MODELING MOOSE HABITAT USE BY AGE, SEX, AND SEASON IN VERMONT, USA USING HIGH-RESOLUTION LIDAR AND NATIONAL LAND COVER DATA

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ABSTRACT: Moose (*Alces alces*) populations have experienced unprecedented declines along the southern periphery of their range, including Vermont, USA. Habitat management may be used to improve the status of the population and health of individuals. To date, however, Vermont wildlife managers have been challenged to effectively use this important tool due to the lack of fine-scale information on moose space use and habitat characteristics. To assess habitat use, we combined more than 40,000 moose locations collected from radio-collared individuals (n = 74), recent land cover data, and high resolution, 3-dimensional lidar (*light detection and ranging*) data to develop Resource Utilization Functions (RUF) by age (mature and young adult), season (dormant and growth), and sex. Each RUF linked home range use to average habitat conditions within 400 m or 1 km of each 30 m^2 pixel within the home range. Across analyses, the top RUF models included both composition (as measured through the National Land Cover Database) and structure (as measured through lidar) variables, and significantly outperformed models that excluded lidar variables. These findings support the notion that lidar is an effective tool for improving the ability of models to estimate patterns of habitat use, especially for larger bodied mammals. Generally speaking, female moose actively used areas with proportionally more regenerating forest (i.e., forage < 3.0 m) and more mature forest (i.e., canopy structure > 6.0 m), while males actively used more high elevation, mixed forest types. Further, moose exhibited important seasonal differences in habitat use that likely reflect temporal changes in energetic and nutritional requirements and behavior across the year. Moose used areas with proportionally more regenerating forest (i.e., forage < 3.0 m) during the growth period and female moose had strong positive associations with lidar-derived canopy structure during the growth (but not the dormant) period. Ultimately, the resultant maps of habitat use provide a means of informing management activities (e.g., the restoration or alteration of habitats to benefit moose) and policies around land use that may contribute to population recovery.

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INTRODUCTION

Moose (*Alces alces*) have experienced declines in many regions along the southern periphery of their distribution in North America (Murray et al. 2006, Jones et al. 2019). In Vermont in the northeastern United

States, moose have declined to the point of requiring new management approaches to improve the status of the population and health of individuals. Habitat management may be an important tool to achieve this end, yet an assessment of fine-scale habitat use by moose in this region is lacking.

Habitat selection is the process in which an animal chooses or selects a particular habitat, given a range of options (Johnson 1980, Beyer et al. 2010). The selection of resources by individuals is thought to occur in a hierarchical manner, from a more coarse-scale examination of where a species selects their geographic range (first-order selection), to the home range of an individual within their geographical range (second-order), and finally to more fine-scale examination of the habitat components within home ranges (third-order, Johnson 1980). Regardless of the available habitat options, habitat selection decisions result in patterns of habitat use, which can be quantified at these same scales (Johnson 1980, Beyer et al. 2010) and is the focus of this study. Common approaches to assess first-and second order habitat use involve detection or non-detection of unmarked individuals across space and time, and the probability a species will exist at a given location (MacKenzie et al. 2017).

Although such modeling approaches are valuable in describing use of locations across a defined geographic extent, they often lack detail regarding resource use by individuals within their home range (i.e., third order) which can provide a more nuanced and finer-scale depiction of the relative importance of specific habitat resources. Resource utilization functions (RUFs) allow estimation of wildlife habitat use within individual home ranges (Marzluff et al. 2004), and RUFs relate home range utilization distribution (UD) to its underlying resources, where the UD is a probability distribution that describes an individual's pattern of space use. RUF models provide the importance of habitat variables within the home range, given the home range has been selected. Population-level RUFs can be derived by aggregating individual RUFs, thus providing an understanding of which habitat variables are most heavily used in aggregate. For example, Marzluff et al. (2004) used this approach to document how Steller's Jays (*Cyanocitta stelleri*) respond to different land cover amounts and types, and Amelon et al. (2014) investigated resource use by eastern red bats (*Lasiurus borealis*) during the maternity season.

RUF models and maps of habitat use that can be produced from them provide important information that can guide decision-making in wildlife management. However, many challenges exist in building models that are of utility, especially for species that occur in a diversity of habitats. Evaluating habitat composition alone (i.e., landcover type) may be insufficient as finer-scale structural features (i.e., the height of vegetation) within habitats may also influence use. For instance, during summer or the vegetative growth period in the northeastern United States (May-Sep), moose consume large quantities of deciduous tree/shrub leaves and stems during their productive state when they recover physically from winter, grow, lactate, and attain pre-winter condition (fat reserves); thus, areas of forest regeneration are highly used and preferred habitat (Schwartz and Renecker 2007). Moreover, moose may alter daily behavior and resource use to avoid thermal stress during summer (Montgomery et al. 2019). Despite its seasonally lower nutritional value, moose continue foraging buds and stems of deciduous regeneration during winter, and commonly consume balsam fir (*Abies balsamea)* (Schwartz et al. 1988). As snow deepens, moose employ energy-conserving behaviors by limiting movement and activity and seeking refuge under canopied coniferous forest (Dussault et al. 2004).

Such life history complexities suggest that coarse scale landcover maps such as the National Land Cover Database (NLCD) alone may be insufficient in estimating RUFs useful for management purposes, particularly for a species that depends on different forest age classes seasonally. Lidar (*light detection and ranging*) is a remote sensing tool used to generate precise, three-dimensional information about the height of vegetation across the landscape (Lefsky et al. 2002). Lidar data are acquired from a fixed-wing aircraft that projects a beam of light towards earth's surface, which is reflected and captured by a sensor. The resulting three-dimensional point cloud records not only the x- and y-coordinates indicating the horizontal location of each point, but also a z-coordinate fixing the vertical location of the point relative to sea level. The point cloud thus captures both ground and aboveground features, including impervious land cover such as buildings and semi-pervious objects such as foliage and branches associated with vegetation (Lefsky et al. 2002). Lidar, combined with NLCD, allows a description of habitat use within home ranges that features combinations of critical habitat, such as structural forage and cover from solar radiation or deep snow. Indeed, studies from other regions (e.g., Isle Royale National Park, Michigan U.S.A, and western Finland) have shown the benefits of lidar in quantifying specific structural conditions used by moose (e.g., Verissimo 2012, Melin et al. 2016). However, lidar data are expensive to produce, and it behooves resource managers in Vermont and the northeastern U.S. to understand if including lidar data in the mapping of habitat use will increase the success of management activities that rely on it (i.e., the value of information; Howard 1966).

Declines in moose health, survival, and fecundity presents concerns for Vermont and for regional moose populations as Vermont provides important connectivity between populations in Maine, New Hampshire, New York (U.S.) and southern Quebec, Canada (Kretser et al. 2011). Although direct management through harvest provides one means of influencing moose density and individual health (Boertje et al. 2019), indirect management through the protection, alteration, or creation of important habitat provides another that may benefit moose. As such, reliable RUF models provide a crucial tool to inform future stewardship for one of the most charismatic and culturally important wildlife species of the region.

We used data from GPS radio-collared moose and multi-scale land cover data to examine third-order habitat use in Vermont. The objectives of this study were to 1) describe general home range habitat characteristics by moose age (mature and young adult), season (dormant and growth), and sex, 2) develop RUF models to determine patterns of utilization within home ranges and their underlying resource variables by age, sex, and season, and 3) apply RUF models to map habitat use and assess the importance of habitats across the study area.

METHODS

Study Area

The study occurred in Essex County in northeastern Vermont, USA, in state wildlife management units E1 and E2 that covered 1,738 km^2 (Fig. 1, mean latitude = 44.77°; mean longitude = -71.74°). This area was selected due to the relatively high density of moose and its importance for Vermont's broader moose population (Pearman-Gillman et al. 2020, VFWD 2020).

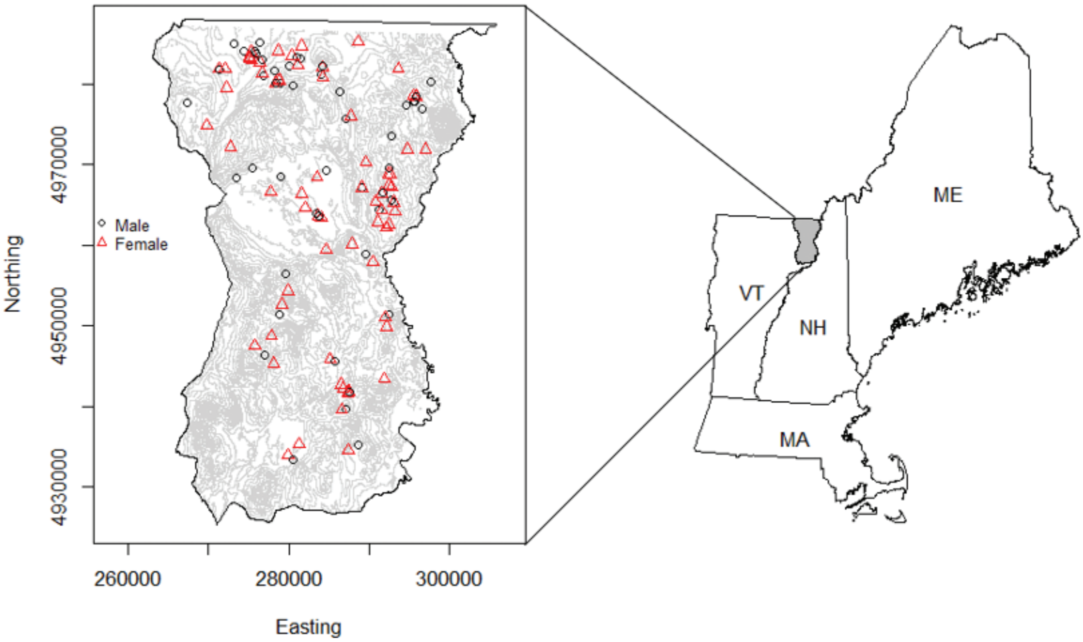

Fig. 1. The location of the study area in northeastern Vermont, USA (1,738 km^2), encompassing Essex County (Wildlife Management Unit E). GPS radio-collars were attached to moose (n = 126) in the area and monitored from 2017 to 2019. The study area was bounded by the Canada-U.S. border to the north, New Hampshire to the east, VT-Route 2 to the south, and VT-Route 114 to the west. Triangles indicate the capture location for all moose throughout the study; red triangles indicate the capture location for female moose (n = 74), while circles indicate where male moose were captured (n = 52). The map on the right shows the study area in relation to other northeastern states (ME = Maine, NH = New Hampshire, and MA = Massachusetts).

The study area has history of logging and mixed geography, characterized by extensive bogs and softwood swamps, and young, intermediate, and mature forest stands. Elevation ranged between 200 to 1000 m. High elevation (> 800 m) forest was dominated by red spruce (*Picea rubens*) and balsam fir. Intermediate elevations (300 – 800 m) consisted primarily of maple (*Acer* spp.), birch (*Betula* spp.), and beech (*Fagus grandifolia*), while the lowland swamps and bogs were dominated by balsam fir, red spruce, black spruce (*P. mariana*), poplar (*Populus* spp.), paper birch (*B. papyrifera*), and alder (*Alnus* spp.).

Vermont experiences 4 distinct seasons including summer (Jun-Aug), fall (Sep-Nov), winter (Dec-Feb), and spring (Mar-May). These seasons were broadly categorized as the dormant season (Oct-Apr in which deciduous trees lacked leaves) and the growth season (May-Sep in which leaves were present). Between 2017 and 2019, the average temperature during the growth season was 15.3 °C, with average precipitation ranging between 100 and 110 cm (NCDC 2019). The average temperature during the dormant season was -3.8 °C, with an average snowfall ranging between 220 and 250 cm (NCDC 2019).

RADIO-COLLARING

To estimate home ranges, 126 moose were captured and fitted with GPS radio-collars. Capturing occurred via helicopter in January of 2017 (n = 30 calves [<1 yr], 30 adult [≥ 1 yr] females), 2018 (n = 30 calves, 6 adult females), and 2019 (n = 30 calves). One radio-collared adult female moose from a New Hampshire study immigrated into the study area in 2018 and was included in our study. Each captured moose was fitted with a Survey Globalstar V7.1 GPS and VHF radio-collar (VECTRONIC Aerospace GmbH, Berlin, Germany). A GPS location of the moose was transmitted from each collar every 13 h. As highly mobile animals, moose can traverse the entirety of their home range within this time span, ensuring that points provided a representative sample of habitat use (Fieberg 2007). All capture, handling, and radio-collaring procedures were reviewed and approved by the University of Vermont Institutional Animal Care and Use Committee (IACUC protocol #17-035).

Objective 1: General Home Range Characteristics

We estimated each individual's home range separately for the growth season and the dormant season across each year (2017–2019) to determine individual habitat use. To avoid bias in measuring habitat use by potentially unhealthy or unrepresentative individuals (e.g., an individual that was limited in its movements due to an infestation of winter ticks *[Dermacentor albipictus]* or brain worm [*Parelaphostrongylus tenuis*]), we removed GPS collar locations as follows. First, if an adult died during the study, GPS coordinates for the two-week period leading up to the mortality event were removed to avoid potentially overestimating habitat use due to behavior associated with brain worm (Lankester 2010). Second, we removed all GPS locations from individuals < 1 year old to ensure that locations were associated with adult age classes. Third, GPS coordinates transmitted from beyond the boundaries of our study area were removed.

After filtering, home range analyses were based on 40,451 locations of 74 moose (219 total home ranges). We used the kernelUD function in the R package, adehabitatHR (Calenge 2011) to estimate 95% fixed kernel home ranges for each moose during each year. We used the ad hoc method to select the smoothing factor (*h*) for each home range. This method tends to outperform the reference and least-squares cross-validation derived smoothing factors by providing robust UD estimates even with autocorrelated data and limiting the number of disjoint home range polygons or 'islands' that can result from under smoothing (Kie 2013).

Within each defined home range, we identified habitat variables important to moose including broad land cover types (deciduous forest, coniferous forest, mixed forest, wetland, developed, and open) from National Landcover Data (USGS 2016a), spatial layers describing anthropogenic influences such as snowmobile trails (VTANR 2019), and terrain characteristics such as elevation models (VCGI 2002) (Table 1).

Lidar data were used to characterize forest age structure within each home range (Table 1). The raw lidar point cloud data (.laz/.las format) for the Connecticut River Basin (which encompassed our study area) was downloaded from the U.S. Geological Survey's open source National Geospatial Program (USGS 2016b). We used lidar point cloud data obtained in early November 2016 (USGS 2016b) and extracted to our study area at the 10 m^2 resolution. The lidar returns were extracted and summarized as the proportion of total returns in each 10 m^2 pixel that fell within 5 vegetative height classifications (open, shrub, forage, cover, and canopy) associated with important life requisites of moose (Table 1, and see Schwartz and Renecker 2007).

We estimated the average kernel home range area for both male and female moose for each season. Additionally, moose were

Table 1. Covariates used to develop Resource Utilization Distribution models describing habitat use for radio-collared moose in Vermont, USA.

Covariate Name	Description	Data Source	Reference
P_Open	Proportion of each home range that was defined as "open" (vegetation between 0.00 - 0.02 m) at a 10 m^2 resolution.	Lidar 2016	USGS 2016b
P_Shrub	Proportion of each home range that was defined as "shrub" (vegetation between > 0.02 - ≤ 2.0 m) at a 10 m^2 resolution. Defined because of its potential importance to moose as a food source, but also to winter ticks as they tend to quest (or seek a host) within this height range.	Lidar 2016	USGS 2016b
P_Forage	Proportion of each home range that was defined as potential "forage" (vegetation ≤ 3.0 m) or vegetation that was within reach of moose at a 10 m^2 resolution.	Lidar 2016	USGS 2016b
P_Cover	Proportion of each home range that was defined as "cover" (vegetation between > 3.0 - < 6.0 m) at a 10 m^2 resolution.	Lidar 2016	USGS 2016b
P_Canopy	Proportion of each home range that was defined as "canopy" (vegetation > 6.0 m) at a 10 m^2 resolution. Defined because of its potential importance to moose as a source of protection for thermal stress or shelter during periods of deep snow.	Lidar 2016	USGS 2016b
P_Wetland	Proportion of each home range defined as "wetland" forest (NLCD emergent and woody wetland classifications were combined to represent general wetlands) at a 30 m^2 resolution.	NLCD 2016	USGS 2016a
P_Deciduous	Proportion of each home range defined as "deciduous" forest (> 75% of the tree species shed foliage simultaneously in response to seasonal change) at a 30 m^2 resolution.	NLCD 2016	USGS 2016a
P_Evergreen	Proportion of each home range defined as "evergreen" forest (> 75% of the tree species maintain their leaves all year) at a 30 m^2 resolution.	NLCD 2016	USGS 2016a
P_Mixed	Proportion of each home range defined as "mixed" forest (neither deciduous nor evergreen species are > 75% of total tree cover) at a 30 m^2 resolution.	NLCD 2016	USGS 2016a
P_OpenWater	Proportion of each home range defined as "open water" (areas of open water, < 25% cover of vegetation or soil) at a 30 m^2 resolution.	NLCD 2016	USGS 2016a
P_Developed	Proportion of each home range defined as "developed" (indication of impervious surfaces, covering all definitions in NLCD legend to represent all development) at a 30 m^2 resolution.	NLCD 2016	USGS 2016a
P_SnoMoTrails	Proportion of each home range defined as "snowmobile trail" (defined by ANR trail maps) at a 30 m^2 resolution.	VCGI 2019	VTANR 2019
Elevation	A measure of the elevation (m) in the study area/100.	VCGI 2002	VCGI 2002

categorized as either "mature adult" or "young adult" (mature = mature at capture, young adult = calf at capture), under the assumption that female adults were not captured as yearlings. No mature male moose were captured during the study, so all males were classified as "young adults".

We used the cellStats function in the R raster package (Hijmans and Van Etten 2012) to calculate the average habitat composition (as measured by NCLD) and structure metrics (as measured by lidar) of each home range, as well as for the overall study area. For each NLCD and lidar variable, we used a linear mixed-effects model (Bates et al. 2015) to determine if the average home range variable differed by sex, season, and age. We included moose identification number as a random effect, as the same moose had multiple home ranges across the study period.

Objective 2: Resource Utilization Function (RUF) Models by Age, Sex, and Season

We estimated a utilization distribution (UD) for each kernel home range; a three-dimensional probability map identifying peaks (frequently-used areas) and valleys (less-used areas) that explains where an individual was most likely to occur within the home range boundary (Worton 1989). We used the kernelUD function in the R package adehabitatHR (Calenge 2011) to estimate 99% kernel UDs for each moose during each season (dormant and growth) and year (2017–2019). UD pixel probabilities were converted to percentiles for interpretation and analysis (Marzluff et al. 2004, Donovan et al. 2011), where pixels of lower UD probabilities (i.e., valleys) had low percentiles while the highest UD probabilities (i.e., peaks) had percentiles closer to 100.

RUF predictor variables included habitat and terrain variables that may define the UD peaks and valleys for each home range (Table 1). For each variable, we used the focal function in the R raster package (Hijmans and Van Etten 2012) to create layers at the 400 m and 1 km scales, in which each pixel's value was the mean value across the given scale, centered on the pixel itself. For example, while a single NLCD pixel (30 m^2) may indicate deciduous forest, its focal value at the 400 m scale provides the proportion of deciduous forest within a 400 m of that cell. This effectively smoothed the resource level at each pixel, allowing analysis of habitat use to more accurately reflect how a moose may perceive and use resources on the landscape (i.e., daily movement patterns; Wattles and DeStefano 2013).

We extracted the underlying raster value for each cell in an individual's UD. Due to computing constraints, large home ranges with more than 500 UD locations were reduced to 500 points by randomly selecting 5 points from each UD percentile. Each record (row) of the dataset was assigned a weight based on a GPS transmission collar bias study (see S1). Weights were computed as the inverse of the estimated transmission rate, such that records with a low probability of successful transmission had higher weights.

A model set of 9 linear regression models was used to relate home range space use to the resource attributes (Table 2). To avoid multicollinearity in any given model, highly correlated variables ($r > 0.5$) were ultimately dropped from consideration as explanatory variables in RUF models. Each RUF model estimated how likely moose were to use a given part of their home range as a function of the smoothed NLCD and lidar variables; UD percentile was used as the response variable. The model set included models that estimated habitat use for moose with the NLCD and lidar variables smoothed at 400 m, NLCD at 1 km and lidar at 400 m, and NLCD at 400 m and lidar at 1 km. We also examined how well NLCD variables only or lidar variables only (at both smoothing scales) estimated habitat use (Table 2). Each RUF model in the set was run with both unstandardized explanatory variables and standardized explanatory variables (z-scores), and with and without the GPS weights (4 analyses of the model set per home range). For each analysis, the models were ranked using Akaike's Information Criterion (AIC) to identify the best-fit model (Burnham and Anderson 2002).

The AIC ranks were averaged across the individual home range models to identify

Table 2. The 9 Resource Utilization Functions (models) analyzed for each radio-collared moose (n = 74) in northeastern Vermont, USA. Models include combinations of NLCD (National Land Cover) and Lidar (*light detection and ranging*) variable classes smoothed at two scales (400 m and 1 km). The formula defines the utilization distribution percentiles (PCT100) as a function of the different resources within each model (100th percentile representing core-use areas and 1st percentile representing valleys or areas of least-use).

Model	Formula	K
1. Intercept	PCT100 ~ 1	1
2. NLCD (400m) & Lidar (400m)	PCT100 ~ nlcd_evergreen_400m + nlcd_mixed_400m + nlcd_wetland_400m + forage_400m + canopy_400m + Elevation	7
3. NLCD (1km) & Lidar (1km)	PCT100 ~ nlcd_evergreen_1km + nlcd_mixed_1km + nlcd_wetland_1km + forage_1km + canopy_1km + Elevation_s	7
4. NLCD (400m) & Lidar (1km)	PCT100 ~ nlcd_evergreen_400m + nlcd_mixed_400m + nlcd_wetland_400m + forage_1km + canopy_1km + Elevation	7
5. NLCD (1km) & Lidar (400m)	PCT100 ~ nlcd_evergreen_1km + nlcd_mixed_1km + nlcd_wetland_1km + forage_400m + canopy_400m + Elevation_s	7
6. Lidar (400m)	PCT100 ~ forage_400m + cover_400m + canopy_400m	4
7. Lidar (1km)	PCT100 ~ open_1km + forage_1km + canopy_1km + Elevation	5
8. NLCD (400m)	PCT100 ~ nlcd_evergreen_400m + nlcd_mixed_400m + nlcd_wetland_400m + nlcd_open_400m + Elevation	6
9. NLCD (1km)	PCT100 ~ nlcd_evergreen_1km + nlcd_mixed_1km + nlcd_wetland_1km + nlcd_open_1km + Elevation	6

a single, best model to estimate habitat use for moose by age, sex, and season. The population level RUF by age, sex, and season was estimated by averaging the regression coefficients across individuals (Marzluff et al. 2004). As such, individual animals were treated as the experimental unit, resulting in unbiased model coefficients for population level RUFs (Millspaugh et al. 2006). Following Marzluff et al. (2004), the top-ranked, unstandardized, weighted models were used to create maps of habitat use, while the top-ranked, standardized models were used to identify the most important variables across moose.

Objective 3: Mapping Moose Habitat Use

We created habitat use rasters for each age, sex, and season using the averaged unstandardized coefficients from analyses where GPS radio-collar bias study weights were applied. We used the overlay function in the raster package (Hijmans et al. 2015) to compute a score estimating habitat use by moose for each 10 m^2 cell within the study area by multiplying each resource variable in the raster stack by its corresponding averaged unstandardized coefficient. The resultant maps contained cell values that described habitat use for moose by age, season, and sex.

RESULTS

Objective 1: General Home Range Characteristics

We calculated kernel home ranges for 57 females and 17 males (Table 3). Average home range area was nearly the same during the dormant season for both mature and young female moose (40 and 39 km^2, respectively; Table 3). Female home range areas increased during the growth season for both mature and young individuals (+ 4 and + 19 km^2, respectively). Male home

Table 3. Mean home range size and proportion of vertical structure and forest type for moose in Vermont, USA by sex, age (mature and young), and across two seasons for vegetation (dormant and growth) from 2017 to 2019. The "Freq" row indicates the number of home ranges analyzed for the given sex, season, and age. The study area mean column provides the overall proportion of each habitat feature for the entire study area. ANOVA results indicate the effect of each covariate (sex, season, and age) on each habitat variable. Values in parentheses are standard deviations for home range habitat proportions and probabilities for ANOVA results.

Sex	Female	Female	Female	Female	Male	Male		ANOVA F-Stat(p-value)			
Season	Dormant	Dormant	Growth	Growth	Dormant	Growth					
Age	Mature	Young	Mature	Young	Young	Young					
Freq	37	16	33	19	15	17					
HR Area (km^2)	40.54 (51.33)	39.96 (43.84)	44.04 (57.92)	58.93 (53.37)	100.37 (114.56)	111.02 (166.01)	Study Area Mean	Intercept	Sex	Season	Age
P_Open	0.33 (0.04)	0.33 (0.04)	0.34 (0.03)	0.34 (0.03)	0.32 (0.04)	0.34 (0.03)	0.35	F = 8910.80 (0.00)	F = 0.00 (0.98)	F = 53.61 (0.00)	F = 0.01 (0.93)
P_Shrub	0.17 (0.02)	0.17 (0.02)	0.17 (0.02)	0.17 (0.02)	0.17 (0.02)	0.17 (0.01)	0.16	F = 5872.03 (0.00)	F = 0.31 (0.58)	F = 2.74 (0.10)	F = 1.59 (0.21)
P_Forage	0.20 (0.03)	0.20 (0.03)	0.20 (0.03)	0.20 (0.03)	0.20 (0.02)	0.19 (0.01)	0.18	F = 5325.28 (0.00)	F = 0.36 (0.55)	F = 6.27 (0.01)	F = 1.58 (0.21)
P_Cover	0.10 (0.02)	0.10 (0.02)	0.10 (0.02)	0.10 (0.02)	0.10 (0.02)	0.10 (0.01)	0.09	F = 3111.80 (0.00)	F = 0.08 (0.78)	F = 25.26 (0.00)	F = 0.30 (0.59)
P_Canopy	0.37 (0.05)	0.37 (0.05)	0.36 (0.04)	0.36 (0.04)	0.38 (0.03)	0.37 (0.02)	0.37	F = 7935.82 (0.00)	F = 0.06 (0.81)	F = 4.82 (0.03)	F = 0.89 (0.35)
P_Deciduous	0.41 (0.14)	0.41 (0.14)	0.46 (0.11)	0.46 (0.11)	0.42 (0.13)	0.45 (0.10)	0.44	F = 1263.50 (0.00)	F = 0.14 (0.71)	F = 28.12 (0.00)	F = 2.42 (0.12)
P_Evergreen	0.13 (0.11)	0.13 (0.11)	0.11 (0.07)	0.11 (0.07)	0.13 (0.07)	0.11 (0.05)	0.12	F = 181.24 (0.00)	F = 0.33 (0.57)	F = 18.82 (0.00)	F = 0.05 (0.82)
P_Mixed	0.28 (0.08)	0.28 (0.08)	0.27 (0.07)	0.27 (0.07)	0.29 (0.07)	0.28 (0.06)	0.28	F = 1357.08 (0.00)	F = 0.53 (0.47)	F = 3.43 (0.06)	F = 1.21 (0.27)
P_Wetland	0.08 (0.09)	0.08 (0.09)	0.06 (0.06)	0.06 (0.06)	0.09 (0.10)	0.07 (0.07)	0.07	F = 78.26 (0.00)	F = 0.33 (0.57)	F = 16.87 (0.00)	F = 0.27 (0.60)
P_OpenWater	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.02)	0.01	F = 39.12 (0.00)	F = 0.77 (0.38)	F = 1.96 (0.16)	F = 0.00 (0.95)
P_Developed	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.02	F = 294.75 (0.00)	F = 0.18 (0.67)	F = 0.04 (0.85)	F = 0.31 (0.58)
P_SnoMoTrails	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.02	F = 250.44 (0.00)	F = 0.80 (0.37)	F = 3.21 (0.07)	F = 1.42 (0.24)

ranges were much larger than female home ranges during the dormant (100 km²) and growth (111 km²) seasons. Like females, male home ranges were larger during the growth season (Table 3).

The overall composition of home ranges for males and females, both mature and young, did not vary significantly (Fig. 2). The mean cover type and vertical structure values within home ranges were similar to the habitat composition of the study area. In terms of NLCD composition, the average home range was largely deciduous and mixed forest, but forest composition differed slightly between the dormant and growth seasons, with higher proportion of deciduous forest during the growth season (e.g., 0.46 for females) than the dormant season (e.g., 0.41 for females; Fig. 2). The percentage of development (including snowmobile trails) in the average home range was very low due to undeveloped nature of the study area. Unlike the NLCD, the vertical forest structure of home ranges as measured through lidar remained relatively constant across seasons (~35% canopy and ~ 33% open forest),

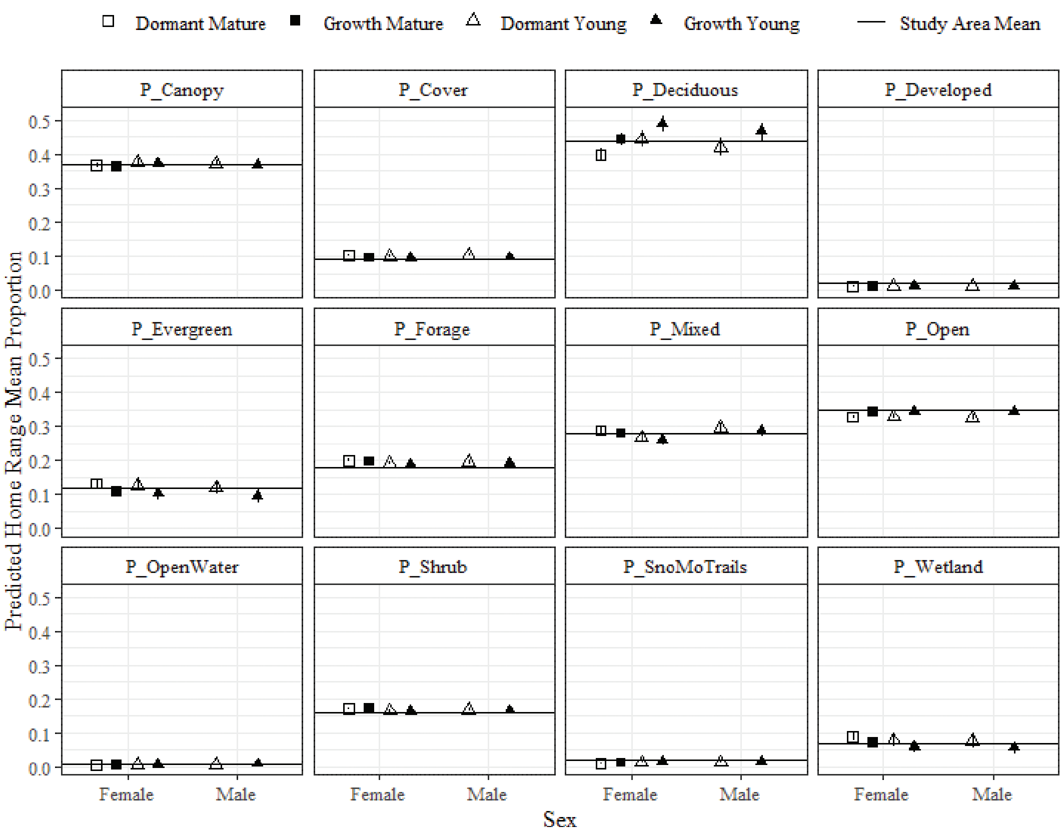

Fig. 2. ANOVA results estimating habitat composition of moose (n=74) across sex and season (dormant and growth) during 2017–2019 in northeastern Vermont, USA. Lidar covariates described the vertical structure of the forest (P_Open, P_Shrub, P_Forage, P_Cover, and P_Canopy), while the NLCD (P_Deciduous, P_Mixed, P_Evergreen, P_Wetland, P_Developed, P_OpenWater) and VCGI (P_SnoMoTrails) covariates described the forest type. The y-axis is the home range mean proportion (± SD) of each habitat feature across all moose. The horizontal line indicates the average proportion of each habitat feature across the entire study area.

but there was a slight increase in the overall proportion of "open" from the dormant season to the growth season (Fig. 2).

Objective 2. Resource Utilization Functions

Each RUF model in the Table 2 model set was run with both unstandardized explanatory variables and standardized explanatory variables (z-scores), and with and without the GPS weights (S1), resulting in 4 analyses of the model set per home range. Across analyses and across moose, the top ranked model was the model in which both NLCD and lidar resources were measured at 1 km² (Fig. 3). The models that were least supported in estimating moose habitat use included the intercept model and those that included only NLCD habitat types or only lidar vertical structure at the 400 m scale. There was very little variation in the rankings of the models with or without radio-collar bias weights applied, and little variation in rankings between models where coefficients were standardized versus unstandardized (Fig. 3).

Average adjusted R-squared values ranged from 0.00 (intercept model) to 0.34 (top model) across all models (Fig. 4). As expected, the top model (NLCD and lidar at

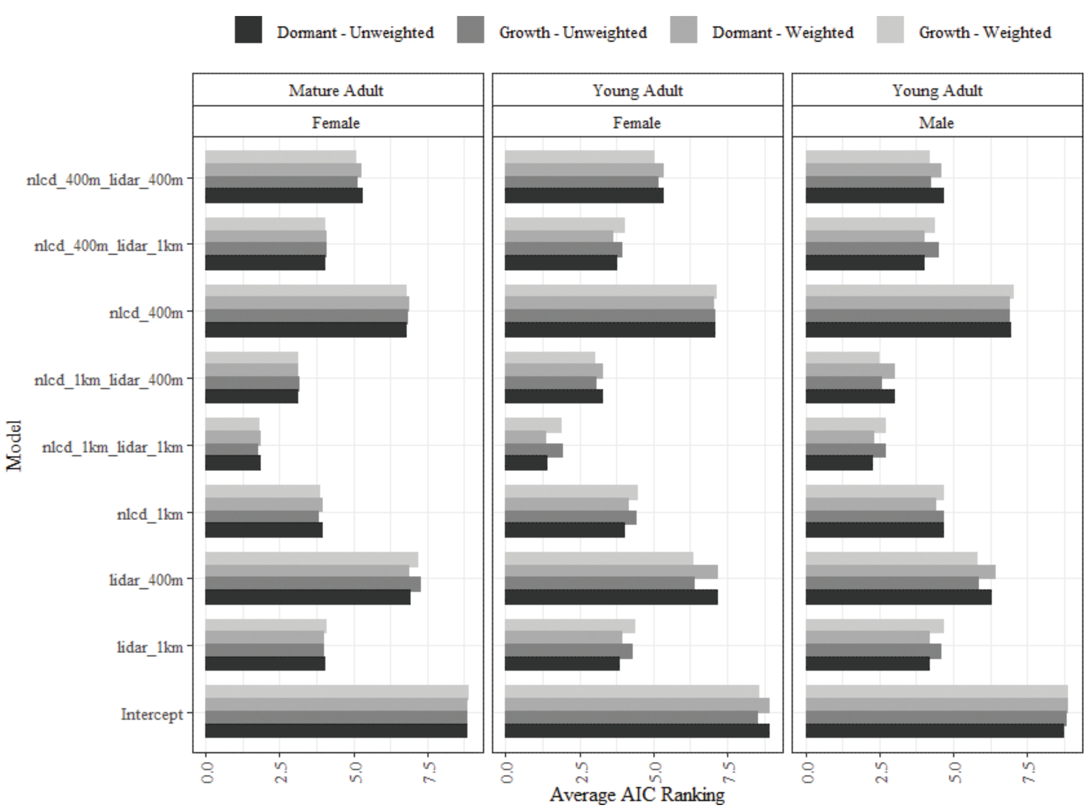

Fig. 3. Average AIC ranking for each RUF model for moose in northeastern Vermont, USA. For each home range, 9 RUF models were evaluated and ranked with AIC approaches. Bars indicate the average ranking across individuals by age, sex, and season (dormant and growth). The lowest AIC ranking on average describes the top model for estimating habitat use. RUF models were evaluated for each group with and without radio-collar bias weights (S1).

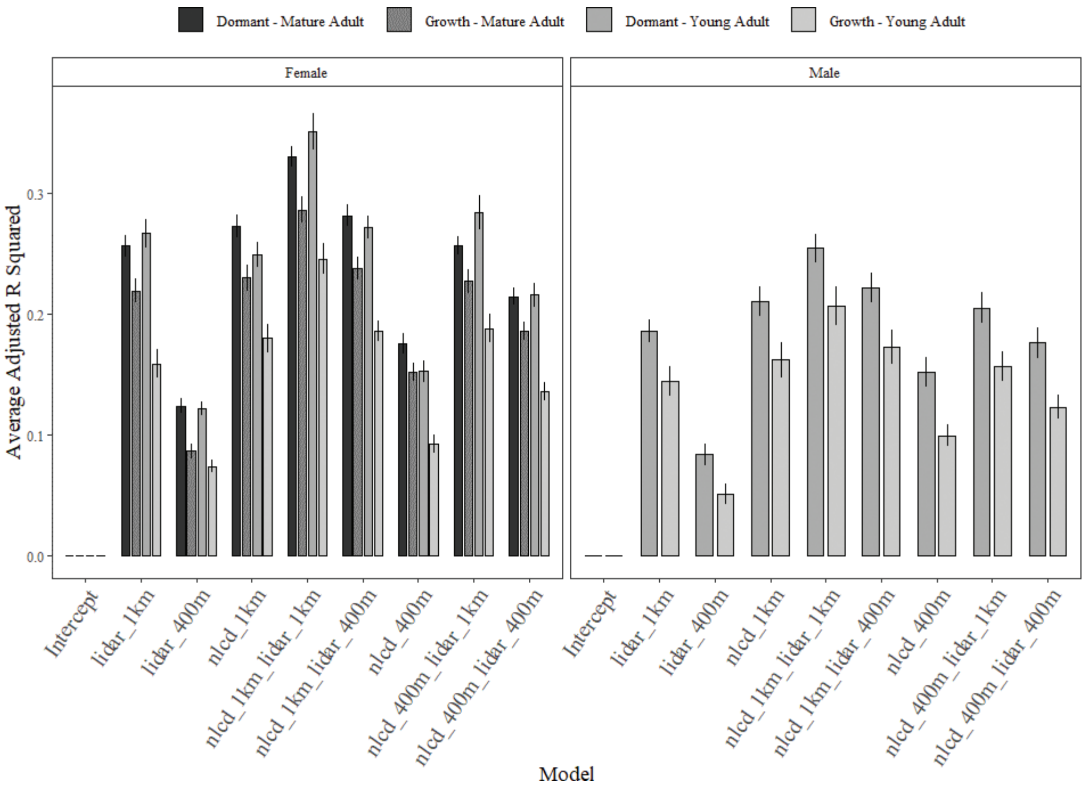

Fig. 4. Adjusted R-Squared values across the models in the RUF model set for moose in northeastern Vermont, USA. The average adjusted R-squared values (y-axis) show how well each of the models (x-axis) estimated habitat use; error bars are standard errors. No mature male moose were radio-collared for the study, thus all males are categorized as "young adult".

1 km^2) was on average the best fit model for both male and female moose during the dormant period and the growth period. Female moose habitat use was more consistent than male, with mature females being the most consistent (Fig. 4).

The top model estimated UD percentiles as a function of the proportion of evergreen, mixed, and wetland forests (within 1 km^2), as well as forage and canopy structure (within 1 km^2), and elevation (model 3, Table 2). Some of the NLCD and lidar habitat variables in this top model were correlated with other variables that were intentionally excluded from the model function (Fig. 5). For example, deciduous forest was relatively widespread in the study area and meaningful to moose habitat use but was not included in any model as it was strongly negatively correlated with evergreen forest. Therefore, we interpreted strong negative effects of evergreen forest in a model as positive effects of deciduous forest; this was the case during the growth period for all moose.

The average standardized betas from the top model indicated the relative importance of resources within moose home ranges (Fig. 6). During the growth season, the amount of vegetation classified as forage (height ≤ 3.0 m) within 1 km of a given location within a home range was highly important in shaping the UD surface, especially for females. This pattern held for young females

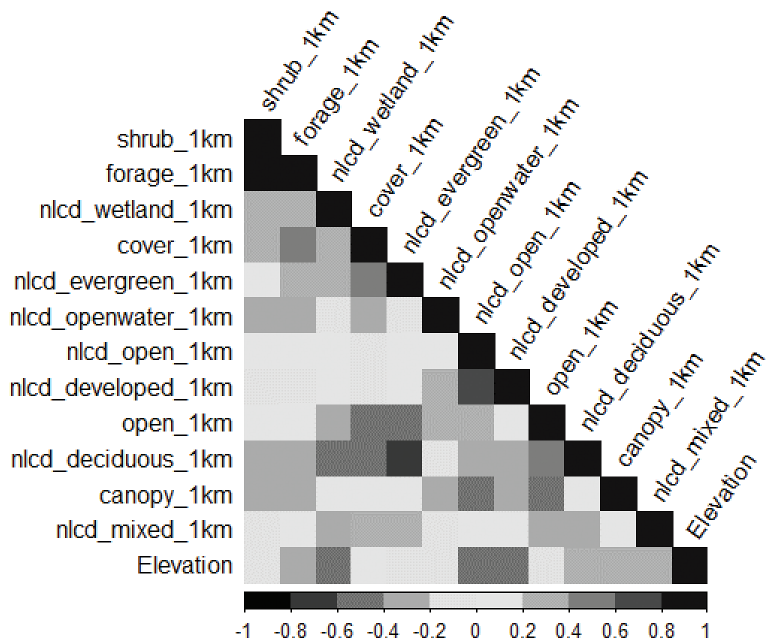

Fig. 5. Correlations between 2016 National Land Cover Database (NLCD) and lidar variables used to describe habitat use for moose in northeastern Vermont, USA. Darker cells represent highly correlated variables, while the lighter cells indicate variables that were less correlated.

during the dormant season (Fig. 6). Forage habitat was strongly associated with use for young male moose as well, but higher elevations and the proportion of mixed forests were of greater importance in estimating UD percentile during both the dormant and the growth seasons. All moose had a negative association with evergreen forests, much more so during the growth period. Areas of an individual's home range that were classified as wetland habitat typically had low UD percentiles, except during the dormant season for females and the growth period for males, where there was increased use. The canopy classification (vegetation > 6.0 m) was a positive predictor of use for young female moose during the growth period. Notably, young females did not heavily use forest classified as coniferous (mixed or evergreen classifications) during the dormant season, instead opting for high forage structure in deciduous forest (Fig. 6).

Objective 3. Mapping Moose Habitat Use
We used the unstandardized (Fig. 7), weighted coefficients to create maps of habitat use within the study area (WMUs E1 & E2) for mature and young adult females during the dormant and growth seasons (S2 and S3) and for young adult males during the dormant and growth seasons (S4). As reflected by the RUF coefficients, high quality "hotspots" differ for male vs. female and young vs. mature moose. Maps of habitat use for mature female moose during the growth period are presented for the top model (NLCD & lidar at 1 km^2) and NLCD (1 km^2) only to illustrate differences (Fig. 8).

DISCUSSION

To date, wildlife managers in Vermont have been challenged to effectively employ habitat management as a tool for managing moose populations due to the lack of fine-scale information on moose space use and

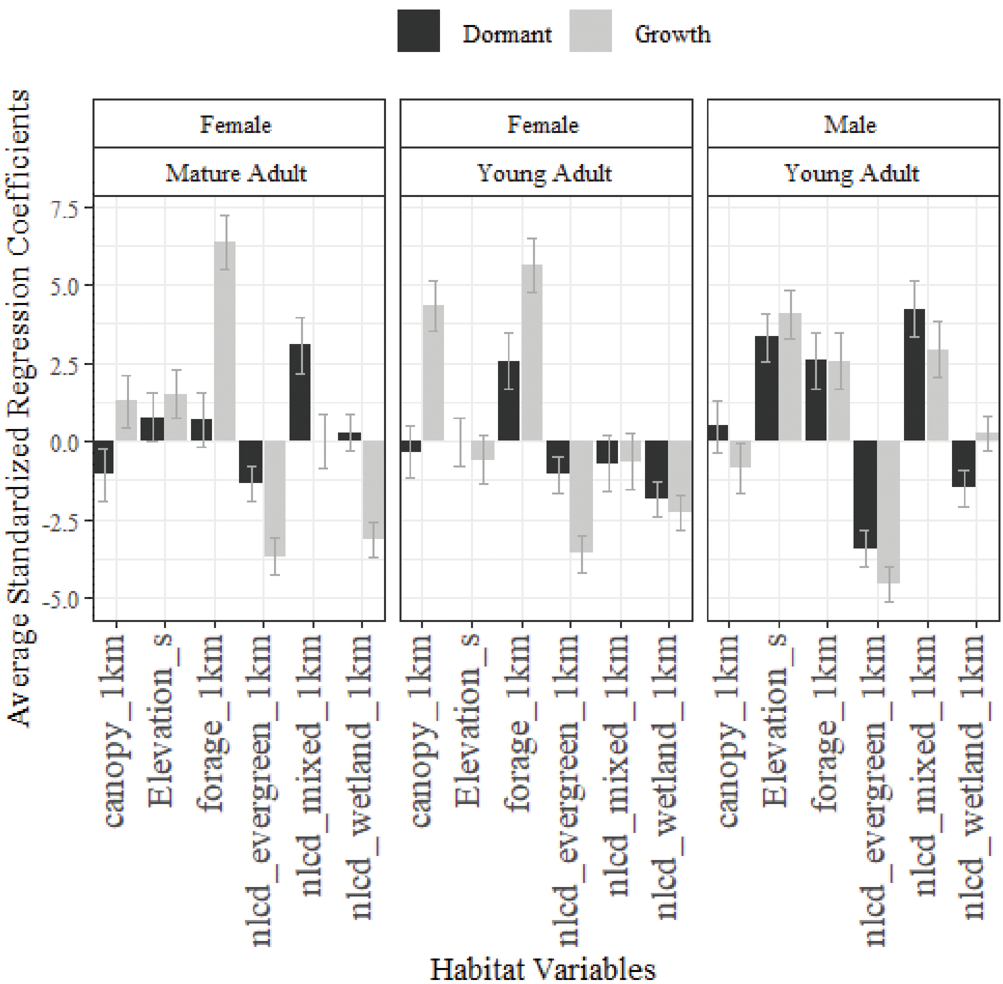

Fig. 6. The relative effects of habitat variables used by sex, age and season for moose in northeastern Vermont, USA. Values represent average standardized regression coefficients across all moose in a given category from the top model. Error bars represent standard error (± SE) for the coefficient estimates.

habitat characteristics in Vermont. Our results help to fill these knowledge gaps by identifying potential "hotspots" indicating areas throughout the landscape of high use by moose. This knowledge may inform wildlife management about the consideration of the spatial distribution of optimal habitats and which forest composition and structure to conserve, modify, or create to promote healthier and more persistent populations of moose across the region.

We examined patterns of habitat use using RUFs based on error-corrected GPS collar data and multi-scale habitat and land cover information. No home range or UD estimation is without error (Powell and Mitchell 2012), but our results appear to be consistent with what is known about moose ecology in the Northeast (Crossley and Gilbert 1983, Healy et al. 2018). For all seasons (dormant and growth), sexes (male and female), and ages (mature and young adult),

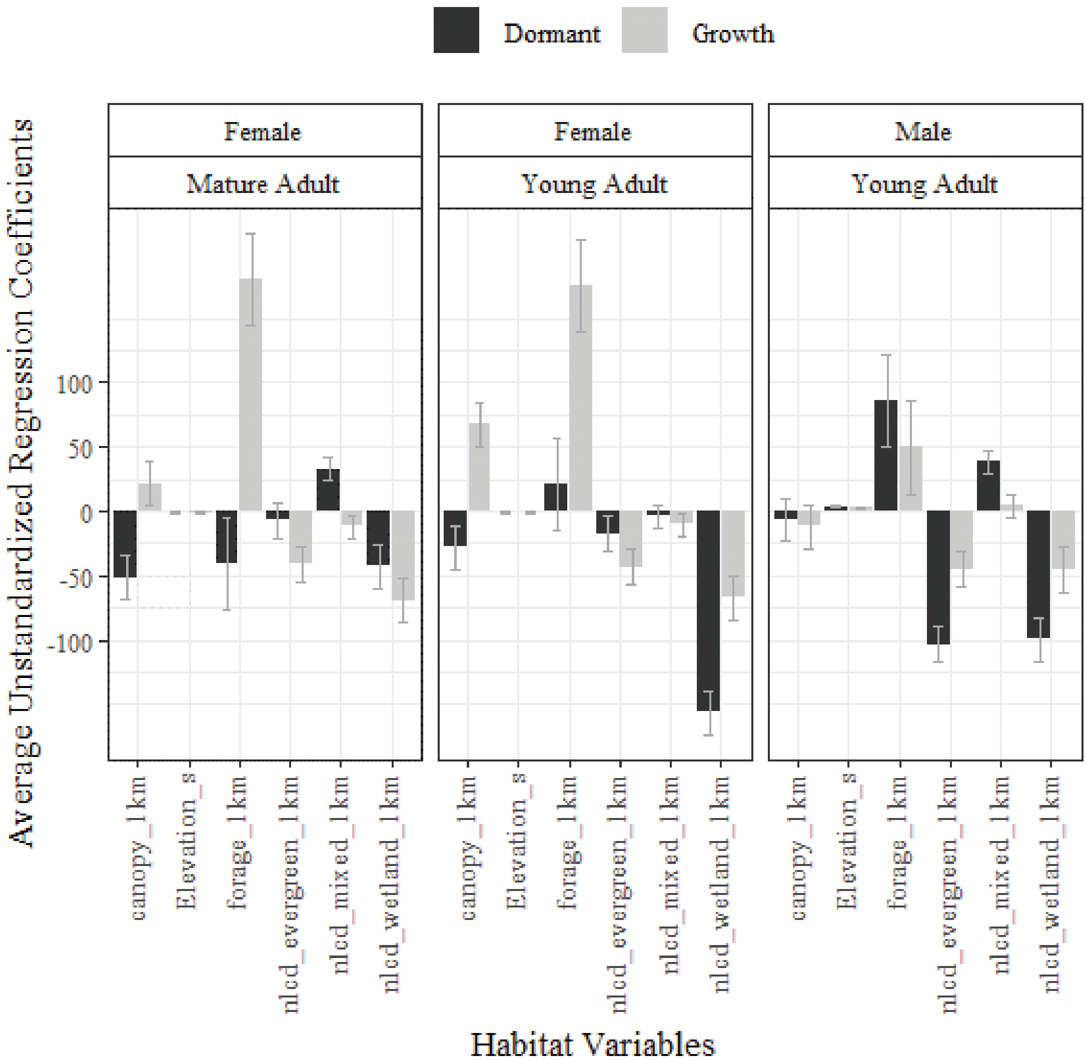

Fig. 7. The effects of habitat variables used by sex, age, and season for moose in northeastern Vermont, USA. Values represent average unstandardized regression coefficients across all moose in a given category from the top model. Error bars represent standard error (± SE) for the coefficient estimates.

the most supported RUF models included both coarse-scale habitat composition (derived from NLCD) and fine-scale structure (derived from lidar) at the 1 km^2 scale. The two least supported models examined habitat use at the 400 m scale using NLCD or lidar data solely, indicating that the combination of composition and structure better explained habitat use. AIC rankings order model support, but the ranking in and of themselves do not convey how much better the top model was relative to the others. AIC weights and ΔAIC metrics convey these differences and suggest that the NLCD + lidar model at the 1 km^2 scale was superior to other models under consideration. For example, for adult females during the dormant season, the "NLCD (1 km^2) and lidar (1 km^2)" performed significantly better than the "NLCD (1 km^2)" model (mean model weights = 0.54

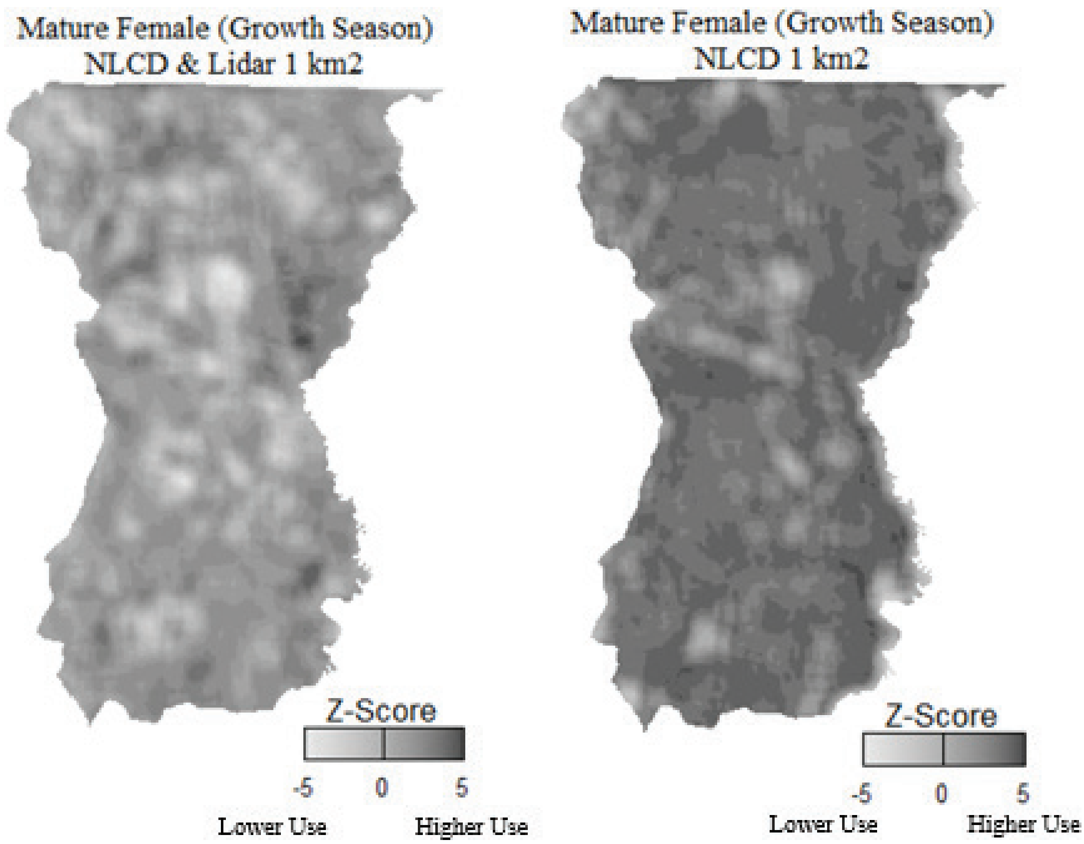

Fig. 8. Habitat use by mature female moose during the growth season using the top NLCD (1 km^2) and lidar (1 km^2) model and the NLCD (1 km^2) only model, based on a Resource Utilization Function in northeastern Vermont, USA. Each map pixel provides a z-score, where 0 indicates average use. Positive scores indicate higher use than average, and negative scores indicate lower use than average.

and 0.15 respectively; median model weights = 0.67 and 0.00 respectively; mean AIC difference = -24.5; median AIC difference = -10.6). These findings support the notion that lidar is an effective tool for improving the ability of models to estimate patterns of habitat use, especially for larger bodied mammals, as other lidar-based studies have focused mainly on birds (e.g., Bradbury et al. 2005).

Moose exhibited important seasonal differences in habitat use that likely reflect temporal changes in energetic and nutritional requirements and behavior associated with certain social activities across the year (Schwartz and Renecker 2007). For instance, during the growth period, moose maximize food intake to meet high energy demands, including lactation, rearing of young, and the accumulation of fat (Shively et al. 2019, Pekins 2020). We found that moose used areas with proportionally more regenerating forest (i.e., forage < 3.0 m) during the growth period, which included areas of recent timber harvest, indicating the importance of focusing on regenerating forest patches. Moose also actively used regenerative forest in the dormant season (although to a lesser extent), presumably to cope with energetic demands associated with heavy tick loads over the winter (Pekins 2020), thus further underlining the essential importance of this habitat type to managers.

Additionally, our results indicated mature and young female moose had strong positive associations with lidar-derived canopy structure during the growth (but not the dormant) period, which suggests that enhancing canopy cover may be an important consideration for managing female habitat use. Given that the Vermont population is near the southern range limit for the species, thermal stress may affect habitat use more so than in other regions (Montgomery et al. 2019, Alston et al. 2020). In contrast to females, elevation was an important predictor of habitat use for young males in both the dormant and growth periods, indicating that the trade-offs between food and temperature may differ by sex or that other factors may be driving use. Although elevation only varied by 800 m, higher elevation can be cooler than lower areas and potentially offset the costs of not using canopied habitats. Certainly moose thermoregulate behaviorally (e.g., Montgomery et al. 2019, Alston et al. 2020), but caution should be used when drawing conclusions about population-level responses from thermal stress (Lowe et al. 2010, Pekins 2020).

In terms of landcover, it is important to emphasize that the effect sizes from our models are relative to the intercept, which encompasses deciduous landcover, the most dominant landcover class in our study area (28% mixed, 44% deciduous, and 12% evergreen). Young male moose used mixed forest types much more than young female moose, which complements other studies of habitat use in New England (Leptich and Gilbert 1989). Mixed forest cover was also used more by mature female moose in the dormant season, thus emphasizing the potential importance of this resource for breeding females. Both evergreen and wetland had negative or no effect on habitat use for both sexes and seasons relative to deciduous forest (the model's intercept). We expected stronger evergreen and wetland signals, as it is well documented that moose seek wetlands in summer and coniferous forest for shelter and as a source of forage in winter (Timmermann and McNicol 1988).

Our results have implications for moose management in this region where declines in moose health, survival, and fecundity have been linked to heavy parasite loads, chief among them winter ticks (Jones et al. 2019, Pekins 2020, Debow et al. 2021). During our study, winter tick epizootics occurred in 2 of 3 years (2018 and 2019), in which calf mortality exceeded 50% and cause of death was attributed to atrophy due to winter tick infestation (Jones et al. 2019, Debow et al. 2021). As a single-host parasite, the prevalence of winter ticks in our study area is largely shaped by the distribution of moose in the fall (when ticks attach to moose) and in the spring (when ticks detach from moose to lay eggs on the forest floor). Thus, areas that are heavily used by moose in both fall and spring may actively promote the host-parasite cycle (Healy et al. 2018), highlighting the concept that habitat use should not be confused with habitat quality (Van Horne 1983). Blouin et al. (2021) found that habitat selection decisions made by adult females during the fall questing period can influence whether their calves survive or not the following spring.

Reducing the impacts of ticks will largely involve efforts to reduce the abundance and distribution of ticks on the landscape, which may be accomplished by reducing moose density through harvest (Ellingwood et al. 2020) or habitat manipulation that aims to reduce high-density moose congregations that may support high tick densities (VFWD 2020). Given this and the need to promote healthy moose on the landscape, the spatial distribution of heavily used habitats (e.g., the amount and distribution of regenerating forest) warrants management attention (Johnson et al. 2002). Previous research indicates that home ranges of young females often overlap with that of the parent cow, leaving questions about how highly distributed optimal habitat on the landscape (i.e., timber harvests) would ultimately impact dispersal behaviors and local densities (Cederlund et al. 1987, Johnson et al. 2002). Future studies on moose habitat use may examine the comparative values of various habitat management options in best reducing high congregations of moose on the landscape while critically providing females with high quality forage and refuge habitat.

Several caveats remain. We did not evaluate the composition of forest species that are used within home ranges or the nutritional landscape (Schrempp et al. 2019) as tree and shrub species vary in nutritional value (Timmermann and McNicol 1988). Failure to recover adequate fat depots during late summer-autumn can predispose individuals to mortality (Schrempp et al. 2019), most notably parasitism by winter ticks regionally (Pekins 2020). Further, locally high seasonal density of moose (browsing) can measurably impact forage quality on the landscape (Persson et al. 2005, Bergeron et al. 2011), and is an important consideration in habitat management.

Ultimately, wildlife and forest managers must balance multiple objectives when developing resource management plans. Maintaining healthy populations of moose while also considering other societal and biological objectives, such as maximizing biodiversity and forest sustainability, can be complex. Structured decision approaches, as suggested by Franklin et al. (2020), can help elucidate tradeoffs. Our aim was to provide science-based information that identified habitat use and importance to moose (and presumably winter ticks) that may be incorporated into decision-making and management frameworks. Ultimately, accurate maps of critical habitats for moose will provide managers guidance when integrating moose population and forest management goals.

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S1: GPS RADIO-COLLAR BIAS STUDY

RUFs estimated from GPS collar data may suffer potential bias if locations are not observed equally. Successful communication between the radio-collar and satellites may depend on habitat types or terrain (e.g., the likelihood of obtaining a GPS coordinate may be lower in evergreen forest than in an open field). Failure to correct for GPS collar bias may in turn bias RUFs (Frair et al. 2004, Horne et al. 2007, Frair et al. 2010).

To account for radio-collar bias, we estimated transmission rates as a function of habitat and terrain by deploying 12 VECTRONIC GPS radio-collars across 60 randomly selected sites that varied by the cover types used in the analysis (deciduous, coniferous, mixed, wetland forests and open habitats). We assumed that habitat cover types affected transmission rate and GPS fix rate (i.e., collection of locations from the GPS satellite system) the same. Cover type of each site was derived from NLCD 2016 land cover classifications at 30 m resolution (USGS 2016a) and confirmed by ground-truthing. Terrain covariates for each site (slope, aspect, and elevation) were also used to account for location bias and derived from U.S. Geological Survey data (Pyle 2002). Sites were stratified by habitat inside a 200 m buffer of VT Rt. 105 from Island Pond, Vermont east to Bloomfield, Vermont and ranged between 268 and 403 m in elevation, 0.01 and 12.28 in slope angle degrees, and included all aspect categories (North as < 45° and ≥ 315°, East as ≥ 45° and < 135°, South as ≥ 135° and < 225°, and West as ≥ 225° and < 315°).

Collars were fastened to a pole positioned downward (mimicking a standing moose) at each trial site, approximately 1 m off the ground. GPS collars were deployed for a minimum of 2 days; when inactive for >5 h, the collars switched to mortality mode, sending a GPS coordinate every half hour for 6 h (12 total transmissions per site, per collar). Each collar was moved to a new, randomly selected site after a minimum of two days until all 60 sites were sampled. Sampling was repeated during two distinct seasons that coincided with the broad seasonal classifications of growth and dormant: "leaf on" (08 July to 29 July 2019) and "leaf off" (08 April to 29 April 2019). Thus, total sample size was: 60 sites * 2 seasons * 12 transmission attempts = 1,440 transmission attempts.

We analyzed the probability of a transmission being successful (1) or unsuccessful (0) as a function of the terrain and cover type variables, while also accounting for the random effect of the individual radio-collar, using mixed-effects logistic regression. Eight models of the covariate data were evaluated to understand effects on transmission probability. Each covariate (cover type, elevation, aspect, slope, season, and intercept) was modelled separately and two models were developed that accounted for combined effects: a model estimating the effect of all covariates together on transmission rate and a model estimating the interaction of season (leaf-on or leaf-off) across cover type variables on transmission.

Akaike's Information Criterion adjusted for small sample size (AICc) and Akaike weights (AICWt) were used to determine the models that best explained the data (Burnham and Anderson 2002). The best-supported model was then applied to objective 3 (analysis of utilization distributions) to correct for collar transmission bias. All analyses were conducted in R (Team 2018). Mixed-effect models were analyzed in the R package lme4 (Bates et al. 2015) and model selection metrics were calculated with the R package AICcmodavg (Mazerolle 2017).

RESULTS

A majority of all GPS collar transmission attempts (76%, n = 1,094 of 1,440) were successful. Of the eight models evaluated, the interaction model was the top-ranking model, carrying 68% of the model weight (Table S1–1). This model examined all landcover and terrain covariates on GPS transmission rates, and further explored the effect of cover type dependent upon season (leaf-off vs. leaf-on). The next best model estimated the effect of all covariates (without interactions) on collar transmission probability and carried 31% of the model weight (Table S1–1).

In the top model (interaction), the leaf-on period, evergreen forest, mixed forest, and higher elevations had significant negative

Table S1–1. Comparison of the 8 mixed effect logistic regression models for GPS transmission bias in northeastern Vermont, USA.

Model	K	LL	AICc	Delta AICc	AICc Wt
1. Interaction	16	-717.24	1466.86	0.00	0.68
2. All	12	-722.10	1468.42	1.55	0.31
3. CoverType	6	-733.74	1479.54	12.68	0.00
4. Slope	3	-747.73	1501.49	34.62	0.00
5. Elevation	3	-760.67	1527.36	60.50	0.00
6. Intercept	2	-765.11	1534.23	67.37	0.00
7. Season	3	-764.66	1535.33	68.47	0.00
8. Aspect	5	-764.73	1539.50	72.63	0.00

Table S1–2. Coefficients (with 95% confidence intervals) of the top mixed effect logistic regression model (interaction) describing the effect of cover types and their interaction with the leaf-on vs. leaf-off period and the effect of terrain characteristics on GPS radio-collar transmission rates.

Model	Parameter	Estimate	Std. Error	Upper 95	Lower 95
Interaction	(Intercept)	4.51	1.00	6.48	2.55
	Leaf-On	-0.93	0.37	-0.21	-1.65
	Evergreen Forest	-1.48	0.35	-0.80	-2.16
	Mixed Forest	-1.00	0.36	-0.31	-1.70
	Open	-0.25	0.42	0.56	-1.07
	Wetland	-0.17	0.44	0.69	-1.04
	Slope	-1.18	0.28	-0.63	-1.72
	Aspect (North)	0.35	0.24	0.81	-0.12
	Aspect (South)	0.16	0.19	0.54	-0.22
	Aspect (West)	0.47	0.24	0.94	0.00
	Elevation	-0.65	0.26	-0.15	-1.16
	Leaf-on: Evergreen Forest	1.34	0.45	2.22	0.45
	Leaf-on: Mixed Forest	0.75	0.44	1.61	-0.11
	Leaf-on: Open	0.75	0.52	1.77	-0.27
	Leaf-on: Wetland	0.53	0.54	1.59	-0.53

impacts (P = <0.05) on transmission probability when compared to the intercept reference (leaf-off, east-facing, deciduous) (Table S1–2). The only significant positive effects on transmission rate was when the aspect was west-facing, and during the leaf-on period in evergreen forest (Table S1–2).

In the all covariate, interaction model, the average probability of transmission was highest in the open and wetland cover types, at a nearly 90% success rate (Fig. S1–1). The lowest probability of a successful GPS transmission was in evergreen forest during the leaf-off period (63% success rate), which we would predict given the denser canopy structure that could impact the relationship of the collar to the satellite. Similarly, transmission rates in all cover types except evergreen forest were lower during the leaf-on period (Fig. S1–1). This decrease in successful transmissions rates from the leaf-off to the leaf-on period was most significant in the deciduous forest type (87% to 73%, respectively), as would be expected in a fully canopied seasonal forest.

We used the predict function from the package lme4 (Bates et al. 2015) to obtain the probability of a successful GPS transmission for each UD value, depending on the UD's covariate values.

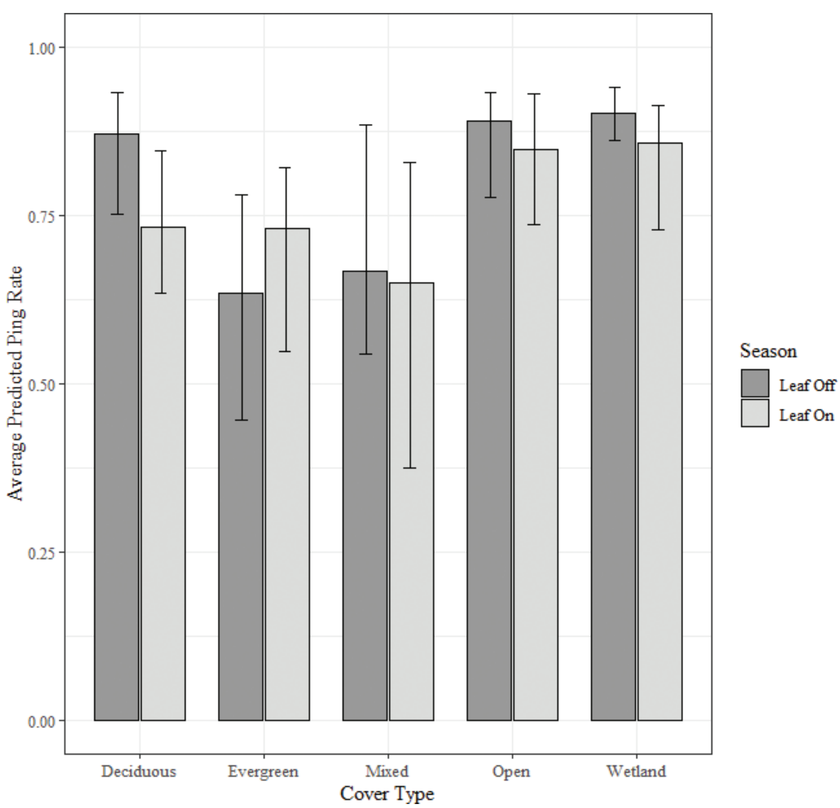
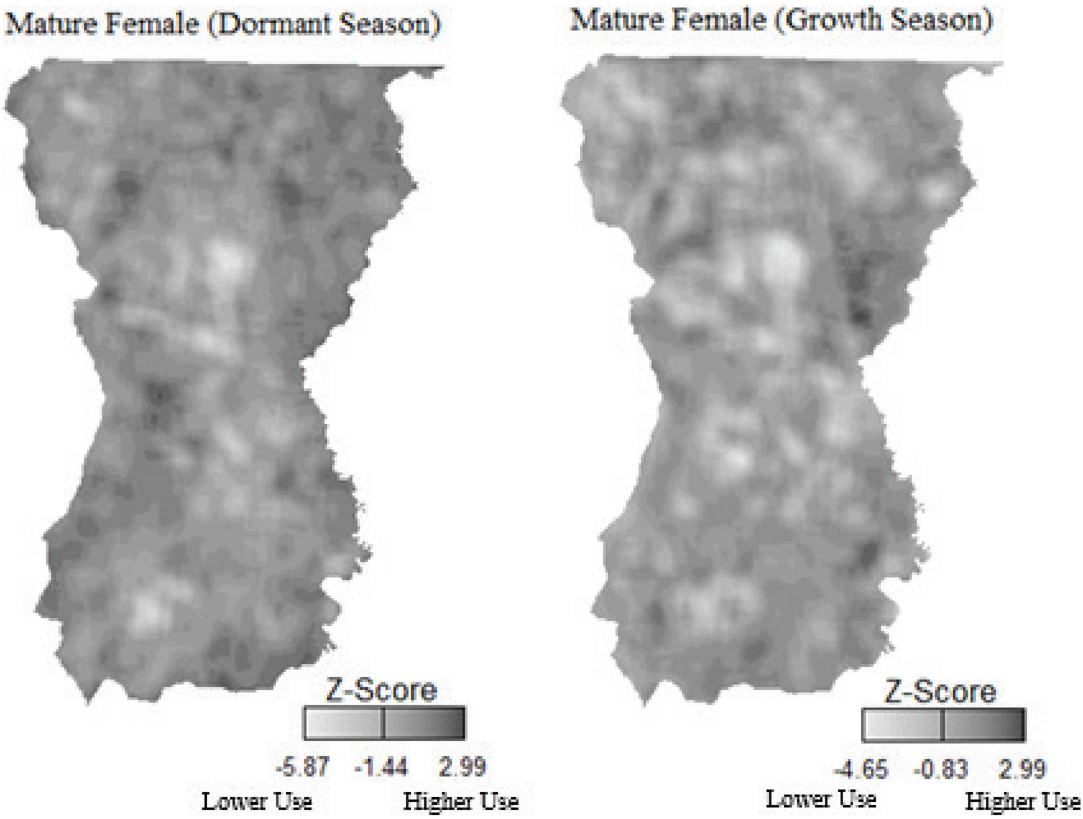
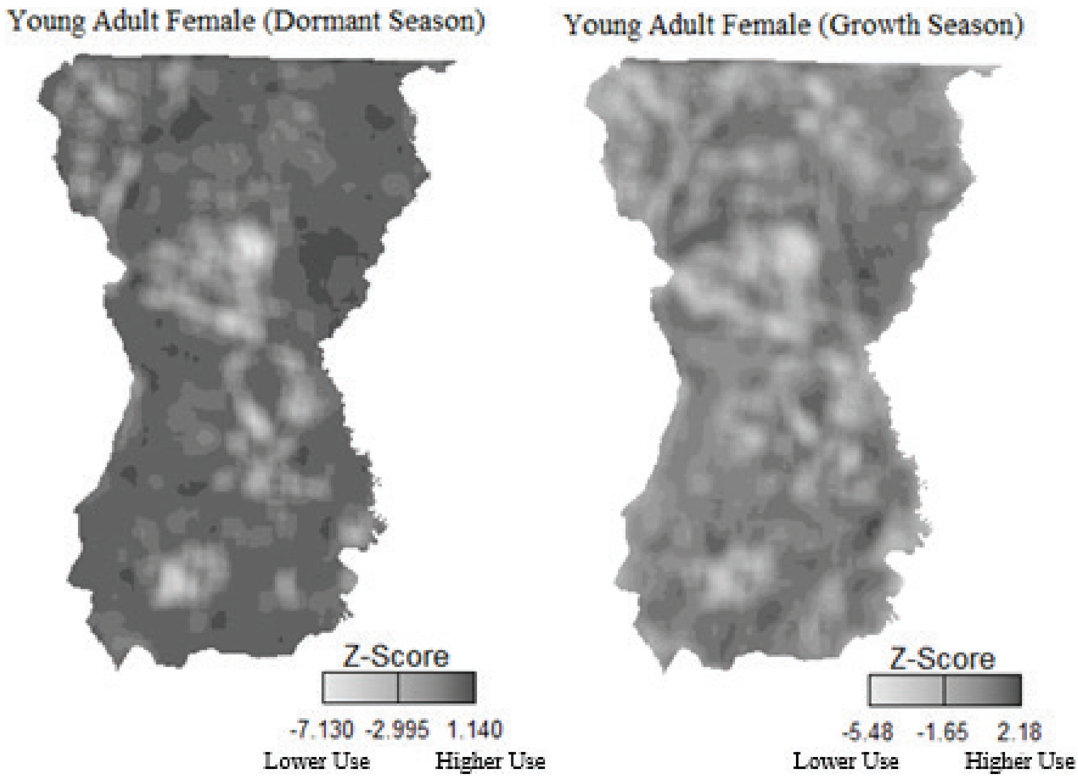


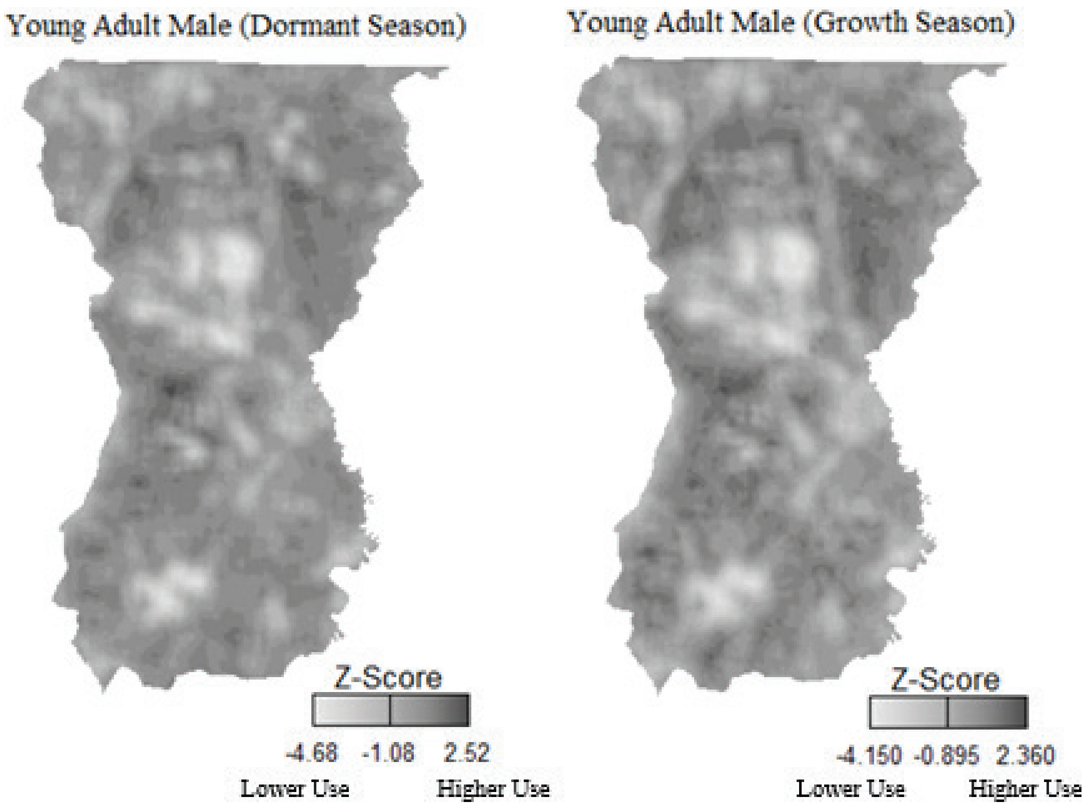
Figure S1–1. The average probability of transmission of Survey Globalstar V7.1 GPS radio-collars placed in five different habitats in northeastern Vermont, USA during a leaf-on and leaf-off period (2019). Vertical bars represent the range in predicted ping rate for any given category. For example, in the deciduous "leaf off" period, predicted ping rates ranged from 0.75 to 0.93, resulting from collars placed at different elevations, aspects, and slopes.



S2. Map of habitat use by mature female moose during the dormant and growth seasons in northeastern Vermont, USA.



S3. Map of habitat use by young adult female moose during the dormant and growth seasons in northeastern Vermont, USA.



S4. Map of habitat use by young adult male moose during the dormant and growth seasons in northeastern Vermont, USA.