WINTER HABITAT SELECTION OF MOOSE IN MAINE AND RUMINATIONS ON THE IMPACT OF CHANGING WEATHER CONDITIONS

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ABSTRACT: Winter habitat use by moose (*Alces alces*) in response to climate change may reflect shifts in biotic and abiotic stressors that pose both environmental challenges and opportunities. Snow depth, temperature, winter length, and forest composition influence moose mobility, habitat use, and access to forage and cover resources. We analyzed habitat selection in winter home ranges of adult female moose (n = 96) over the course of six winters (2014–2019) to explore the influence of winter weather and forest composition on landscape and habitat use. Second order (home range) resource selection functions were estimated using generalized linear mixed models. Moose selected most strongly for forest habitat, specifically evergreen and mixed forests, which had similar strength of selection and represented ~50% of home ranges. The models identified a slight positive association with regenerating forest, although high levels of variance indicated a weak relationship. Contrary to our prediction, we did not detect any influence of weather conditions on winter habitat selection. Maine's mosaic of forest types and commercial forestry seemingly provide adequate food and cover resources for moose regardless of winter conditions, with the three habitat types selected for representing ~70% of home ranges. Due to the coarse resolution of the data we analyzed, more specific data on forest structure such as stand age, canopy, and forage species may be required to identify finer relationships in habitat use and specific resource requirements during winter. It is possible that other factors associated with climate change, such as increases in deer (*Odocoileus virginianus*) populations, parasites, and disease will have greater influence on moose than habitat per se. However, because these potential influences are indirectly related to habitat use by moose, further research is warranted to best understand the multiple factors and relationships affecting winter habitat use.

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INTRODUCTION

Moose (*Alces alces*) population dynamics are largely influenced by forage and cover resources in forest habitats; within Maine's boreal forest moose landscape use is likely driven by access to optimal habitat (Healy et al. 2018). Like other northern regions, Maine is experiencing seasonal shifts in weather from climatic warming, most notably extreme weather events and warmer, shorter, and less snowy winters (Garlick et al. 2019, Fernandez et al. 2020). Changes in winter conditions and length impact moose populations both directly and indirectly through shifts in forest composition, use of forest habitats, bioenergetics, and parasite and disease dynamics (Post and Stenseth 1999, Murray et al. 2006, Ditmer et al. 2018, Lankester 2018). As such, it is critical to understand winter habitat selection and landscape use by moose in the context of changing winter conditions (Maier et al. 2005, Bjørneraas et al. 2011).

After a history of heavy hunting and population decline in the 19th century, moose populations slowly increased in Maine in the early-mid 1900s, with a dramatic increase occurring in the 1980–1990s. The population was estimated as 70,000–80,000 animals in 2012 (MDIFW 2017) with highest densities in the contiguous interior forests of the state (Wattles and Destafano 2011). This increase reflects the reconversion of farmland to forest, changes in forest management, minimal predation, and regulatory protection from hunting (Karns 1998, Foster et al. 2002, Timmermann and Rodgers 2005, Wattles and Destafano 2011, Kantar and Cumberland 2013). More recently, an outbreak of spruce budworm (*Choristoneura fumiferana*) in the 1970s brought on extensive salvage logging and large-scale timber harvests (Irland et al. 1988) that created a mosaic of regenerating forest stands providing ideal habitat and forage resources for moose throughout central and northern Maine (Renecker and Schwartz 1998, Van Beest et al. 2010, Wattles and Destafano 2011, Andreozzi et al. 2016).

Winter habitat provides foraging and cover needs for moose that generally select for food availability over canopy cover (Renecker and Schwartz 1998, Poole and Stuart-Smith 2006). Adult female moose are in negative energy balance in mid to late winter due to low-quality forage and increasing gestational costs, although they have evolved to survive winter in reasonable condition (Regelin et al. 1985, Peek 1998, Schwartz and Renecker 1998, Pekins 2020). In general, moose forage on woody plants, twigs, and fallen leaves in winter (Renecker and Schwartz 1998), favoring maples (*Acer* spp.), birches (*Betula* spp.), other hardwood species, and balsam fir (*Abies balsamea*) (Ludewig and Boyer 1985, Faison et al. 2010). They show preference for regenerating stands (Blouin et al. 2021) with abundant forage that are identified as optimal habitat (Healy et al. 2018) and predictors of moose location in winter (Andreozzi et al. 2016). It is clear that forest habitat in Maine provides adequate winter forage and cover resources given it sustains an abundant moose population.

Overstory cover consisting of dense vertical tree canopy in softwood stands is used during harsh winter conditions and deep snow accumulation (Dussault et al. 2005). While temperature probably has minimal influence on habitat selection (Van Beest et al. 2012), snow depth and snow density can impede mobility and limit access to forage during a time when energy conservation is needed to minimize weight loss (Timmermann and Mcnicol 1988). While moose are well adapted to travel through snow, access to forage is reduced when mobility is hindered by snow depths > 90 cm (Ballenberghe and Ballard 1998, Peek 1998, Courtois et al. 2002). Conversely, minimal snow depth expands mobility, habitat use, and access to forage (Courtois et al. 2002). Climatic warming would presumably affect winter habitat use of moose relative to forage and cover requirements and access.

Climate change is expected to increase the northern range of certain hardwood tree species including maples (*Acer* spp.) and birches (*Betula* spp.) commonly consumed by moose (Rodenhouse et al. 2009, Peterson et al. 2020). Although maple-beech-birch forests are expected to remain the predominant forest type in Maine (Rustad et al. 2012), worst-case climate models predict declines in red maple, yellow birch (*Betula allegheniensis*), and paper birch (*B. papyrifera*) (Prasad et al. 2007). Further, spruce-fir forests and lowland mixed conifer forests that moose use for winter cover and forage (Ludewig and Bowyer 1985, Leptich and Gilbert 1989) are considered vulnerable to climate change (Swanston et al. 2018).

The more immediate influence of climate change is arguably how changing winter conditions influence parasitism and disease in moose (Murray et al. 2006, Dunfey-Ball 2017, Jones et al. 2019, Pekins 2020). Winter tick parasitism is already increasing in frequency and severity with higher infestation rates associated with longer autumnal questing periods where moose density is high (Samuel 2007). Maine moose annually experience high infestation of winter ticks that causes excessive mortality (>50%) of 10–11 month-old moose calves, delayed sexual maturation in yearling cows, and reduced productivity in adult cows (Musante et al. 2007, Elliott 2019, Jones et al. 2019, Pekins 2020). Presumably, milder winters will allow white-tailed deer (*Odocoileus virginianus*) density to increase in areas with large moose populations (Weiskopf et al. 2019); along with increased competition for forage resources, white-tailed deer can pass brainworm (*Parelaphostrongylus tenuis*) to moose that is potentially fatal (Schmitz and Nudds 1994, Murray et al. 2006, Lankester 2010, 2018).

Taken together, shifts in forest composition and less severe winters from climatic warming will influence how moose use and interact with forest habitats (Humphries et al. 2004, Rodenhouse et al. 2009). Since moose respond to habitat resources within a few kilometers of their location (Maier et al. 2005), resources within the home range should prove useful to investigate how moose respond to changes in the larger landscape. Forest resources and environmental variables influence habitat selection and should provide perspective concerning effects of climatic change on resource use and availability, how moose use and respond to shifting environmental conditions and resources (Rodenhouse et al. 2009), and winter distribution of moose on the landscape (Humphries et al. 2004).

The objectives of this study were to determine habitat selection in winter home ranges of adult female moose in Maine and explore how winter weather conditions might influence landscape use through home range selection. We hypothesized that: 1) moose will select habitat features that minimize energy expenditure and maximize forage availability, and 2) that selection for specific habitat features related to forage and cover resources will vary relative to weather conditions and winter severity. If moose select habitat to minimize energy expenditure over winter, we expect to find selection for forest types like mixed forests that provide both forage and overstory cover. If the severity of winter conditions impact habitat selection, we predict greater use of softwood stands in winters with high snowfall, and conversely, greater use of regenerating forests and open areas in winters with less snow accumulation. If this relationship is true, we expect to find that models containing an interaction between habitat variables and winter weather conditions would be better supported than models containing only additive effects of habitat variables. We explored the potential influence of winter weather and forest composition on habitat use at the landscape scale by analyzing winter home ranges of GPS radio-collared adult female moose over the course of 6 years.

STUDY AREA

Maine is in the northeastern United States, has a diverse landscape from rocky coast to interior mountains, and is mostly forested (89%) with northern hardwood, coniferous, and mixed forest types (Butler 2018). Our study included two areas with multiple-aged commercial forests reflecting historical and current forest harvesting and management practices (Wiersma 2009). Historical harvesting in our study areas created a patchy forest landscape favoring regeneration of commercially viable tree species (Barton et al. 2012). More recent harvesting patterns reflect more efficient and larger harvests, and regeneration from the spruce budworm epidemic in the 1970–1980s that resulted in widespread, large-scale salvage harvesting of spruce-fir forests (Irland et al. 1988). Other recent influences include sustainable forestry initiatives, which reduced size of clearcuts leading to an increase in prevalence of partial harvest management, and a dramatic increase in conservation lands beginning in the 1990s (Barton et al. 2012). The forest structure in our two study areas is still influenced by forest harvesting practices and pest and disease stressors that produce a diversity in forest stand age and composition.

The Maine Department of Inland Fisheries and Wildlife (MDIFW) uses 29 Wildlife Management Districts (WMD) to guide local and regional wildlife management (MDIFW 2017). This study occurred in WMD 8 in the western mountains and WMD 2 in the north that are in the New England Adirondack Province ecoregion (Fig. 1): WMD 8 in the Central and Western Mountains region and WMD 2 in the Boundary Plateau-St. John Uplands region (Schlawin and Cutko 2014). Both are comprised of similar landscapes and composed mainly of

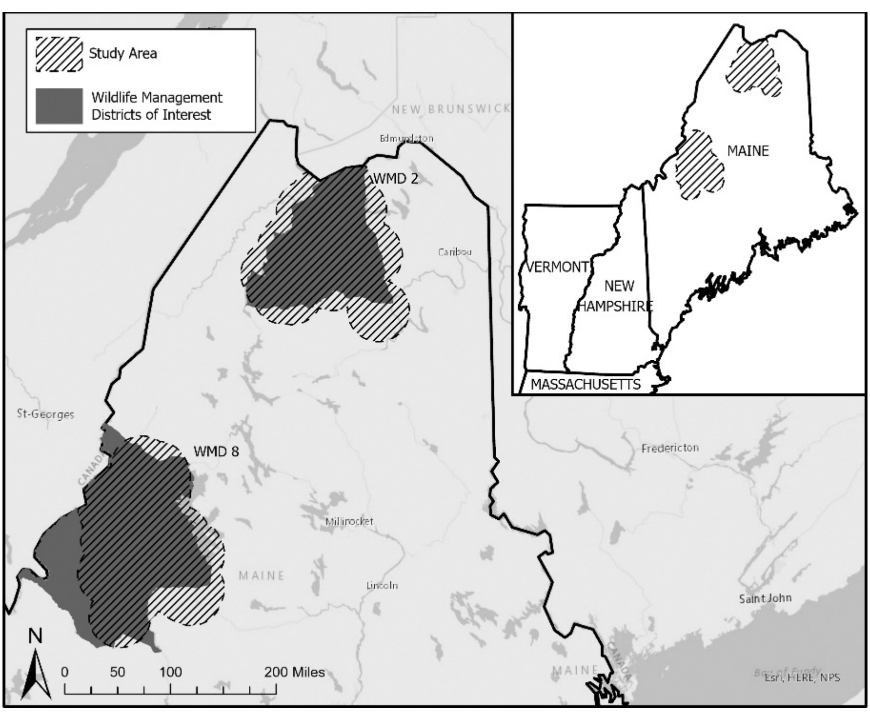

Fig. 1. Location of study area, Wildlife Management Districts (WMD) 2 and 8, in the context of New England (US) and Maine, USA.

Acadian low elevation spruce-fir-hardwood forests (16% and 26%, respectively) and Laurentian-Acadian northern hardwood forests (27% and 26%, respectively); >30% of each is currently in conservation land (Schlawin and Cutko 2014).

We analyzed WMD 8 and WMD 2 jointly to capture a wide range of winter weather conditions in areas with moderate-high moose density, and similar forest habitat and forest harvesting dynamics. The combination of ample suitable habitat, low risk of predation and moose-vehicle-collisions, and conservative moose harvest for 40 years has created a moderate-high population density: ~3.1 moose/km^2 in WMD 2 and 1.7 moose/km^2 in WMD 8 (Kantar and Cumberland 2013). Winter tick parasitism, not habitat, is considered the principal limitation of population growth (MDIFW 2017). White-tailed deer (*Odocoileus virginianus*) density in Maine during our study period was below the management objective of 50% biological carrying capacity (MDIFW 2017).

METHODS

Moose Locations

We acquired location data from 96 GPS radio-collared (Vertex Globalstar, Vectronic) adult females (n = 61 in WMD 8; n = 35 in WMD 2) that were part of a larger demographic study of moose survival in Maine (MDIFW 2017). Locations were collected twice daily at ~ 05:00 and 17:00 hr EST (times shifted with daylight savings time) and downloaded daily via satellite (GPS Plus Vertex Survey Collar, Vectronic Aerospace GmbH, Berlin, Germany). Data were collected for each animal until death or until the collar ceased working; certain individuals were monitored during multiple winters.

These data spanned 6 years starting in winter 2013–2014 and ending in winter 2018–2019.

We used GPS points taken during the winter season to calculate home ranges, and defined winter as 15 December – 15 March. In a typical winter, this period is when forage resources are most limited, ambient temperature coldest, and snow cover most prevalent and likely to impede mobility in open areas (Schwartz and Renecker 1998, Dussault et al. 2005, Scarpitti et al. 2005).

Home Range Generation

To characterize winter habitat, we analyzed second-order resource selection defined as individual home range selection within a species geographical range (Johnson 1980). We examined second-order selection due to limitations in data resolution including coarse weather metrics and temporal bias in GPS location data that restricted our ability to consider resource use within home ranges and other higher-order selection. Kernel Density Estimation (KDE) was used to calculate utilization distribution (UD) (Worton 1989) for individual home ranges using the package adehabitatHR (Calenge 2006, 2011) in the program R (R Core Team 2021). The reference bandwidth for h (h_{ref}) was used to determine smoothing (Blundell et al. 2001, Hemson et al. 2005) and to calculate 95% UD home range polygons for each individual. Individuals with < 30 points in a given winter were precluded from analysis that year (Seaman et al. 1999).

Land cover variables were quantified within each 95% UD polygon to calculate individual habitat use each winter. We characterized the availability of landscape features using a case-control design by calculating mean annual home range size and overlaying this with individual winter home ranges. This approach matched available habitat to the scale moose were selecting habitat within their winter home range (Boyce 2006). This allowed us to compare the composition of an individual winter home range to that available to an individual given its annual movements.

To calculate the median annual-home range size, we determined an annual home range for each individual using KDE and the 95% UD. We included individuals with GPS locations available for at least 6 months in a single year to establish annual ranges reflective of use through multiple seasons, and then calculated the mean area of annual home ranges from these individuals. We calculated the radius equivalent to the mean annual home range size to use as the estimated distance an individual might travel to access available habitat during the study period. Using the calculated average mean radius value, we created circular plots with a radius of 5.44 km from the center point of each winter home range polygon to characterize available habitat for each individual, where the entire polygon including the home range was treated as available habitat.

Environmental Variables

We used elevation, slope, and land cover as variables to assess determinants of moose habitat selection based on relationships from past research. Elevation and slope influence late winter ranges of moose and can proxy for other environmental conditions such as local snow depth (Poole and Stuart-Smith 2006). Elevation was obtained from Digital Elevation Models (DEM) and calculated as an average for each home range polygon. Slope was calculated from DEMs using ArcGIS and averaged within each home range.

Classification of landscape composition was determined using the 2016 National Land Cover Database ((NLCD 2016) NLCD 2016). Land cover variables that composed < 5% of the available landscape were excluded from the analysis due to their limited presence and presumed low biological significance. Five land cover variables were included in our analysis: mixed forest, evergreen forest, deciduous forest, regenerating (shrub forest, herbaceous forest, shrub scrub, herbaceous), and wetlands (woody wetlands and emergent herbaceous wetlands). The NLCD product used in this study included spectrally transitioning shrub (shrub forest) and grassland (herbaceous forest) variables that are considered early successional habitats (Healy et al. 2018, Homer et al. 2020); therefore, we combined spectrally transitioning shrub, spectrally transitioning grass, herbaceous, and shrub scrub into a single regenerating forest variable. Likewise, woody wetlands and emergent herbaceous wetlands were combined into a single wetlands variable.

Mixed, evergreen, and deciduous forest land cover variables encompass mature (>5 m tall) forested landscapes (NLCD 2016). The mixed forest land cover variable includes both evergreen and deciduous tree species (NLCD 2016) that provide cover and forage for moose. Evergreen forests were composed mainly of spruce and fir species, with northern white cedar (*Thuja occidentalis*) and eastern hemlock (*Tsuga canadensis*) also present (Butler 2018). The principal hardwoods in both the mixed and deciduous land cover variables were maples, birches, and American beech (*Fagus grandifolia*) (Butler 2018). The evergreen variable principally provides cover and the deciduous variable principally forage for moose during winter (Ludewig and Boyer 1985, Dussault et al. 2005, Faison et al. 2010). The regenerating forest variable includes young trees and shrubs that are preferred winter forage for moose (Blouin et al. 2021); while the data lacked information about tree height, this land cover variable is generally a more open landscape (NLCD 2016). Using these adjusted NLCD categories, we created a GIS raster layer for each landscape class and then intersected those with the unique, individual winter home ranges and associated available habitat polygons to generate estimates of percent cover to use in the models.

We used multiple winter weather variables from the NOAA Global Historical Climate Network Daily Summaries (NOAA 2019) and the Maine Cooperative Snow Survey (MCSS) (MDACF 2019) to assess if weather influenced habitat use. Measurements were collected at a single point location (weather station) representative of the study area in each WMD. In each winter, we calculated a mean value of five weather variables: 1) minimum temperature, 2) maximum temperature, 3) precipitation, 4) snowfall, and 5) average snow depth. Snow depth was obtained from the MCSS (MDACF 2019).

There was considerable variation in average snow depth and maximum temperature over the course of the study (Fig. 2). On average, WMD 8 had slightly higher maximum winter temperatures and slightly lower snow depths than WMD 2 (Fig. 2). Winter 2015–2016 was considered abnormally mild compared to the other years, with higher temperatures and lower snow depth in both WMDs (Fig. 2), in contrast to the winters of 2013–2014 and 2018–2019 which were considered more severe. As expected, many of the climate variables were correlated (Appendix 1); high correlation (>|0.60|) was found between snow depth and snowfall (0.75), snowfall and precipitation (0.78), and minimum and maximum temperature (0.89). As a result, we considered climate variables separately in our model set.

Statistical Analysis

Resource Selection was estimated using generalized linear mixed models (GLMM) in R (R Core Team 2021). Slope and

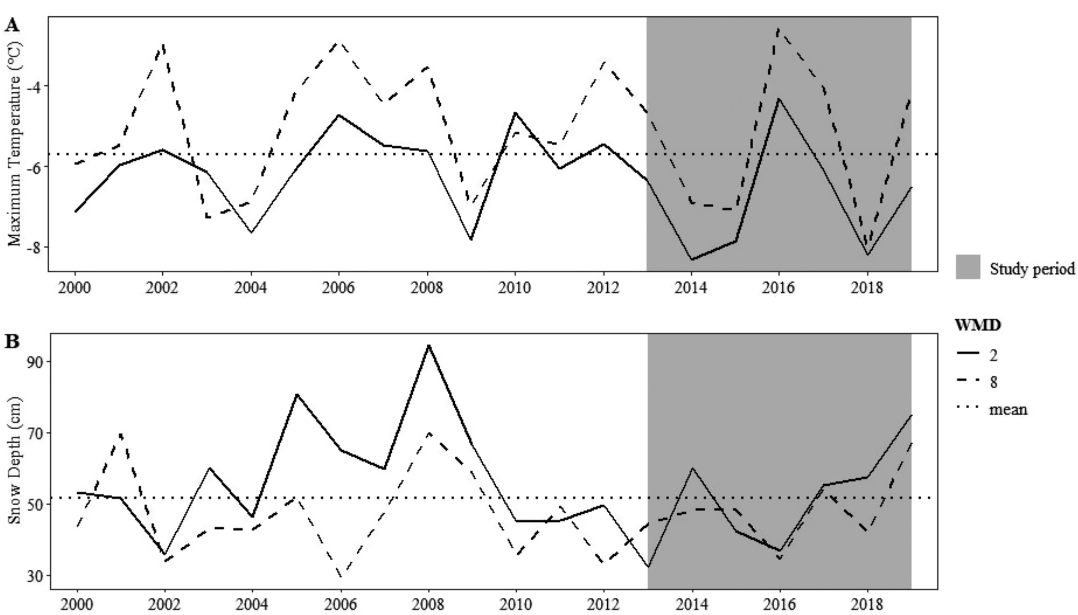

Fig. 2. Average winter snow depth (cm) and average winter maximum temperature (°C) from 2000 to 2019, including study period from 2013 to 2019, for WMD 2 and 8 in Maine, USA. The 20-year mean average snow depth was 51 cm and mean average maximum temperature was −6°C for both WMD's combined.

elevation were included in the model selection process and the resulting beta values were assessed for significance. All land cover variables were included as fixed effects, with individual and WMD included as random effects (Manly et al. 2002, Hebblewhite and Merrill 2008). We assessed the influence of weather conditions on habitat selection by examining interactions between weather variables and land cover variables. Collinearity of variables was assessed using Pearson correlation coefficients. Any variables with correlations >0.600 were not included in the same model; collinearity was dealt with by removing highly correlated variables from the same model based on ecological relevance (Graham 2003). Any variable removed from a model due to high correlation with another variable retained in the model was subsequently tested in the same model (in place of the retained variable) to evaluate which was better supported. Evergreen and deciduous forests were correlated and close to the 0.600 threshold (−0.57); given that both are dominant components of the landscape, we assessed each independently to determine the covariate effects.

Model fit was assessed using Akaike's Information Criterion (AIC) which compares each model's complexity to the variance explained by the model (Burnham and Anderson 2002). The model with the lowest AIC was selected as the model with best fit to the data. To assess significance of model variables, we compared the beta estimates and associated standard errors; if the 95% confidence intervals surrounding beta estimates did not overlap zero, it suggested a significant effect ($P < 0.05$). We also investigated the influence of slope and elevation on selection. Although elevation was supported in our modeling framework, the beta estimates were not significant and the 95% confidence intervals overlapped zero; therefore, elevation was not included in our base model. We retained all landcover variables in the base model in order to investigate potential interactions with climate variables. Beta estimates and their associated variance were assessed to compare strengths of associations of habitat and weather variables on habitat selection.

We used a two-step process to identify our final model. First, we identified a base model that contained the land cover variables supported by our model selection process. Then we included the weather variables as interaction terms with the land cover variables to assess the influence of winter weather on selection. Interactions between each weather variable and each land cover variable were tested one at a time. The resulting model fits were compared to the base model.

RESULTS

A total of 222 winter home ranges were calculated using 96 adult female moose during the 6-year study period. Winter home range size varied widely, averaging 13.7 ± 11.9 km^2 (SD) with most between 1 and 21 km^2; major outliers were excluded as determined by values 1.5 interquartile ranges above the third quartile. Most annual home ranges were between 8 and 50 km^2. Available habitat was mostly forest (85.7%) with mixed, evergreen, and deciduous forest constituting 30%, 20%, and 19% of the landscape, respectively. Regenerating forest comprised 17% of the landscape, with wetlands (8.9%) and other open land cover variables comprising the remainder (5.4%; Table 1).

Resource Selection

Model selection did not support the inclusion of slope or elevation in the base model. We investigated potential support for inclusion of elevation; however, delta AIC was < 2.0 with its addition and model outputs

Table 1. Land cover composition for used and available landscape and associated standard deviation. Estimates calculated from average winter home ranges and associated available habitat for 96 female moose in Maine, 2013–2019.

Land class	Composition (%) of available landscape (sd)	Composition (%) of used landscape (sd)
Mixed Forest	30.05 (7.62)	31.93 (10.92)
Evergreen Forest	20.29 (7.47)	22.48 (12.64)
Deciduous Forest	18.66 (8.98)	16.93 (13.26)
Regenerating Forest	16.65 (4.76)	16.70 (8.10)
Wetlands	8.93 (4.53)	8.75 (6.75)
Open Water[1]	3.00 (3.71)	1.16 (2.70)
Developed[1]	2.08 (0.80)	1.78 (1.36)
Barren Land[1]	0.30 (0.29)	0.25 (0.46)
Crops/Pasture[1]	0.01 (0.11)	0.01 (0.08)

[1]Land class was excluded from analysis since it comprised less than 5% of the landscape.

Table 2. GLMM model results to determine the best model of winter resource selection of female adult moose in Maine, 2013–2019. Number of model variables (K), Akaike's information criterion (AIC) scores, differences in AIC (ΔAIC) scores.

Model	K	AIC	ΔAIC
Evergreen_Forest + Mixed_Forest + Regenerating_Forest + Wetlands + **Elevation +** (1|WMD) + (1|ID)	7	610.9	−1.80
Evergreen_Forest + Mixed_Forest + Regenerating_Forest + Wetlands + (1|WMD) + (1|ID)	6	612.7	0
Evergreen_Forest + Mixed_Forest + Regenerating_Forest + Wetlands + **Slope +** (1|WMD) + (1|ID)	7	613.9	1.20
Deciduous_Forest + Mixed_Forest + Regenerating_Forest + Wetlands + (1|WMD) + (1|ID)	6	623.5	10.8

Note: AIC=Akaike Information Criteria value, ΔAIC=difference between model AIC and lowest (best) model AIC.

identified borderline significance and a small effect size for the estimate ($\beta = 0.003$, SE = 0.002, $P = 0.05$). We also investigated the influence of deciduous forest on winter habitat selection independently from evergreen forest given that evergreen and deciduous forest cover variables were highly correlated (0.60). Models containing evergreen forest outperformed those containing deciduous forest (Table 2), indicating evergreen forest is a better predictor of winter habitat selection. Evergreen forest was included in the base model along with the other major land cover variables to investigate potential interactions between land cover and climate on selection.

Moose primarily selected for forested habitat types during winter. The final model contained only additive effects of the land-cover variables (evergreen, mixed, and regenerating forest, and wetlands) as predictors of winter habitat selection. In general, moose had strong and similar selection for evergreen and mixed forests during winter (Table 3), with slightly stronger selection for evergreen. Moose were more likely to have moderate to high levels of evergreen or mixed forest component in their winter

Table 3. Model derived beta estimates and standard errors of best habitat selection model based on winter home range characteristics of female adult moose in Maine, 2013–2019.

Evergreen_Forest + Mixed_Forest + Regenerating_Forest + Wetlands + (1|WMD) + (1|ID)		
Model variable	Estimate (SE)	95% CI
Evergreen forest	0.037*** (0.011)	0.016, 0.059
Mixed forest	0.040*** (0.012)	0.016, 0.066
Regenerating forest	0.022 (0.016)	−0.009, 0.054
Wetlands	0.005 (0.019)	−0.032, 0.041

Note: *$p < 0.1$;**$p < 0.05$;***$p < 0.01$

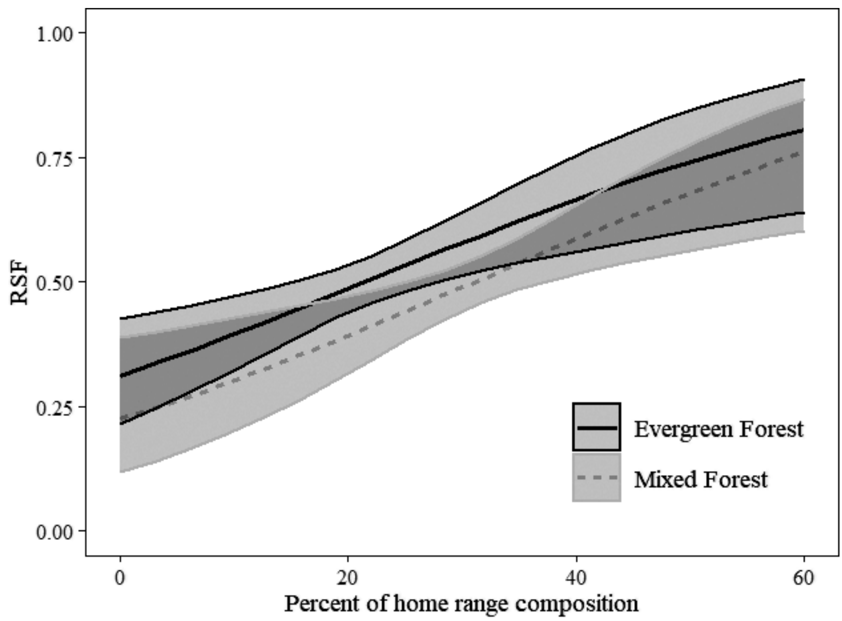

Fig. 3. Resource Selection Functions (RSF) depicting relative predictive probability of use and 95% confidence intervals for significant land classes, evergreen and mixed forest, for winter resource selection of female adult moose in Maine, 2013–2019.

home range (Fig. 3). There was a positive influence of regenerating forest on selection; however, we did not identify significant support for effects of regenerating forests and wetlands on habitat selection when considering beta estimates and their associated variance (Table 3).

Our second objective was to identify variation in selection due to changes in winter conditions related to winter severity. However, we failed to detect support for any interactions between weather variables (average snow depth or average min temperature) and land cover variables on selection of winter home range characteristics (Table 4). We also investigated potential interactions between deciduous forest and weather variables to explore if use of those areas might increase during less severe winters. Again, we did not detect any significant interactions between weather and land cover variables (Table 4). Consequently, our final

Table 4. Model results, number of model variables (K), Akaike's information criterion (AIC) scores, differences in AIC (ΔAIC) scores, from assessment of interactions between land cover variables and yearly winter severity metrics to determine the best model of winter resource selection of female adult moose in Maine, 2013–2019. Interactions between each weather variable and each land cover variable were tested in the base model individually. The base model contained an additive effect of land cover variables (*Evergreen_Forest + Mixed_Forest + Regenerating_Forest + Wetlands + (1|WMD) + (1|ID))*.

Model variable	Interaction term variable		K	AIC	ΔAIC
	Snow Depth	Min Temp			
Base Model	**NA**	**NA**	**6**	**612.7**	**0.0**
Regenerating Forest	−0.0008	NA	7	616.6	3.9
	NA	−0.0021	7	616.3	3.6
Evergreen Forest	0.0013	NA	7	616.2	3.5
	NA	−0.0016	7	616.2	3.5
Mixed Forest	0.0012	NA	7	616.4	3.7
	NA	−0.0011	7	616.5	3.8
Wetlands	0.0032	NA	7	616.1	3.4
	NA	−0.0036	7	616.0	3.3
Deciduous Forest[1]	−0.0027	NA	7	625.9	13.2
	NA	0.0015	7	627.0	14.3

[1]Deciduous forest was evaluated for interactions in the model in place of evergreen forest due to high correlation between variables.

model (AIC = 612.7) contained only the additive effects of the four major land cover variables: evergreen forest, mixed forest, regenerating forest, and wetlands.

DISCUSSION

Female adult moose showed strong selection for forested areas during winter, with slightly greater selection for evergreen than mixed forest, although both types were preferred. There was a slight preference for regenerating forest, although this relationship was highly variable among individuals; wetlands were not selected for during winter. Slope and elevation did not appear to be important components of winter habitat; however, it is possible they are utilized to mediate micro-habitat conditions at a finer scale than analyzed. Our results highlight the value of both mixed forest and evergreen forest land cover types as components of winter habitat, and suggest that both are important for moose in this region. Moreover, we did not identify a difference in selection of specific habitat types based on weather variables as we found no strong patterns to indicate any dramatic shift in habitat selection associated with overall winter conditions.

Our hypothesis that moose would select for evergreen habitats more in winters with higher amounts of snow was not supported, suggesting that selection for evergreen forests was insensitive to changes in winter conditions. Multiple explanations include that evergreen forests are commonly used regardless of winter conditions, the high availability of evergreen forest in the study area masks their selection, or winter conditions during the study were moderate and selective use of evergreen forest was unnecessary. Although moose mobility and subsequent use of evergreen forest with higher forest canopy and lower snow depth occurs at snow depths >69 cm (Peek 1998, Ballenberghe and Ballard 1998), the highest average snow depth in our study was only 56 cm. Any of the previous explanations could be true, however, it is likely that the ~50% combination of mixed and evergreen forest in Maine's complex forest matrix provides sufficient canopy cover at the winter home range scale.

The Maine forest is abundant with varied types, age classes, and regeneration patterns (Wiersma 2009, Butler 2018) to sustain a large moose population. Because mixed forest represents >30% of the available forest in the region, it presumably provides sufficient winter forage and cover in typical winters and may either negate or mask possible selection for evergreen and deciduous forest types. Previous regional research indicated that moose select largely for forested habitat at the home range scale (Wattles and Destefano 2013), and in Maine had preference for red maple (*Acer rubrum*) found in deciduous and mixed forest stands (DeGraaf et al. 1992). Further, moose tend to favor young regeneration stands for forage (Blouin et al. 2021), with optimal habitat consisting of forest openings 4–16 years post-harvest (Healy et al. 2018). Although we expected to find selective use of regenerating forests in mild winters due to unrestricted access and movement, surprisingly, we did not identify a relationship or influence between winter conditions and use of regenerating forest. While there was positive selection for regenerating forests, there was high variability among animals; other metrics including regenerating tree species and age class might explain some of this variability with regard to that land cover type.

We found minimal to no relationship between winter weather conditions and home range habitat selection at the second-order resource selection scale. Since winter conditions in Maine are predicted to change due to climate change, it is important to consider the possible impacts of warmer temperatures, less snow, and other metrics on individual and populations of moose. Analyses with finer scale winter severity metrics and moose movement data might help identify any such relationships between winter conditions and fine-scale landscape and resource use (e.g., species composition, age class, canopy cover) by moose (Herfindal et al. 2009).

Use of higher-order selection of specific habitat patches and resources within the home range would aid in identifying finer habitat use and relationships (Johnson 1980). For example, if winter severity and snow depth decline overall due to climate change, as predicted in Maine (Fernandez et al. 2020), moose may increasingly use certain forest habitats such as regenerating stands. Indeed, Andreozzi et al. (2016) found that proximity to recent timber cuts was a predictor of winter landscape use, yet we were unable to evaluate this relationship at the second order scale. Concentrated moose browsing during winter can alter species composition, abundance, and diversity of tree and shrub species (Pastor and Naiman 1992, Thompson and Curran 1993, Poole and Stuart-Smith 2006, Christenson et al. 2014, Faison et al. 2016), effectively influencing forest composition and productivity. Although research did not identify substantial impacts of such in the region after peak moose numbers (Bergeron et al. 2011, Andreozzi et al. 2014), it is of concern in the commercial forest landscape of Maine with implications for both forest and wildlife management.

Our analyses at the second order suggest that moose currently access and use regenerating habitats with minimal restriction during winter, and Dunfey-Ball (2017) found that the current availability and creation of such habitat was optimal for moose in Maine. Shorter winters due to climate change may have greatest impact via increased parasitism of moose by winter ticks (Musante et al. 2010, Pekins 2020). In Maine and New Hampshire in 2014–2019, winter tick parasitism caused >50% mortality of 9–10 month old calves, delayed maturation of yearling females, and reduced twinning and birth rates of adult females (Jones et al. 2017, 2019). Ironically, Healy et al. (2018) found that moose prefer young forest openings and their selective use of this habitat coincides with winter tick drop-off in spring and questing in autumn, facilitating a feedback loop of high tick abundance and infestation risk to moose (Healy et al. 2020, Powers and Pekins 2020).

Milder winters associated with climate change will presumably lead to increased deer abundance and overlap with moose in Maine, increasing exposure and transmission of brainworm (*Parelaphostrongylus tenuis)* to moose. Brainworm is a potentially fatal disease to moose carried by, but benign in deer (Lankester 2010, 2018). As with most diseases and parasites, the relative abundance of brainworm and winter ticks is host-density dependent, and healthy moose are not necessarily resistant to the effects of either as the impact of both is "dose dependent." Therefore, increased mobility, access, and use of regenerating habitats would likely provide minimal advantage relative to risk at the individual or population level of moose. Theoretically, advantage would come from broader habitat use by moose that would reduce overlap with deer and exposure to brainworm infection, as well as local tick abundance.

Winter habitat of moose in Maine consists largely of managed stands in coniferous and mixed forests that provide sufficient forage and canopy cover. Our second-order analysis makes clear that more detailed data are required to describe winter habitat use at the finer scale of tree species and stand age (DeGraaf et al. 1992). We assume that local winter conditions could influence fine-scale habitat use, and that identification of any relationship between specific winter metrics and specific habitat use is useful for forest and moose management. Such information would inform current management strategies, and importantly, provide a foundation to assess future impacts of climate change on the health and productivity of moose and forest habitats in Maine.

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APPENDICES

Appendix 1: Matrix of correlation for predictor variables.

Variables	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)
(1) Precipitation	1.00												
(2) Snowfall	0.78	1.00											
(3) Max temperature	0.15	−0.07	1.00										
(4) Min temperature	0.19	−0.20	0.89	1.00									
(5) Snow depth	0.47	0.75	−0.23	−0.45	1.00								
(6) Slope	0.01	−0.06	−0.00	0.07	−0.08	1.00							
(7) Elevation	−0.25	−0.13	0.07	−0.03	−0.10	0.54	1.00						
(8) Deciduous forest	−0.08	−0.10	0.07	0.08	−0.10	0.61	0.57	1.00					
(9) Evergreen forest	−0.04	0.04	0.02	−0.01	0.00	−0.36	−0.21	−0.57	1.00				
(10) Mixed forest	0.25	0.10	−0.08	−0.00	0.09	0.03	−0.22	−0.21	−0.36	1.00			
(11) Developed	−0.01	0.13	0.05	−0.03	0.11	−0.19	0.01	−0.16	0.06	−0.22	1.00		
(12) Regenerating forest	−0.08	−0.10	−0.01	−0.02	−0.04	0.08	0.04	−0.13	−0.24	−0.10	0.01	1.00	
(13) Wetlands	−0.02	0.05	−0.06	−0.10	0.05	−0.57	−0.40	−0.39	0.18	−0.29	0.24	−0.16	1.00