, respectively; home range overlap in Berlin and Jackman was ≥20%. An increasing trend in overlap occurred from Aroostook to Berlin to Jackman; home (*P* = 0.04) and core range overlaps (*P* = 0.01) were higher in Jackman than Aroostook (Table 2). At all sites, the proportion of overlap declined (~2–5 fold) from home to core ranges.

Across sites, the average proportion of optimal habitat in seasonally overlapping home and core ranges was similar: 12–23% in home and 8–26% in core ranges. This proportion exceeded the proportional availability of optimal habitat at each site (Table 3, Fig. 3). In contrast to seasonal overlap, the proportion of optimal habitat overlap was similar between home and core ranges, except in Berlin. The proportion of optimal habitat in home range overlap was 1.8X higher in Jackman than in Aroostook (*P* < 0.00); the proportion in Berlin was similar to that at both Maine sites. The proportion of optimal habitat in core range was not different (*P* < 0.05) among sites, although the overlap in Jackman was 1.7–3.1X higher than at Aroostook and Berlin (Table 3). As with seasonal overlap, individual variation in overlap existed (0–75%).

DISCUSSION

Range size

Home and core range sizes during questing increased from south (Berlin) to north (Aroostook), a pattern likely reflecting the similar population density gradient at these sites. In general, the larger ranges during

Table 2. Overlap of home (HR) and core (CR) ranges for moose that survived subsequent drop-off and questing seasons at each site in Maine (Aroostook, Jackman) and New Hampshire (Berlin), USA (2014–2017).

Range	Aroostook			Berlin			Jackman		
	n	Mean (± SE) Overlap	Range Overlap	n	Mean (± SE) Overlap	Range Overlap	n	Mean (± SE) Overlap	Range Overlap
HR	25	15.1 ± 2.0%	1–40%	7	19.9 ± 6.0%	7–54%	75	24.3 ± 1.8%	0–73%
CR	13	3.1 ± 1.2%	0–24%	4	7.9 ± 4.2%	0–29%	56	8.8 ± 1.1%	0–43%

Table 3. Proportion of home (HR) and core (CR) overlap that was composed of optimal habitat used by moose in Maine and New Hampshire, USA (2014–2017).

Range	Aroostook		Berlin		Jackman	
	Mean (± SE) Cuts (%)	Range Cuts (%)	Mean (± SE) Cuts (%)	Range Cuts (%)	Mean (± SE) Cuts (%)	Range Cuts (%)
HR	12.4 ± 2.8	0–75.0	17.0 ± 5.7	1.7–46.3	23.0 ± 1.7	0–68.0
CR	14.8 ± 5.2	0–66.7	8.2 ± 4.7	0–18.9	25.8 ± 2.9	0–75.0

questing reflect higher movement and activity during breeding season. The ranges were similar to those reported in previous studies at the Berlin site and in Massachusetts (Table 4).

Habitat use

Use of optimal habitat was higher than proportionally available within home and core ranges. This selective use is well documented regionally, year-round, and in boreal forests at large (Belovsky 1981, Renecker and Hudson 1992, Scarpitti et al. 2005, Scarpitti 2006, Bjørneraas et al. 2011, Lenarz et al. 2011, Terry 2015). Although the relative difference between availability and use of cuts was lowest in Jackman, both availability and use of cuts were highest there, with use proportionally up to 25% higher than the other sites (Fig. 3). Moose generally displayed higher use of optimal habitat during questing than drop-off, despite larger home ranges during questing. This stronger habitat selection, despite larger home range, may ensure questing success and high tick abundance on moose despite their increased activity and movement during breeding. Overall, this analysis provides strong evidence of selective use during the short and critical periods of drop-off and questing during the life cycle of winter ticks.

One limitation of describing habitat use from location data is that the GPS radio-collars were programmed to transmit coordinates only twice daily. Although home range composition can be reasonably defined, there is no estimate for the amount of time moose spend in each habitat type. Moose, like other ruminants, spend most time in three activities—feeding, resting, and ruminating (Renecker and Schwartz 1997). Daily activity budgets indicate that time spent per activity changes seasonally, but feeding generally occupies 30–40% of each day (Risenhoover 1987, Renecker and Hudson 1989, Van Ballenberghe and Miquelle 1990). The bulk of forage consumption by moose is within optimal habitat, because it provides highest quality forage and is concentrated spatially (Renecker and Schwartz 1997). Therefore, time spent in cuts is presumably higher than the proportional availability of cuts in the core range.

The high use of optimal habitat by moose during drop-off and questing is important because the survival of winter tick larvae is highest in open cover types; tick

Table 4. A comparison of home range sizes during late winter, spring, and autumn for moose in Maine and New Hampshire, USA (2014–2017).

Location	Drop-off HR		Questing HR		Method	Source
	Size (km^2)	Drop-off Dates	Size (km^2)	Questing Dates		
New Hampshire	14.2 ± 2.3	15 Mar. – 5 May	11.8 ± 2.6	15 Sept. – 26 Nov.	95% KDE	This study
Western Maine	9.4 ± 0.7	15 Mar. – 5 May	23.2 ± 3.0	15 Sept. – 26 Nov.	95% KDE	This study
Northern Maine	21.6 ± 6.1	15 Mar. – 5 May	37.0 ± 7.3	15 Sept. – 26 Nov.	95% KDE	This study
New Hampshire	~15.2	Late-winter + spring = 16 Feb. – 15 Jun.	24.7	Fall = 16 Sept. – 15 Dec.	90% KDE (VHF)	Scarpitti 2006
Massachusetts	~ 12.0	Late-winter + spring = 1 Jan. – 31 May	~11.4	Fall + early-winter = 1 Sept. – 31 Dec.	95% KDE	Wattles & DeStefano 2013

density declines as canopy cover exceeds 60% closure (Drew and Samuel 1986, Aalangdong 1994, Terry 2015) because restricted sunlight and cooler temperatures impact the activity and efficiency of winter ticks during questing (Drew and Samuel 1986, Aalangdong 1994). With the exception of years characterized by especially hot and dry conditions, open habitats are more conducive to successful larval transmission than closed habitats (Addison et al. 2016). In an assessment of randomly selected cover types crossing fall movement paths of GPS-collared moose, Terry (2015) found that 70% of locations categorized as regenerating habitat contained ticks; a greater proportion than in any other cover type. In combination, selective habitat use by moose and higher survival of larval ticks provides favorable conditions to promote local abundance of winter ticks in optimal moose habitat.

Seasonal overlap

Moose display seasonal range fidelity (Welch et al. 2000, Ofstad 2013), and unsurprisingly, all but 3 of 106 adult moose that survived consecutive questing and drop-off periods exhibited some degree of seasonal home range overlap. Average home range overlap was 15–24%, with the greatest overlap in Jackman and the least in Aroostook. Core range overlap was lower at 3–9%, but followed the same site trend. Importantly, the seasonal proportional overlap of optimal habitat in home and core ranges exceeded the absolute proportion in home and core ranges. The drop-off period in this study spanned portions of the late-winter and spring seasons as defined by Scarpitti (2006), who found 22% overlap in late-winter and fall home ranges, and 33% overlaps in spring and fall home ranges; core range overlaps were 10% and 16%, respectively.

Optimal habitat was 12–23% of the seasonal home range overlaps of 102 of 106 moose. Interestingly, core range overlaps contained a greater proportion of optimal habitat (15–26%) than home range overlaps at all sites except Berlin (8%) which had a small sample size (4 moose). These data indicate that moose not only select cuts, but also use the same cuts during both the drop-off and questing seasons, and presumably identical feeding sites and paths within the same cuts. It is possible that moose contract offspring larvae in the fall from adult ticks that dropped from them the previous spring. This is consistent with Terry (2015) who found some degree of self-overlap on spring and fall movement paths of radio-collared moose (4.6%).

Understanding when and where moose acquire winter ticks is key to predicting the occurrence and relative severity of winter tick epizootics. Unfortunately, current estimates of field abundance of winter ticks are not available, and such estimates are rare overall. Local larval abundance has been measured only once by Bergeron and Pekins (2014) who reported a regional density of 0.07–0.16 winter ticks/m^2, and maximum density of 0.40–0.64 ticks/m^2 within individual cuts. These measurements occurred in autumn 2008 and 2009, neither preceding a spring with an epizootic. Hence, these estimates should be considered conservative, particularly during years when weather conditions favor larval survival and extended questing.

Overall, relative tick abundance on the landscape is fundamentally a function of moose density (Samuel 2004), larval survival, and the length of the questing period (Dunfey-Ball 2017). Of consequence is that these relationships are gradually affected by climate change influences that lengthen the questing period. Predicting the relative influence of these factors on tick loads of moose, and ultimately the occurrence of an epizootic, requires further work measuring field abundance of ticks.

CONCLUSION

This analysis indicates that moose in northern New England selectively use optimal habitat during the drop-off and questing seasons of winter ticks, and that field abundance measurements should focus on these habitats. Importantly, this relationship was found despite cuts being underestimated due to the difficulty in using Landsat imagery to discern smaller openings associated with partial harvesting, and possibly misclassifying older age classes of optimal habitat (4–16 years). Considering that moose spend 30–40% of daily activity feeding in optimal habitat that ranged from 9–19% availability at the study sites, it follows that winter tick abundance on the landscape is concentrated in proportionally small, but selectively used optimal habitat. Again, this is a conservative conclusion as moose commonly bed in cuts during both seasons, presumably increasing the local abundance of gravid adult female ticks during drop off, and subsequently, tick loads on moose after questing. Winter tick abundance on the landscape is ultimately a function of multiple characteristics of the behavior, physiology, and local abundance of moose and winter ticks that are linked to dynamic processes of forest harvesting, weather events, and climate change. Assuming continuation of the current trend of sustained forest harvest in northern New England that produces near 20% availability of optimal moose habitat and high moose density, the near-term occurrence of winter tick epizootics will primarily be a function of annual weather events that limit survival of winter tick larvae in autumn.

ACKNOWLEDGEMENTS

Funding for this project was provided in part through Wildlife Restoration Program grant No. F13AF01123 (NH W-104-R-1) to N.H. Fish and Game Department from the U.S. Fish and Wildlife Service, Division of Wildlife and Sport Fish Restoration with matching funds provided by the University of New Hampshire. We are additionally grateful to MDIFW for providing access to the locational data used to complete this study, and to K. Ball and H. Grybas for their input and advice on data analysis techniques.

REFERENCES

Aalangdong, O. I. 1994. Winter tick (*Dermacentor albipictus*) ecology and transmission in Elk Island National Park, Alberta. M. S. Thesis, University of Alberta, Edmonton, Alberta, Canada.

Addison, E. M., R. F. McLaughlin, P. A. Addison, and J. D. Smith. 2016. Recruitment of winter ticks (*Dermacentor albipictus*) in contrasting forest habitats, Ontario, Canada. Alces 52: 29–40.

Andreozzi, H. A., P. J. Pekins, and L. E. Kantar. 2016. Using aerial survey observations to identify winter habitat use of moose in northern Maine. Alces 52: 41–53.

Ballard, W. B., J. S. Whitman, and D. J. Reed. 1991. Population dynamics of moose in south-central Alaska. Wildlife Monographs 114: 3–49.

Belovsky, G. E. 1981. Food plant selection by a generalist herbivore: the moose. Ecology 62: 1020–1030.

Bergeron, D. H. 2011. Assessing relationships of moose populations, winter ticks, and forest regeneration in northern New Hampshire. M.S. Thesis, University of New Hampshire, Durham, New Hampshire, USA.

_____, and P. J. Pekins. 2014. Evaluating the usefulness of three indices for assessing winter tick abundance in northern New Hampshire. Alces 50: 1–15.

_____, _____, and K. Rines. 2013. Temporal assessment of physical characteristics and reproductive status of moose in New Hampshire. Alces 49: 39–48.

BEYER, H. L. 2015. Geospatial Modelling Environment (Version 0.7.4.0). <http://www.spatialecology.com/gme> (accessed April 2018).

BJØRNERAAS, K., E. J. SOLBERG, I. HERFINDAL, B. VAN MOORTER, C. M. ROLANDSEN, J-P. TREMBLAY, C. SKARPE, B-E. SÆTHER, R. ERIKSEN, and R. ASTRUP. 2011. Moose (*Alces alces)* habitat use at multiple temporal scales in a human-altered landscape. Wildlife Biology 17: 44–54.

CEDERLUND, G., and H. OKARMA. 1988. Home range and habitat use of adult female moose. The Journal of Wildlife Management 52: 336–343.

_____, and H. Sand. 1994. Home-range size in relation to age and sex in moose. Journal of Mammalogy 75(4): 1005–1012.

_____, F. SANDEGREN, and K. LARSSON. 1987. Summer movements of female moose and dispersal of their offspring. The Journal of Wildlife Management 51: 342–352.

DEGRAAF, R. M., M. YAMASAKI, W. B. LEAK, and J. W. LANIER. 1992. New England wildlife: management of forested habitats. General technical report NE – 144. USDA Forest Service, Northeast Forest Experimental Station, Radnor, Pennsylvania, USA.

DREW, M. L., and W. M. SAMUEL. 1986. Reproduction of the winter tick, *Dermacentor albipictus*, under field conditions in Alberta, Canada. Canadian Journal of Zoology 64: 714–721.

DUNFEY-BALL, K. R. 2017. Yearling moose dispersal in a declining population in northern New England and moose and winter tick epizootics in northern New England's changing climate. M.S. Thesis, University of New Hampshire, Durham, New Hampshire, USA.

Ellingwood, D. 2018. Assessing the impact of winter ticks on moose condition and population dynamics in northern New Hampshire. M. S. Thesis. University of New Hampshire, Durham, New Hampshire, USA.

GASAWAY, W. C., S. D. DUBOIS, and K. L. BRINK. 1980. Dispersal of subadult moose from a low-density population in interior Alaska. Transactions of the North American Moose Conference and Workshop 16: 314–337.

GODDARD, J. 1970. Movements of moose in a heavily hunted area of Ontario. The Journal of Wildlife Management 34: 439–445.

GREGSON, J. D. 1956. The *Ixodoidea* of Canada. Science Service, Entomology Division, Canada Department of Agriculture. Publication 930.

JARRON, L. R., T. HERMOSILLA, N. C. COOPS, M. A. WULDER, J. C. WHITE, G. W. HOBART, and D. G. LECKIE. 2017. Differentiation of alternate harvesting practices using annual time series of Landsat data. Forests 8 (15): 1–13.

JONES, H., P. J. Pekins, L. E. Kantar, D. Ellingwood, M. O'Neil, I. Sidor, and A. Lichtenwalner. 2018. Mortality assessment of calf moose during successive years of winter tick epizootics in New Hampshire and Maine. Canadian Journal of Zoology 96: in press.

_____, _____, _____, M. O'NEIL, and D. ELLINGWOOD. 2017. Fecundity and summer calf survival of moose during 3 successive years of winter tick epizootics. Alces 53: 85 – 98.

KANTAR, L. E., and R. CUMBERLAND. 2013. Using a double-count aerial survey to estimate moose abundance in Maine. Alces 49: 29–37.

LANKESTER, M. W., and W. M. SAMUEL. 1998. Pests, parasites, and diseases. Pages 479–517 *in* A. W. Franzmann, and C. C. Schwartz, editors. Ecology and Management of the North American Moose. The Wildlife Management Institute, Washington D. C., USA.

LENARZ, M. S., R. G. WRIGHT, M. W. SCHRAGE, and A. J. EDWARDS. 2011. Compositional analysis of moose habitat in northeastern Minnesota. Alces 47: 135–149.

LYNCH G. M., and L. E. MORGANTINI. 1984. Sex and age differential in seasonal home range size of moose in northcentral Alberta, 1971–1979. Alces 20: 61–78.

Maine Forest Service (MFS). 1999. The State of the Forest and Recommendations for Forest Sustainability Standards. Augusta, Maine, USA.

_____. 2015. Silvicultural Activities Report including Annual Report on Clearcutting and Precommercial Activities. Augusta, Maine, USA.

_____. 2016. Silvicultural Activities Report including Annual Report on Clearcutting and Precommercial Activities. Augusta, Maine, USA.

McCaskill, G. L., T. Albright, C. J. Barnett, B. J. Butler, S. J. Crocker, C. M. Kurtz, and C. W. Woodall. 2016. Maine Forests 2013. U. S. Forest Service, Newtown Square, Pennsylvania, USA.

McCulley, A. A., K. L. Parker, and M. P. Gillingham. 2017. Yukon moose: II. Range sizes, movement rates, and use of elevation and land cover by males and females. Alces 53: 1–21.

McPherson, M., A. W. Shostak, and W. M. Samuel. 2000. Climbing simulated vegetation to heights of ungulate hosts by larvae of the winter tick, *Dermacentor albipictus* (Packard) (Acari: Ixodidae). Journal of Medical Entomology 37: 114–120.

Musante, A. R, P. J. Pekins, and D. L. Scarpitti. 2010. Characteristics and dynamics of a regional moose *Alces alces* population in the northeastern United States. Wildlife Biology 16: 185–204.

Ofstad, E. 2013. Seasonal variation in site fidelity of moose (*Alces alces*). M.S. Thesis, Norwegian University of Science and Technology, Trondheim, Norway.

Peek, J. M. 1997. Habitat relationships. Pages 351–376 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and Management of the North American Moose. The Wildlife Management Institute, Washington D. C., USA.

_____, D. L. Urich, and R. J. Mackie. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildlife Monographs 48: 3–65.

Renecker, L. A., and R. J. Hudson. 1989. Seasonal activity budgets of moose in aspen dominated boreal forests. The Journal of Wildlife Management 53: 296–302.

_____, and _____. 1992. Habitat and forage selection of moose in the aspen-dominated boreal forest, Central Alberta. Alces 28: 189–201.

_____, and C. C. Schwartz. 1997. Food habits and feeding behavior. Pages 401–439 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and Management of the North American Moose. The Wildlife Management Institute, Washington D. C., USA.

Risenhoover, K. L. 1987. Winter foraging strategies of moose in subarctic and boreal forest habitats. Ph. D. thesis, Michigan Technological University, Houghton, Michigan, USA.

Roussel, Y. E., E. Audy, and F. Potvin. 1975. Preliminary study of seasonal moose movements in Laurentides Provincial Park, Quebec. Canadian Field-Naturalist 88: 47–52.

R Studio Team. 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, Massachusetts, USA. <http://www.rstudio.com/> (accessed April 2018).

Samuel, W. M. 2004. White as a Ghost: Winter Ticks and Moose. Natural History Series, Volume 1. Federation of Alberta Naturalists, Edmonton, Alberta, Canada.

_____. 2007. Factors affecting epizootics of winter ticks and mortality of moose. Alces 43: 39–48.

_____, M. S. Mooring, and O. I. Aalangdong. 2000. Adaptations of winter ticks (*Dermacentor albipictus*) to invade moose and moose to evade ticks. Alces 36: 183–195.

Scarpitti, D. R. 2006. Seasonal home range, habitat use, and neonatal habitat characteristics of cow moose in northern

New Hampshire. M. S. Thesis. University of New Hampshire, Durham, New Hampshire, USA.

_____, C. Habeck, A. R. Musante, and P. J. Pekins. 2005. Integrating habitat use and population dynamics of moose in northern New Hampshire. Alces 41: 25–36.

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. The Journal of Wildlife Management 63: 739–747.

Terry, J. 2015. The habitat of winter ticks (*Dermacentor albipictus*) in the moose (*Alces alces*) range of northeast Minnesota. M.S. Thesis, University of Minnesota, Duluth, Minnesota, USA.

Thompson, M. E., J. R. Gilbert, G. J. Matula, Jr., and K. I. Morris. 1995. Seasonal habitat use by moose on managed forest lands in northern Maine. Alces 31: 233–245.

Timmermann, H. R., and J. G. McNicol. 1988. Moose habitat needs. The Forestry Chronicle 64: 238–245.

Van Ballenberghe, V., and D. G. Miquelle. 1990. Activity of moose during spring and summer in interior Alaska. The Journal of Wildlife Management 54: 391–396.

Wattles. D. W., and S. DeStefano. 2013. Space use and movements of moose in Massachusetts: implications for conservation of large mammals in a fragmented environment. Alces 49: 65–81.

Welch, I. D., A. R. Rodgers, and R. S. McKinley. 2000. Timber harvest and calving site fidelity of moose in northwestern Ontario. Alces 36: 93–103.

Wilson, E. H., and S. A. Sader. 2002. Detection of forest harvest type using multiple dates of Landsat TM imagery. Remote Sensing of Environment 80: 385–396.

Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. The Journal of Wildlife Management 59: 794–800.