



HABITAT USE AND SELECTION BY ADULT FEMALE MOOSE IN NORTHWESTERN MONTANA: VEGETATION TYPES, FOREST DISTURBANCE, AND THERMAL REFUGE

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ABSTRACT: We studied summer and winter habitat use and selection of 34 GPS radio-collared adult female moose (*Alces alces*) living in largely managed coniferous forests in the Cabinet and Salish Mountains in northwestern Montana during 2013-2022. We built resource-selection function (RSF) models at the 2nd and 3rd order scales, and supplemented them by examining functional response to resource availability. We also assessed whether habitat selection was influenced by ambient temperature and used independently obtained field data to gain insight about the abundance of 2 important dietary shrubs, *Salix* spp. and *Ceanothus velutinus*. Moose selected strongly for intermediate elevations, denser canopy cover, and riparian habitats, but against non-vegetated and pine-dominated stands. As expected given their preference for deciduous shrubs, moose selectively used cut stands after the initial decade post-timber harvest. We observed a subtle preference for uneven-aged versus even-aged treated stands. Although uncommon, burned areas were used by moose, particularly ~15-35 years post-burn when conditions were conducive for *Salix* spp. and *C. velutinus*. Moose made subtle adjustments in habitat selection based on time-of-day and the prevailing temperature, exhibiting behavior consistent with the hypothesis that they seek cooler microclimates to aid thermoregulation. To benefit moose, habitat management in these and similar systems should diversify forest structure by setting back succession through timber harvest and allowing fires where possible, while providing mature proximate coniferous canopy for thermal relief.

ALCES VOL. 59: 69 – 98 (2024)

Key words: *Alces alces*, habitat, Montana, moose, selection, shrubs, thermal cover, timber harvest, vegetation type, wildfire

The fundamental strategies of moose (*Alces alces*) to locate and use required resources and avoid mortality are reasonably well understood (Peek 1998, Bowyer et al. 2003). However, local populations encounter a variety of biophysical characteristics and climatic regimes, and thus exploit habitat resources in subtly different ways. In turn, managers are best equipped to adapt and respond when they understand local

habitat choices. Although moose consume portions of coniferous trees, particularly during winter, those occupying temperate forests in western North America obtain most forage and nutritional requirements from deciduous shrubs (Jenkins and Wright 1988, Shipley 2010). Deciduous shrubs in these forests evolved to take advantage of sunlight reaching the forest floor from canopy disturbances associated mostly with

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fire (Street et al. 2015b, Brown et al. 2018) and other less frequent natural disturbances (Stephenson et al. 2006). Forest vegetation communities reset by disturbance to early successional stages typically include high biomass of deciduous shrubs and are consequently important foraging habitat for moose (Shrempp et al. 2019). More recently, timber harvests in northwestern Montana during the 20th century became the principal disturbance that created these early seral stages. However, timber harvests have since declined in the region (Proffitt et al. 2019) as moose populations concurrently declined in the 1990s and 2000s in Montana (DeCesare et al. 2014). One hypothesis is that the nutritional carrying capacity of moose is declining as forest maturation gradually reduces available forage. The relationships among foraging behavior, population response, forest disturbance, and the temporal pattern in availability of early successional forests as a nutritional limiting factor to moose in northwestern Montana remains largely unexplored.

Given the potential effects of climate change, the role of thermal cover for moose has received increased attention for southern populations presumed most challenged by warming (Schwab and Pitt 1991, van Beest et al. 2012, McCann et al. 2013, Melin et al. 2014, Alston et al. 2020, Borowik et al. 2020). Nutritious forage in early successional stages provides maximal benefit for moose, but daily use may be tempered by conditions (heat) prohibitive to lengthy exposures in open habitat. In contrast, although mature forests may provide fewer nutritional resources for moose, their canopy cover and microhabitats provide important thermal relief. Thus, moose likely face daily tradeoffs to effectively balance use of foraging habitat and thermal refuge (Dussault et al. 2004).

In the Rocky Mountains of North America, most investigations of moose-habitat

relationships have occurred in relatively xeric and cold environments at high elevations where coniferous forests are typically simple in structure and composition, and large patches of contiguous, willow (*Salix* spp.) riparian communities favored by moose are prominent (Knowlton 1960, Van Dyke et al. 1995, Tyers 2003). In environments such as southwestern Montana, Yellowstone National Park, and northern Colorado, moose typically forage in shrub-dominated climax communities, occasionally seeking refuge from snow or warm temperatures in mature conifers (Kufeld and Bowden 1996, Burkholder et al. 2022).

In warmer, more mesic coniferous forests of the Rocky Mountains, Matchett (1985) studied habitat selection of moose in managed habitats of the Yaak River drainage of northwestern Montana. Moose selected stands with a history of timber harvest, particularly small (< 12 ha) clearcuts and stands harvested 15-30 years prior. Similarly, in the North Fork of the Flathead River of Montana and adjacent British Columbia, Langley (1993) found that moose selected habitats characterized as marsh and early-seral sapling forests in summer, and riparian and conifer-dominated stands in winter. In an area of central Idaho where early seral stages were uncommon, Pierce and Peek (1984) found selective use of open habitats in summer and mature and old-growth stands in winter. The use of mature stands in winter was attributed, in part, to their function as snow-intercepts. Focusing on finer-grained selection in nearby southeastern British Columbia, Poole and Stuart-Smith (2005) found that moose in late winter concentrated time and foraging activity where deciduous shrubs (particularly *Salix* spp.) were disproportionately abundant. Further north in British Columbia, Mumma et al. (2021) also found like Matchett (1985), that moose generally selected cutblocks > 8 but

< 25 years old; the degree of selection varied by vegetation composition. Lastly, Francis et al. (2021) concluded that moose prioritized forage over security, selecting for burns in spring, deciduous stands in spring and fall, and wetlands in summer in the southern portions of the Mumma et al. (2021) study areas.

Here, we report on habitat use and selection of adult female moose in the Cabinet and Salish Mountains of northwestern Montana, an area subject to long-term management-focused research (Newby and DeCesare 2020). We used location data from GPS-monitored moose (2013–2023) to examine use and selection of habitat resources relative to abundance, and to relate these patterns to the biological needs of moose and habitat management options available to managers.

Our primary objective was to understand the relative importance of habitat resources during summer and winter, thereby providing the basis for more effective management of moose populations and habitats. To this end, we constructed resource selection function (RSF) models for both seasons at the 2nd (landscape) and 3rd (home range) order scales. Within this heavily forested area, we hypothesized that moose would prefer disturbed habitat patches sufficiently open to allow vigorous growth of shrubs, their primary food source (Renecker and Schwartz 1998, Shipley 2010). We further hypothesized that use of disturbed areas by moose would be highest when shrub production is maximal, ~ 1–3 decades post-disturbance (Matchett 1985, Mumma et al. 2021). Although the RSF method is well established for analyzing habitat selection, it can be misleading if important resources are sufficiently abundant that proportional use is unlikely to exceed availability, or if selection itself varies as a function of availability (Mysterud and Ims 1998, Beyer et al. 2010, Holbrook et al. 2019). Additionally, because the study moose varied

not only in their relative preference, but in the ensemble of resources available to them, an RSF approach that considered all animals was necessarily constrained in its ability to illuminate selection of rare resources (Gillingham and Parker 2008, Fieberg et al. 2010). Thus, we supplemented RSF modelling with examination of functional responses to the availability of resources (Bjørneraas et al. 2012), providing graphical depictions that added nuance to our understanding of use patterns and allowing inclusion of resources that certain animals had no opportunity to encounter.

An additional objective was to gain insight into whether and how topographic and forest-stand characteristics influenced the relative abundance of plant species likely to be important components of moose diets. To this end, field vegetation data gathered originally to inform studies of habitat use and migration by sympatric mule deer (*Odocoileus hemionus*) were used to assess variation in the abundance (i.e., biomass) of shrubs presumed important forage for moose (Peterson et al. 2022, Hayes et al. 2022). Specifically, we developed linear models to elucidate which, if any habitat features found important in RSF analyses (and others we were unable to incorporate in RSF models) also predicted available biomass of selected shrub species.

Our final objective was to understand the influence of temperature variation on moose habitat selection. Toward this end, we tested whether moose responded to hourly and daily variation in ambient temperatures by selecting habitats predicted to provide thermal refuge in the Cabinet-Salish Mountains area (DeCesare et al. 2023). To test hypotheses relating habitat use to daily and hourly variation in temperature, we developed linear regression models of habitat use that used temperature and hour-of-day as predictors, and predictor response variables that DeCesare et al. (2023) found produced small-scale geographic thermal refuges.

METHODS

Study Area

We defined the Cabinet-Salish Mountains study area as the union of the watersheds (HUC-6) in the Kootenai River drainage, centered on approximately 48.2°N, 115.5°W (Fig. 1). The study area varied in elevation from 660 to 2,494 m. We expanded the area beyond these drainage boundaries where necessary to allow inclusion of areas within moose home ranges. The study area had a modified maritime-continental climate with mean January temperatures of -8.1 to -0.8 °C, mean July temperatures of 7.7 to 25.0 °C, and mean annual precipitation of 91.4 cm. Characterized by dense forest of diverse conifer species, the most common trees were Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and Ponderosa pine (*P. ponderosa*) on drier sites, and Engelmann spruce (*Picea engelmannii*), western larch (*Larix occidentalis*), grand fir (*Abies grandis*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) on more mesic sites (Wilson and Miles 2000). Prominent deciduous species occurring mostly in moist or riparian areas were aspen (*Populus tremuloides*), black cottonwood (*P. trichocarpa*), and Sitka alder (*Alnus viridis*). Most of the study area was managed by the Kootenai National Forest, with a substantial minority held by large, commercial timber production companies. Most of the study area was managed for commercial timber harvest with the exception of the western-most extent, part of the designated Cabinet Mountains Wilderness Area. Recently burned areas were rare with ~ 1.5% of the study area experiencing wildfire from 1985 to 2020. Other large herbivores included white-tailed (*Odocoileus virginianus*) and mule deer, mountain goats (*Oreamnos americanus*), and elk (*Cervus canadensis*). Potential predators included wolves (*Canis lupus*), mountain lions (*Puma concolor*), and black (*Ursus americanus*) and grizzly bears (*U. arctos*).

Study Animals and Locational Data

We captured adult female moose via helicopter, immobilizing them with a combination of xylazine (20–50 mg/animal) and either carfentanil (3.3–3.9 mg/animal) or etorphine (8–10 mg/animal), which was reversed with tolazoline (600–800 mg/animal) and naltrexone (400–600 mg/animal), respectively. All capture and handling was conducted according to protocols approved by the Animal Care and Use Committee (Permit FWP12-2012) of Montana Fish, Wildlife and Parks.

Sixty-two adult female moose (age \geq 1.5 years old) were captured during winters 2013 through 2021, of which 42 were equipped with GPS-transmitting collars during some of the monitoring period. We defined the summer season as 15 May to 15 September and the winter season as 1 January to 30 March. We selected these dates to exclude variation in habitat selection that might be influenced by biological and anthropogenic factors including the breeding period, moose hunting season (which began 15 September annually), and spring and fall migrations (typically completed by 15 May and 1 January, respectively). We limited analyses to data from 34 animals providing >100 GPS locations with positional dilution of precision (PDOP) of 4 or lower in that season (Table S1); 1 animal was excluded in winter and 2 in summer due to insufficient locations in that season only. A total of 21,286 GPS locations were analyzed with similar amounts in each season. Data for each moose were pooled within season across years; monitoring per animal averaged 1,116 days (range = 339 – 2,794 days).

Collars were programmed to obtain and transmit (via Globalstar satellites) locations every 23 h on 9 moose (16% of data), and every 13 h for 28 moose (84% of data). To address potential biases that might result from

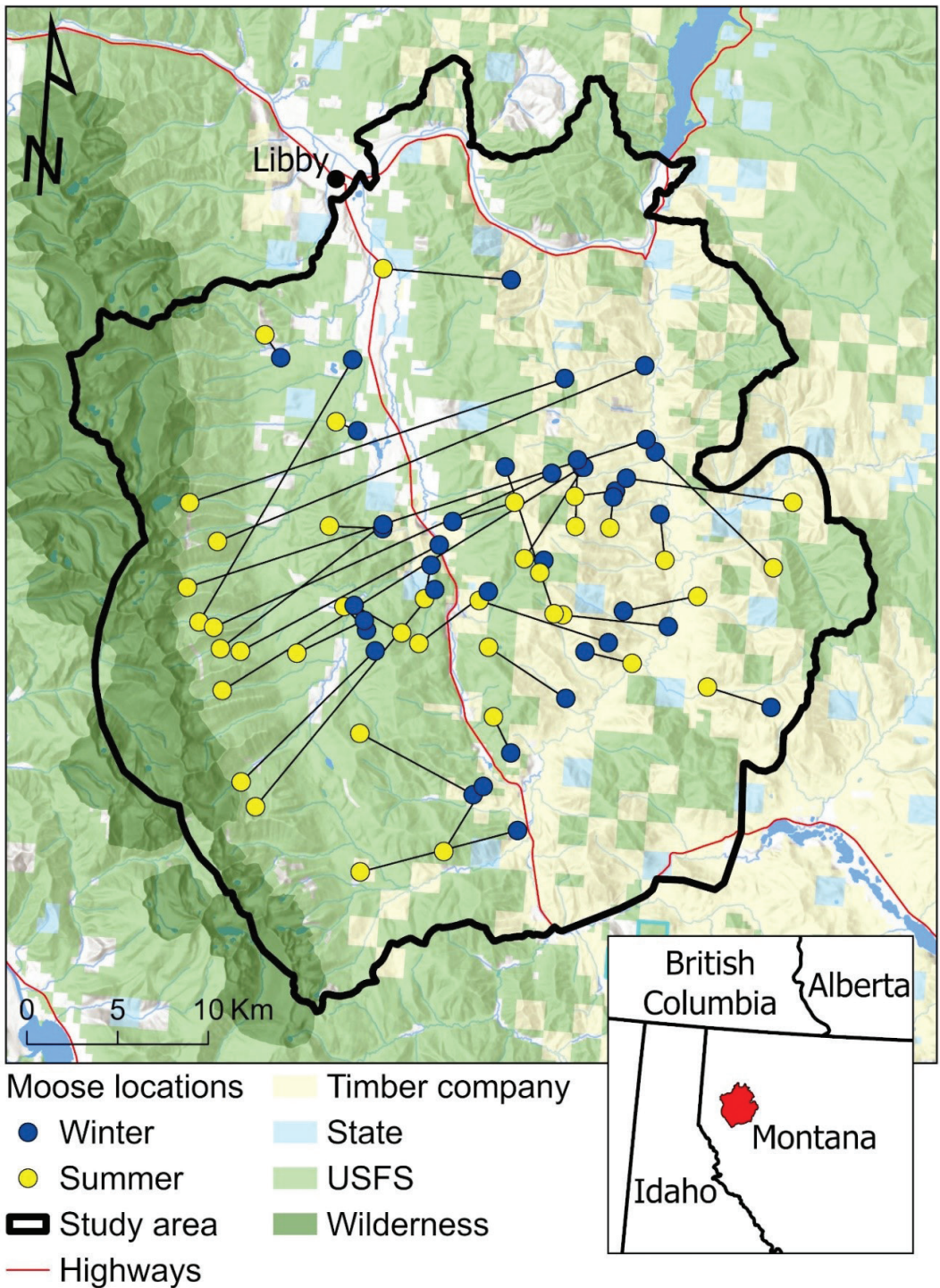


Fig. 1. The Cabinet-Salish study area showing representative adult female moose locations during winter (blue, when captured) and summer (yellow, location closest in time to 15 July in the first year of monitoring), and land ownership in northwestern Montana, 2013-2022.

habitat-induced variation in remote transmission of data via Globalstar satellites, we followed the protocol of Peterson et al. (2022) to estimate the probability of a successfully transmitted fix (P_{fix} ; Frair et al. 2010). A sample of 14 collars from animals that died or were recaptured provided the opportunity to compare fixes received remotely to fixes recorded only on the collar (not transmitted). Overall, 52.6% of store-on-board fixes were transmitted to the satellite; these fixes identified usable data for the other 20 collars for which we had transmitted data only. We used logistic regression to estimate and predict P_{fix} (see Supporting Material, Tables S2, S3, Fig. S1), and then weighted locations in subsequent habitat analyses by $1/P_{fix}$ (Frair et al. 2010).

Habitat Attributes

To quantify physical site characteristics that we hypothesized could affect habitat selection, we estimated metrics of topography using a digital elevation model (DEM) from the USGS 3D Elevation Program (USGS 2019). From this DEM we derived elevation (m), aspect, slope ($^{\circ}$), and a topographic position index (TPI). We used a trigonometric transformation of aspect ($\cos[\text{aspect}-45]$; McCune and Keon 2002) that varied from -1 to 1 along a southwest to northeast gradient. We estimated TPI as the difference in elevation between any given pixel and the average elevation of the surrounding neighborhood (1 km radius), thus discriminating the gradient of landforms from drainages (negative values) to ridges (positive values; Weiss 2001).

We categorized vegetation by collapsing categories developed by the NatureServe consortium (NatureServe 2018) that were mapped as vector-shape files as part of the LANDFIRE Existing Vegetation Type (EVT) GIS layer in 2020 (LANDFIRE 2020). To quantify where and when timber

harvest had occurred on the study area, we used a vector shape-file map of timber harvest cutting units periodically updated by the U.S. Forest Service (USFS 2023). We aggregated 34 unique harvest types into 4 categories (even-aged, uneven-aged, shelterwood, and uncategorized); clearcuts and seed-tree cuts were considered as even-aged, and we further simplified these to even-aged and uneven-aged for small sample sizes (Tables S4, S5). Following Matchett (1985), we hypothesized that shrub production (i.e., and thus moose habitat use) would be optimal in stands regenerating from disturbance \sim 10-30 years previously. Thus, we considered a separate variable for harvested stands 10-29 years-old in the year each moose was monitored. Because Matchett (1985) recommended that harvest units be relatively small to encourage use by moose, we also included the area of harvested polygons in our analyses.

We identified previously burned areas with the National USFS Final Fire Perimeter feature layer, a vector shape file updated periodically by the U.S. Forest Service and available publicly on the FSGeodata Clearinghouse (<https://data/fs.usda.gov>). We used geographic information on locations of paved primary and secondary highways in Montana from the Montana Department of Transportation (<https://gis.mdt.opendata.arcgis.com>). Spatial analyses of all hypothesized predictors (Tables 1, S6) were conducted in ArcGIS Pro 3.0.3 (Esri, Redlands, California, USA).

Resource Selection Analyses

We modeled resource selection during summer and winter at two orders of selection (Johnson 1980): 2nd order in which selection of home ranges was assessed relative to the entire study area, and 3rd order in which selection of used sites was assessed relative

Table 1. Predictive variables considered in logistic regression models comparing use with availability at 2 spatial scales (2nd and 3rd order) and 2 seasons (winter and summer), Cabinet-Salish study area of northwestern Montana, 2013-2022.

Variable category	Variables
Topography	Elevation ² , Slope ² , Aspect, Topographic Position
Canopy	Canopy cover ² , Stand age ²
Vegetative characteristic of habitat	Vegetation type ^a
Forest management	Harvested (10-29 years prior), Harvested (< 10 or < 29 years prior), Harvest block size, Harvest type (even-aged, uneven-aged, unidentified)
Linear features	Distance from water, Distance from highway

Notes:

1. Superscripted variables = included a quadratic term to allow the potential for nonlinearity in response.
2. Slope² was examined but consistently found to be both highly correlated with, and an inferior predictor than elevation²; it did not appear in top models.

^a Due to lack of convergence caused by limited sample size, fewer levels of vegetation types and harvest types were modeled in 3rd order and 2nd order winter models than 2nd order summer models.

to those available within an individual home range. We developed 95% kernel density multi-year home ranges (Calenge 2006) for each moose for each season. In developing kernel density home ranges, we used the reference value for bandwidth except when doing so produced multiple polygons in close proximity to each other, in which cases we adjusted the bandwidth manually to connect those polygons (Kie et al. 2010). At both spatial scales and for each season, we generated random points equal to 10 times the number of used points for each moose as recommended by Muff et al. (2020). Throughout, we used a 2-stage model-fitting approach, in which we averaged across models initially fit for each individual animal to account for unequal sampling and autocorrelation of GPS fixes (Murtaugh 2007, Fieberg et al. 2010), acknowledging that it most likely inflated coefficient variances and thus provided a conservative picture of predictor significance at the population level (Fieberg et al. 2010). Specifically, we first identified a global model for fitting to each individual by selecting the most parsimonious model structure from a suite of candidate models using a standard model selection

approach (Burnham and Anderson 2002) applied to the pooled data set across all individuals. We applied this model to each individual moose separately to estimate individual-level coefficients and their standard errors (Table S7). We then produced population level RSFs by averaging the coefficients across all individuals weighted by the reciprocal of their standard errors. Following Murtaugh (2007), we assumed the resulting weighted mean coefficients divided by their weighted standard errors had *t* distributions, and calculated the statistical significance of the population-level RSF coefficients assuming normality.

We fit logistic regression models (Manly et al. 2002) of the form $w(x) = \beta_{ix_1} \dots + \beta_{ix_j}$, where $w(x)$ was the resource function (i.e., relative probability) based on predictor variables x_i ; the coefficients (β_i) were estimated using package `glmmTMB` (Brooks et al. 2017) with binomial error structures. When initially identifying the global model using all pooled data, we weighted used points by $1/Pfix$ (see above) and available points by 1,000 (Muff et al. 2020). We began model selection with univariate models, adding additional predictors

to the most parsimonious univariate model only when uncorrelated ($r < 0.5$), and ensured variance inflation factors (VIF) for all covariates were < 3 (Zuur et al. 2007) using the `check_collinearity` function in R package Performance (Lüdecke et al. 2021). When necessary, we reduced the levels of categorical variables included within the top pooled-data model in order to achieve convergence for that model at the 2nd stage (Beyer et al. 2010). We transformed elevations and both distance-based predictors from meters to kilometers and divided raw TPI values by 1,000 to optimize model convergence. Because areas previously burned by wildfire were rare in the study area and only a few moose had access to them, we were unable to account for burns directly in the RSF models (see below).

In our approach to orders of selection, we adopted a nested design to allow development of a single scale-integrated predictive map that included selection patterns among both 2nd and 3rd orders (sensu DeCesare et al. 2012). To this end, we assumed that animal locations from GPS collars represented resource use at the 3rd order scale, but in 2nd order analyses we represented resource use by generating random locations sampled within each animal's home range (with the n equal to the number of location points for that animal in that season). This nested structure facilitated producing maps that represented predictions integrated across both scales of selection, one for summer and one for winter.

Finally, to validate the scale-integrated RSF models, we grouped model predictions into 10 equal-area bins ranked according to predicted selection values (i.e., bin 1 representing the least likely to be selected and bin 10 the most likely). We then used Spearman's rank correlation to assess the degree to which moose used habitat in each bin in accordance with their relative rank

(Boyce et al. 2002). A positive correlation between the frequency of moose GPS locations and the relative bin ranking would suggest a reasonable model. We conducted tests using 2 independent data sets for both summer and winter maps. First, as an internal validation we used the same used locations employed in developing the models. Second, as an external validation we used data collected in the year after analyses were conducted (i.e., 2023). That is, the external validation asked how well our map developed from 2013-2022 data predicted patterns of use in 2023.

Functional Responses to Habitat Availability

Because RSF models require that home ranges for all sampled animals have at least some presence of each level for resources considered (which was untrue in our case), and because selection and avoidance patterns can be misleading in some cases (Mysterud and Ims 1998, Holbrook et al. 2019), we examined selection ratios and functional responses to habitat availability for specific selected resources. To quantify use of burned areas, we calculated Manly selection ratios (Manly et al. 2002, Gillingham and Parker 2008) of points used by moose to available points on each burn. To examine functional responses, we regressed the proportion of used locations for each individual (as in the RSF approach, weighted by *Pfix* to account for biases of GPS collars acquiring a location) on the proportion of that resource available within each animal's home range. We adopted the additive approach of Mysterud and Ims (1998; approach 1 of Holbrook et al. 2019) in considering slopes and intercepts of linear, 2nd (quadratic), and 3rd order (cubic) polynomial relationships. We assessed the fit of these 3 nested candidate models using log-likelihood ratio tests (Program `lmtest`

version 0.9-40, Zeileis and Hothorn 2002), where we retained lower order polynomials unless the higher order model was significant at $\alpha < 0.05$. Points falling near a reference line with slope = 1 (i.e., used = available) would indicate that use was proportional to availability at all abundances of that resource, whereas points above that line would reflect selection (use greater than availability) and below the line avoidance (use less than availability). We concluded that slopes differed from the 1:1 reference line when their 95% confidence intervals did not include 1.0. This approach provided a way to assess if selection or avoidance depended on resource abundance, while also allowing examination of specific resources that could not be included in population-averaged RSF models due to lack of availability for some individual moose. For both summer and winter, we examined functional responses of moose to availability of vegetation type, timber harvest type, timber harvest age, and area burned by wildfire.

Abundance of Shrubs

To further explore the forage relationships underlying selection patterns in our RSF models, we used field data on shrub species composition and biomass to describe difference in forage associated with our categorical, GIS-based depictions of vegetation. We used data gathered 1 June - 31 August in 2017, 2018, and 2019 as part of research on sympatric mule deer (Hayes et al. 2022, Peterson et al. 2022) to aid our inferences about possible motivations in habitat selection by moose. Vegetation plots consisted of 40-m long transects placed along elevation contours in upland habitats (including montane riparian, but excluding riverine areas), and selected in a stratified random fashion within disturbance regimes (i.e., timber harvest, prescribed fire, and wildfire) identified a priori. Plots thus provided unbiased

samples of vegetation within each disturbance regime, but not necessarily within the study area overall. In most cases, paired supplementary reference plots were established between 100 m and 1.5 km from plots in specified disturbances in forested stands without recent (< 35 years) disturbance. Species-specific biomass data for all plots represented the mean of dry-weight values from 3 1-m² quadrats systematically placed within each (see Hayes et al. 2022 and Peterson et al. 2022 for details). We limited our inference to data from the 320 plots that Peterson et al. (2022) and Hayes et al. (2022) had categorized as being located within the slightly larger boundary of their overlapping study area of the same name.

We summarized occurrence and biomass of shrub species identified as important moose forage (*Salix* spp. and *Ceanothus* spp.; DeCesare et al. 2022) relative to categories of vegetation type and disturbance history. We then examined a suite of fixed-effects models that predicted biomass of these 2 shrubs as functions of the habitat characteristics we found useful in explaining habitat selection. All regressions of shrub biomass from independent predictors used negative binomial error structures, and were implemented in R 4.2.2. (R Core Team 2021) using program glm.nb from the MASS package, version 7.3-58.3; we selected the most parsimonious model using AIC_c.

Thermal Influences on Habitat Use

DeCesare et al. (2023) developed models predicting how ambient temperature at microsites within the study area varied as a function of environmental covariates (i.e., canopy cover, elevation, aspect, topographic position, forest type), and with time of day (quantified in 3-h increments, e.g., at 0000, 0300, 0600 hr; Borowik et al. 2020, Burkholder et al. 2022). We further asked if habitat use patterns were consistent with the

hypothesis that moose responded to prevailing temperatures by selecting for cooler and against warmer microsites. Specifically, we asked if the spatiotemporal temperature patterns characterizing the study area were reflected in use patterns by moose. We reasoned that if moose chose sites in part for thermal reasons, we would observe patterns explainable by the work of DeCesare et al. (2023) at the 3rd order level of selection (i.e., sites actually used), but not necessarily at the 2nd order. That is, these analyses investigated whether moose altered their use of specific habitats at a fine scale in response to daily and hourly temperatures, but assumed that multi-year home ranges were not responsive to potential thermal stress.

DeCesare et al. (2023) modeled Δt (difference between temperatures at a specific site and that at a reference station) as functions of hypothesized habitat covariates. Here we reversed that logic by modeling use of those same covariates as functions of daily maximum temperature and time-of-day (the latter because DeCesare et al. (2023) had shown that accounting for daily cycles was necessary to interpret the effects of these habitat variables). We obtained the maximum temperature for each date in our telemetry data set from the centrally located SNOTEL station at Poorman Creek (48° 8' North, 115° 37' West, elevation 1555 m). We tested for significant relationships between use of elevation, canopy cover, topographic position, and (cosine-transformed) aspect with daily maximum temperature, hour-of-day (in 3-h increments), and their interaction. We did not test for associations between vegetation type and these thermal predictors because our definition of vegetation type differed from the one used by DeCesare et al. (2023). As in the RSF analyses, we used the 2-stage approach of Murtaugh (2007) to avoid inflating statistical significance that would have resulted from

considering all moose as a single pooled sample, and we weighted observations by $1/P_{fix}$ to account for collar fix bias (Frair et al. 2010). Finally, for tests in which hour-of-day was a significant predictor of resource use, we computed the correlation coefficient between the predicted use value at that time-of-day, and the β coefficients relating the effects of a given covariate on temperature as estimated previously for the same time-of-day (see Tables 2, 3 in DeCesare et al. 2023).

RESULTS

Resource Selection Functions

Summer home ranges were located disproportionately at intermediate elevations (Table 2a) and characterized by mesic mixed conifer and spruce-fir forests versus dry mixed-conifer forests (Fig. 2a). In comparison to the study area, they had lower proportions of non-vegetated areas, larger areas of riparian habitat, and larger proportions of patches subjected to previous timber harvest, regardless of type or age of cut (Fig. 2b). Within their home ranges, moose selected for intermediate (albeit somewhat higher) elevations and concave topography (e.g., stream drainages) consistent with their use of riparian habitats and proximity to water (Table 2b), intermediate canopy cover, and harvested versus unharvested forest stands (Table 2b).

Winter home ranges were also located disproportionately at intermediate elevations with more riparian habitat than available generally. They contained significantly less shrubland and non-vegetated lands (Fig. 2a, Table 2c). As in summer, winter home ranges had larger proportions of patches subjected to previous timber harvest (Figure 2b), both in the hypothesized optimum (10–29 years) regeneration age as well as both younger and older ages, regardless of type, than the study area generally.

Table 2. Top ranking resource selection models relating resource use to availability for adult female moose, Cabinet-Salish study area, northwestern Montana, 2013-2022.

a. Summer, 2nd order				
	Estimate	Standard error	<i>t</i>	<i>P</i>
Intercept	-13.500	1.100	-12.273	<0.001
Elevation	5.830	1.800	3.239	0.003
Elevation ²	-2.130	0.644	-3.307	0.002
Aspect	0.017	0.038	0.459	0.650
Topographic Position	0.812	0.793	1.024	0.314
Harvest age 10-29 years ^a	0.712	0.108	6.593	<0.001
Harvest other age ^a	0.457	0.088	5.205	<0.001
Harvest size	-1.61 ⁻⁰⁴	4.34 ⁻⁰⁴	-0.370	0.714
Non-vegetated ^b	-0.327	0.084	-3.902	<0.001
Mesic mixed conifer	0.409	0.116	3.526	<0.001
Pine ^b	0.121	0.106	1.142	0.262
Riparian ^b	0.553	0.126	4.389	<0.001
Shrubland ^b	-0.108	0.105	-1.029	0.312
Spruce-Fir ^b	0.470	0.108	4.352	<0.001
Steppe-Grassland ^b	0.046	0.119	0.387	0.701
Distance from highway	0.032	0.028	1.123	0.270
Distance to water	0.146	0.139	1.050	0.302

^aReference category: Unharvested

^bReference category: Dry mixed conifer

b. Summer, 3rd order, (Table 2, continued)

	Estimate	Standard error	<i>t</i>	<i>P</i>
Intercept	-17.700	1.700	-10.412	<0.001
Elevation	12.400	2.870	4.321	<0.001
Elevation ²	-4.460	1.190	-3.748	<0.001
Topographic Position	-9.820	1.360	-7.221	<0.001
Aspect	0.158	0.066	2.394	0.023
Canopy cover	0.031	0.007	4.433	<0.001
Canopy cover ²	-3.64 ⁻⁰⁴	7.46 ⁻⁰⁵	-4.879	<0.001
Harvested ¹	0.464	0.092	5.033	<0.001
Mesic Mixed Conifer ²	0.057	0.069	0.827	0.415
Pine ^b	-0.091	0.073	-1.251	0.220
Riparian ^b	1.540	0.137	11.241	<0.001
Distance to water	-0.468	0.169	-2.769	0.009

¹Reference category: Unharvested

²Reference category: Includes dry mixed conifer, spruce-fir, and shrublands

c. Winter, 2nd order (Table 2, continued)

	Estimate	Standard error	<i>t</i>	<i>P</i>
Intercept	-18.900	1.400	-13.500	<0.001
Elevation	16.600	2.360	7.034	<0.001
Elevation ²	-6.880	0.941	-7.311	<0.001
Aspect	0.015	0.047	0.317	0.753
Topographic Position	0.013	0.878	0.015	0.988
Mesic Mixed Conifer ^a	-0.015	0.103	-0.150	0.882
Non-vegetated ^a	-0.267	0.097	-2.747	0.010
Pine ^a	-0.109	0.065	-1.685	0.102
Riparian ^a	0.500	0.163	3.067	0.004
Shrubland ^a	-0.332	0.056	-5.982	<0.001
Harvest age 10-29 years ^b	0.851	0.100	8.544	<0.001
Harvest other age ^b	0.669	0.099	6.730	<0.001
Harvest size	0.001	0.001	1.596	0.121
Distance from highway	0.029	0.029	0.976	0.337
Distance from water	0.298	0.176	1.693	0.100

^aReference category: Combined dry mixed conifer, steppe-grassland, and spruce-fir

^bReference category: Unharvested

d. Winter, 3rd order (Table 2, continued)

	Estimate	Standard error	<i>t</i>	<i>P</i>
Intercept	-8.850	0.161	-54.969	<0.001
Canopy cover	0.007	0.006	1.2457	0.222
Canopy cover ²	-1.76 ⁻⁰⁴	5.31 ⁻⁰⁵	-3.315	0.002
Topographic index	3.370	1.830	1.842	0.075
Mixed mesic conifer ^a	0.047	0.069	0.686	0.498
Non-vegetated ^a	-0.290	0.105	-2.762	0.010
Pine	-0.267	0.070	-3.793	0.001
Harvested ^b	0.348	0.096	3.610	0.001
Distance from water	0.207	0.174	1.190	0.243

^aReference category: Includes dry mixed conifer, spruce-fir, shrubland, and riparian

^bReference category: Unharvested

Within their home ranges, moose in winter selected for lower canopy cover than available generally. They selected harvested over unharvested stands (Table 2d.), but avoided stands dominated by lodgepole or Ponderosa pine, as well as non-vegetated stands relative to dry mixed-conifer forests,

spruce-fir, and riparian areas. No selection or avoidance in elevation was found; however, in contrast to summer, moose selected for convex topography (i.e., ridges rather than valleys; Table 3d).

Viewed as predictive surfaces, the integrated RSFs illustrated complex and

Table 3. Comparison of models predicting biomass (g/m^2) of *Salix* spp. and *Ceanothus* spp. shrubs from biophysical variables included in top resource selection functions at either 2nd or 3rd order during either season, Cabinet-Salish study area, northwestern Montana, 2013-22. Reference category was dry forest.

	AIC	Δ AIC	k	weight
Vegetation type \times wildfire	277.7	0.0	11	0.4408
Wildfire + prescribed fire	278.3	0.6	3	0.3275
Wildfire	281.4	3.7	3	0.0710
Vegetation type	282.1	4.4	6	0.0490
Vegetation type \times (canopy cover + canopy cover ²)	282.6	4.9	7	0.0387
Elevation + elevation ²	284.5	6.7	4	0.0152
Timber harvest < 25 years old	284.5	6.8	3	0.0150
Canopy cover + canopy cover ²	284.9	7.2	3	0.0121
Timber harvest	285.2	7.5	5	0.0106

fine-scale juxtaposition of selected habitat resources during summer and winter. Selection against high elevations in winter (Fig. 3a) is seen in the prominent extent of white color on the western side of the study area where the Cabinet Mountains ridges and peaks exceed 2600 m, whereas selection for harvested areas in winter is evident by the

linear boundaries that typify cutting units. Selection for harvested areas in summer is illustrated similarly by darker color (Fig. 3b) and in contrast to winter, selection for higher elevations in the Cabinet Range is seen in more extensive color (green), although the narrow extent of white identifies avoidance of the highest ridges and peaks.

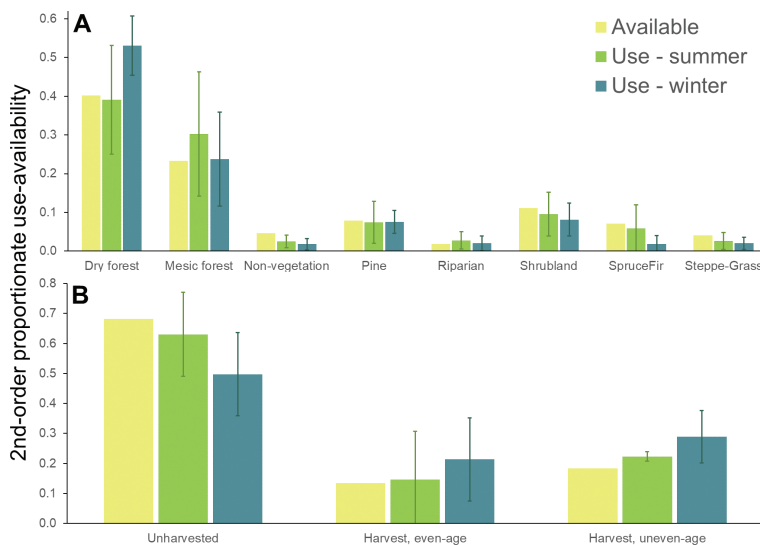


Fig. 2. Proportion of a. coarsely defined vegetation types, and b. coarsely defined timber harvest types used and available during summer and winter at the 2nd order of selection for adult female moose in the Cabinet-Salish study area, northwestern Montana, 2013-22. Error bars are standard error estimates.

Validation of both maps suggested that the models were reasonably predictive (Fig. 4). Patterns illustrating how used locations were distributed among equal-probability bins of map pixels were similar between seasons, and when using the locations used to generate the models and withheld locations collected in 2023. In all four validations, proportional use increased progressively according to the predicted quality of the 10 equal-area bins (Spearman's $\rho = 0.988$, $P < 0.001$, Fig. 4).

Functional Responses to Habitat Availability

Use of mesic forests in summer home ranges was higher than availability (most points were above the 1:1 line denoting use =

availability), but this modest selection was not related to the abundance of mesic forest (Fig. 5). Moose use of dry forests was slightly greater than relative abundance when that abundance was low, but crossed over so that it was lower than available when dry forests were plentiful within home ranges (slope = 0.59, 95% CI = 0.26–0.92; Figure 5). Pine forests were avoided at all levels of availability (Fig. 5). In contrast, moose exhibited selection for riparian habitats with no indication that preference for these habitats was saturated (slope = 3.47, 95% CI = 1.86–5.08) at even the highest proportions of availability within home ranges; albeit, availability was never high (Fig. 5).

Habitat selection patterns in winter were generally similar to those in summer, although

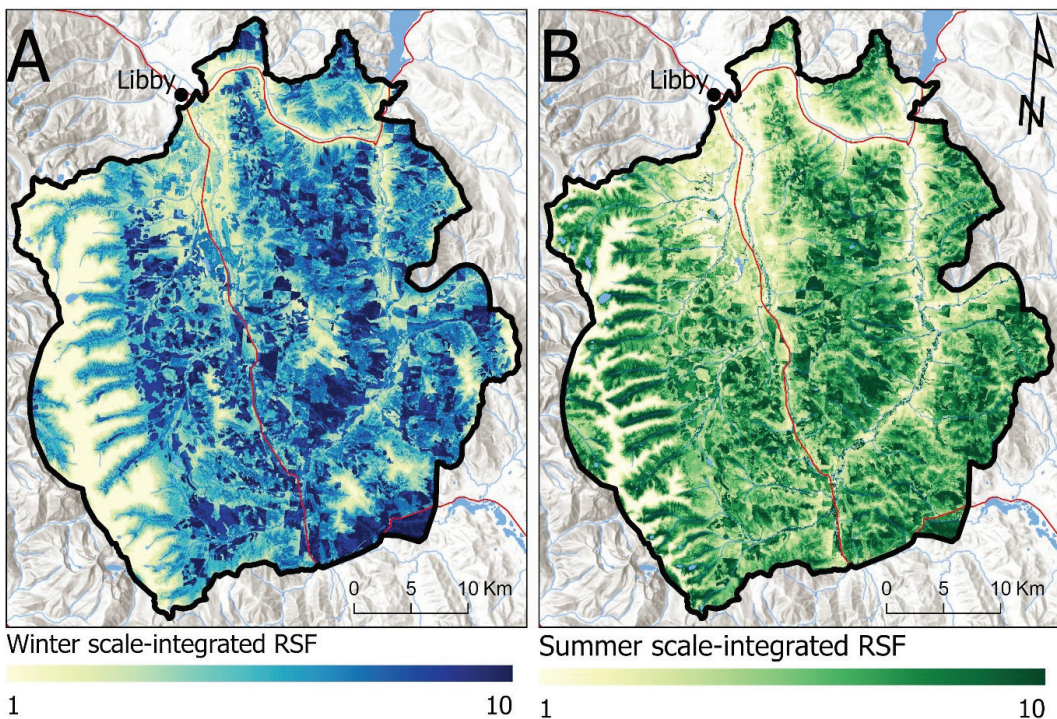


Fig. 3. Predictive maps of adult female moose habitat selection developed by integrating best-fitting resource selection function (RSF) equations at the 2nd and 3rd orders of selection and categorizing RSFs into 10 equal-area bins ranked from low (1) to high (10) relative probability of use during A) winter and B) summer seasons, northwestern Montana, 2013–22. Note that neither predictive map illustrates selection for burned areas because they could not be accommodated in the RSF approach.

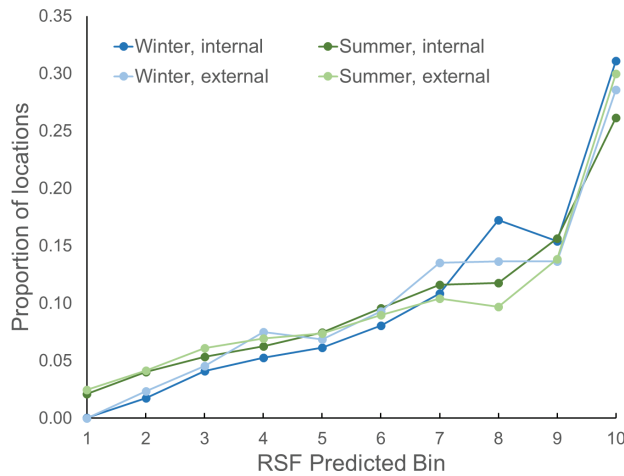


Fig. 4. Validation plots using moose location points used to develop the resource selection function (RSF) models for moose in the Cabinet-Salish mountains, 2013-22, in winter (n = 11,288) and summer (n = 10,835), as well as external validation using independent moose locations recorded during winter (n = 1,825) and summer (n = 2,511) of 2023.

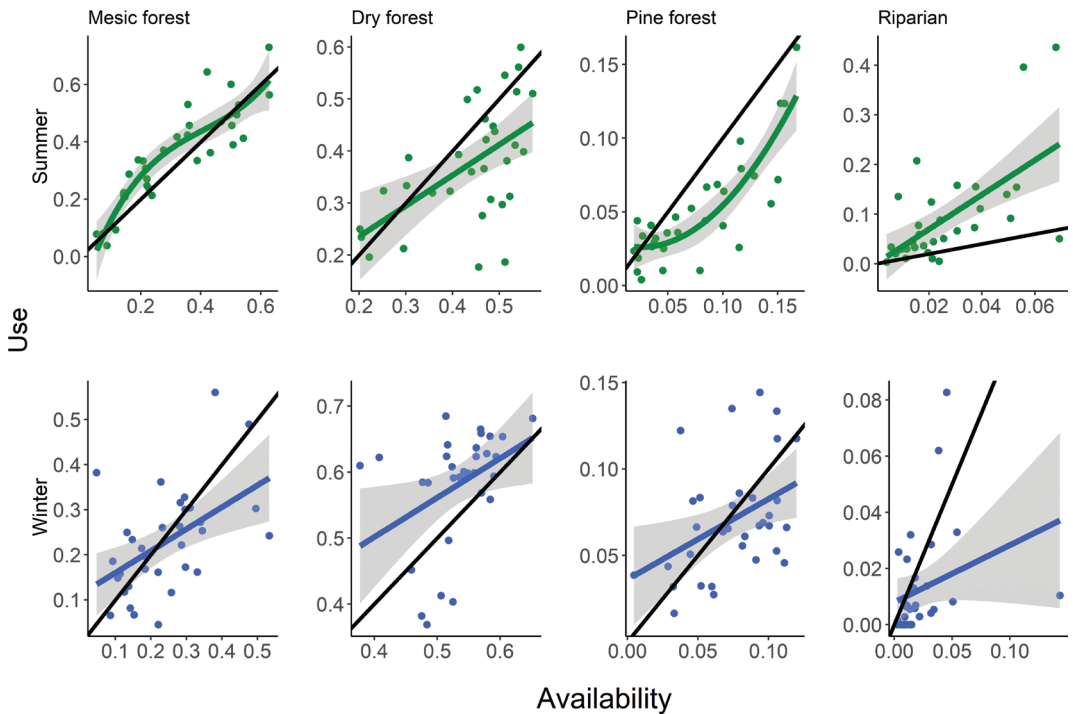


Fig. 5. Relationships characterizing functional responses in habitat use for adult female moose across 4 coarsely defined vegetation types and during summer and winter in the Cabinet-Salish study area of northwestern Montana, 2013-22. Data points represent proportions used by and available to 32 moose used to develop relationships: green (summer) and blue (winter) lines = best fitting regression (likelihood ratio test, $\alpha = 0.05$), gray shaded area represents 1 standard error. Solid black lines indicate proportional (used = available) habitat use. Note that scales differ among panels.

the magnitudes of preference were tempered. Use of the 4 vegetation types (mesic forest, dry forest, pine forest, riparian) tended to exceed availability in home ranges where the resource was relatively uncommon, but was less than availability when the resource was common; slopes were significantly < 1.0 for all but dry forests (Fig. 5).

Use of areas subjected to even-aged timber harvests (regardless of harvest age) was not different from availability in either season (Fig. 6). Moose displayed modest selection for areas of uneven-aged timber harvests in both seasons, with the magnitude of selection invariant across the range of availability (Fig. 6). Moose fell into either of two distinct categories in their relative use of undisturbed (i.e., unharvested) forest. Most animals used

these stands less than available, yet a few individuals used them nearly exclusively, particularly in summer when use by 5 moose was > 90% with 4 of 5 home ranges > 70% undisturbed forest (Fig. 6).

Use of recently harvested (< 10 years) stands varied with no clear pattern during summer, and winter use was not different from availability (Fig. 7). In contrast, most moose used 10–29 year-old harvested stands in greater proportion than availability (most points about the reference line) in both seasons; the preference level did not vary with proportional availability (95% confidence intervals included 1.0; Fig. 7). Use of older-aged (30+ year) cut areas was similar to availability in summer and higher than availability in winter (Fig. 7), although winter

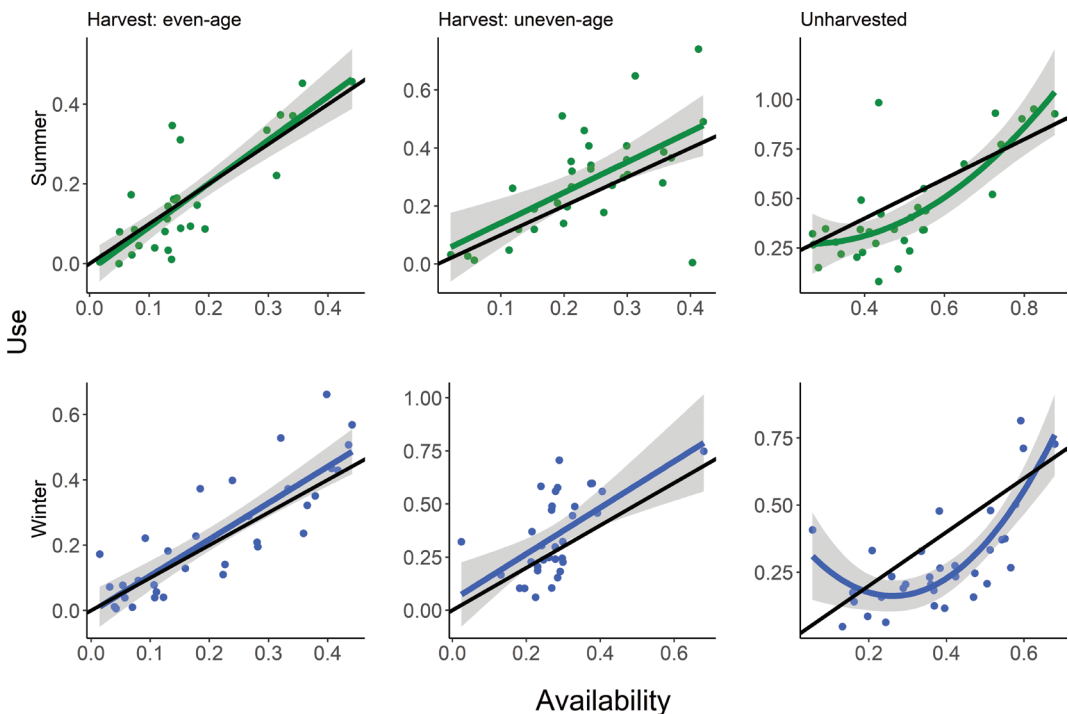


Fig. 6. Relationships characterizing functional responses in habitat use for adult female moose across 3 disturbance regimes in the Cabinet-Salish study area of northwestern Montana, 2013–22. Data points indicate 32 moose used to develop relationships: green (summer) and blue (winter) lines = best fitting regression (likelihood ratio test, $\alpha = 0.05$), gray shaded area represents 1 standard error. Solid black lines indicate proportional (used = available) habitat use. Note that scales differ among panels.

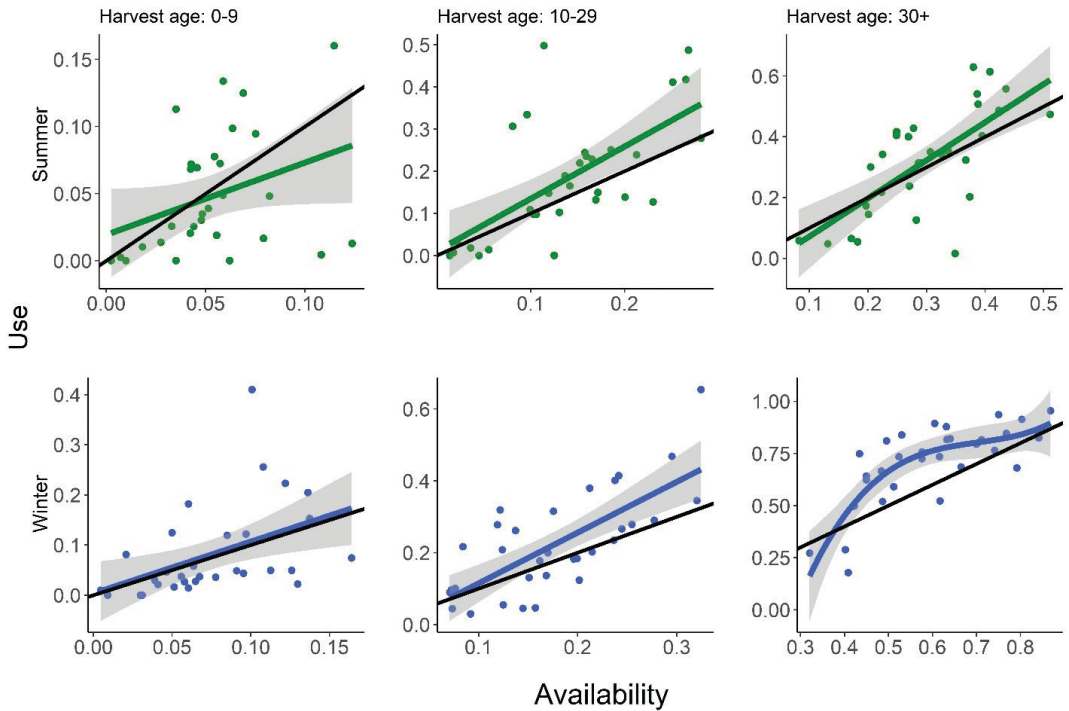


Fig. 7. Relationships characterizing functional responses in habitat use by age of timber harvest for adult female moose in the Cabinet-Salish study area of northwestern Montana, 2013-22. Data points indicate 32 moose used to develop relationships, green (summer), and blue (winter) lines = best fitting regression (likelihood ratio test, $\alpha = 0.05$), gray shaded area represents 1 standard error. Solid black lines indicate proportional (used = available) habitat use. Note that scales differ among panels.

preference declined gradually as these areas comprised $> 60\%$ of the home range (Fig. 7).

Burns were uncommon components of home ranges during summer ($\bar{x} = 2.2\%$, $SD = 3.7\%$, maximum = 16.7%) and winter ($\bar{x} = 0.8\%$, $SD = 1.4\%$, maximum = 6.0%). Use of burns was also uncommon, although use was usually higher than expected had there been no selection. Selection ratios were > 1.0 for 9 of the 12 seasonal comparisons of use and availability for wildfires that burned between 1990 and 2017 (Table S8). Use of burns by individual moose was typically higher in summer ($\bar{x} = 4.7\%$, $SD = 9.6\%$, maximum = 44.8%) than winter ($\bar{x} = 1.3\%$, $SD = 2.4\%$, maximum = 8.6%).

The greater selection for burns in summer than winter is also evident in the

functional response to burn availability (Fig. 8). Most moose with access to burns in summer used them more than available, although no strong relationship was found between selection and availability (slope = 1.52 , $95\% CI = 0.58-2.46$; Fig. 8). Both availability and use of burns were lower in winter (Fig. 8), and although a few moose preferentially used the small proportion of burns available, selection declined with availability (slope = 0.44 , $95\% CI = 0.16-0.73$). Considering both seasons together, use was highest for burns 26–35 years old relative to availability (Fig. 9).

Abundance of Shrubs

Categorized as vegetation types as per the RSF analyses, biomass of *Salix* and

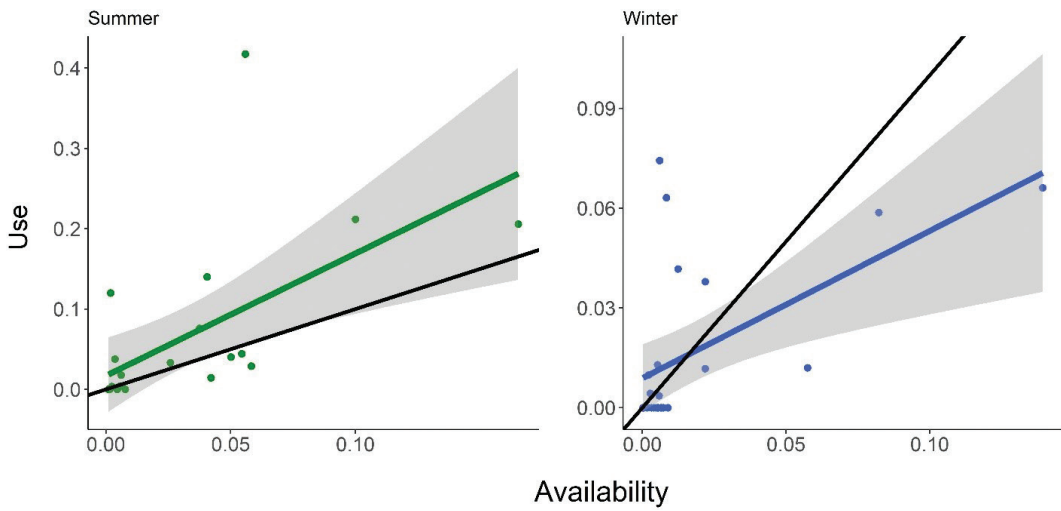


Fig. 8. Relationships characterizing functional responses in habitat use by use of recently burned area for adult female moose in the Cabinet-Salish study area of northwestern Montana, 2013-2022. Data points indicate 32 moose used to develop relationships: green (summer), and blue (winter) lines = best fitting regression (likelihood ratio test, $\alpha = 0.05$), gray shaded area represents 1 standard error. Solid black lines indicate proportional (used = available) habitat use. Note that scales differ among panels.

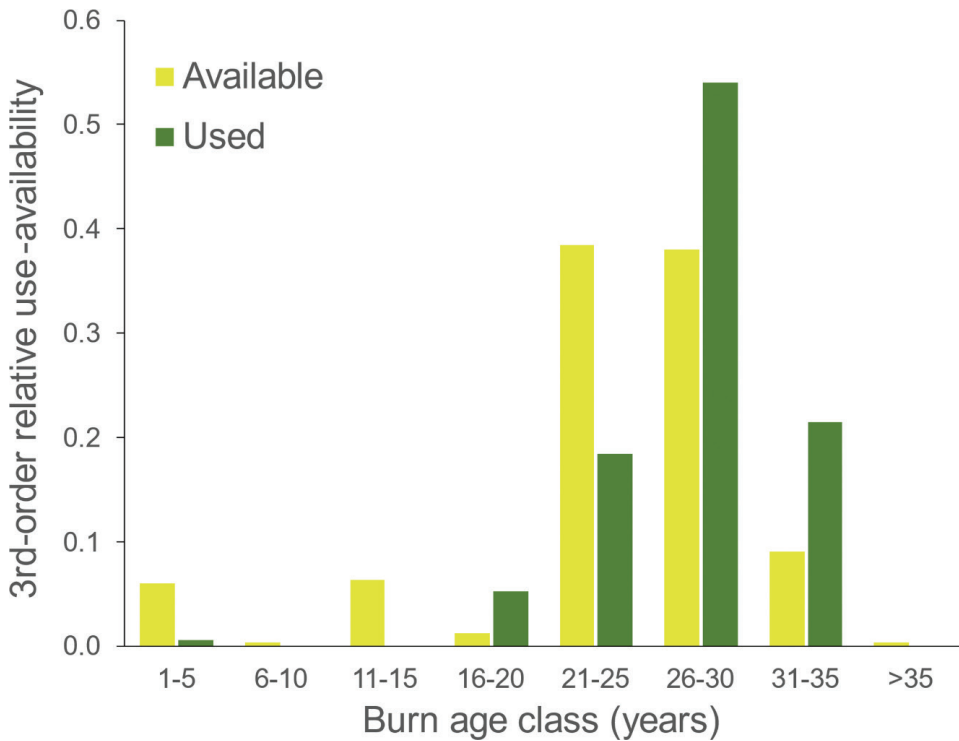


Fig. 9. Proportionate use and availability in burned areas by age-category for adult female moose with non-zero availability in their summer or winter home ranges Cabinet-Salish study area of northwestern Montana, 2013-2022.

Ceanothus varied but was generally highest in the steppe-grassland type and lowest in the mesic and pine forest types (Fig. 10a). Considered in terms of stand disturbance, mean biomass of both was significantly higher in stands categorized as having experienced wildfire (n = 37) than in uneven-aged timber harvest stands (n = 116), or in stands without disturbance (n = 128; Fig.

10b). No plots categorized as even-aged harvest (n = 19) had measurable biomass of either shrub.

The top model predicting biomass (g/m²) of *Salix* and *Ceanothus* incorporated the interaction of vegetation type with recent (< 35 years) wildfire, accounting for ~44% of model weight within the suite of candidate models (Table 3). Wildfire was present in the

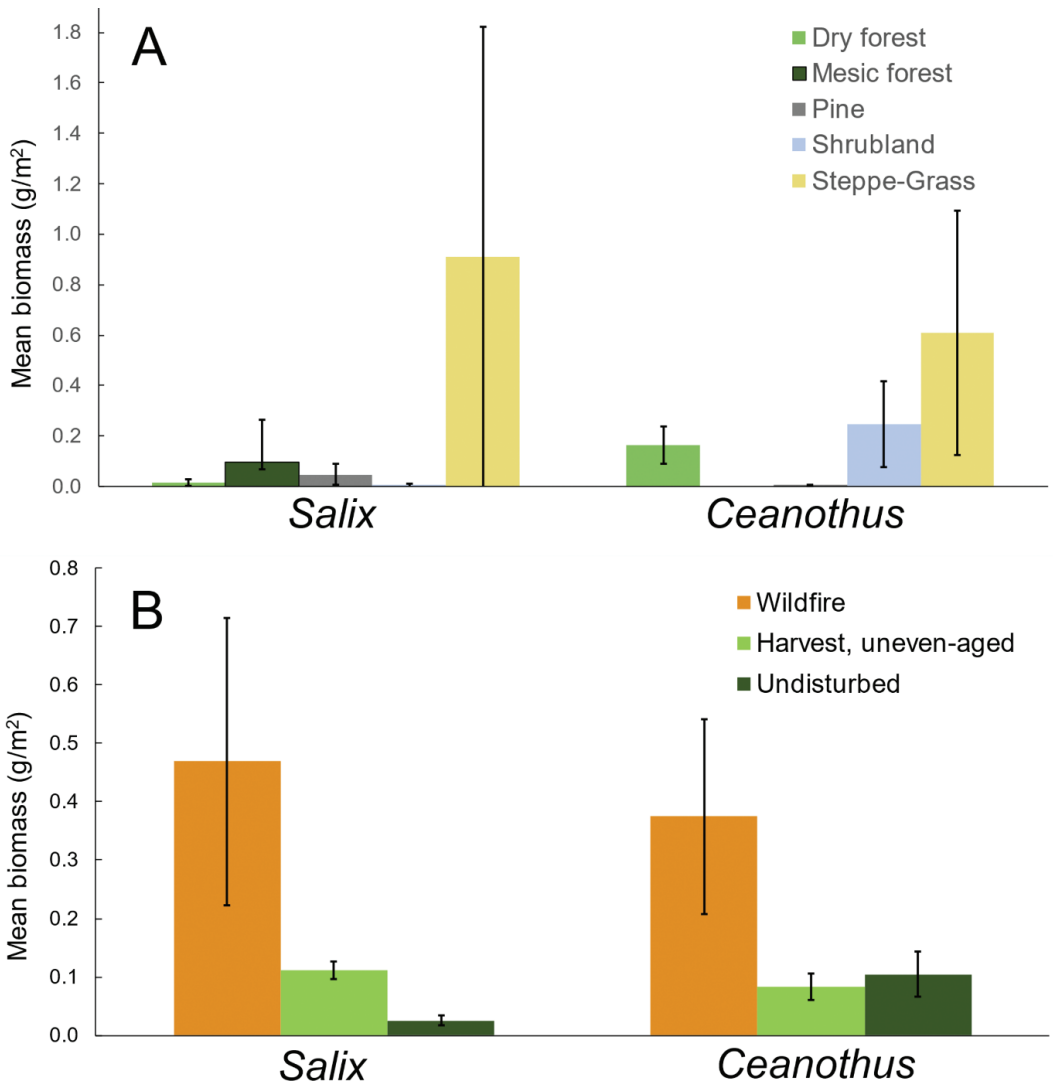


Fig. 10. Estimated mean biomass (g /m²) of shrub genera *Salix* and *Ceanothus* as estimated from 320 field plots measured by Hayes et al. (2022), and summarized by A) coarsely defined vegetation types and B) disturbance regimes, Cabinet-Salish study area of northwestern Montana, 2013-2022. Error bars represent standard errors.

top 3 models, together accounting for ~ 84% of model weight. These shrubs were predicted to be more available in steppe-grasslands and where wildfire occurred in vegetation types categorized as shrubland (Table 4).

Thermal Influences on Habitat Use

The top-ranked model predicting elevation used by moose in summer included maximum daily temperature, but not hour-of-day. Elevation was a positive function of daily maximum temperature (elevation used = $1085.0 + 2.350 [\pm 0.888 \text{ SE}] \text{ temperature}$; $t = 2.614$, $P = 0.014$). Similarly, the top-ranked model in winter included temperature (elevation used = $1146.0 + 2.10 [\pm 0.680 \text{ SE}] \times \text{temperature}$); $t = 3.099$, $P < 0.004$), but not hour-of-day.

The top-ranked model predicting use of canopy cover in summer included time-of-day, but not maximum daily temperature (Table S9a); use of canopy cover was highly correlated with Δt ($r = -0.936$, $P < 0.001$; Fig. 11a). That is, in early morning when the temperature differential as a function of canopy was positive (areas with denser canopy were warmer than sparser canopy areas), moose used forests with lower canopy cover.

In mid-afternoon, when the temperature differential as a function of canopy was negative (areas with denser canopy cover were cooler), moose tended to use more closed forest (Fig. 11a). In winter, both maximum daily temperature (canopy cover = $0.405 [\text{SE} = 0.091] \times \text{temperature}$; $t = 4.441$, $P < 0.001$) and time-of-day predicted use of canopy cover (Table S9b, Fig. 11b; interactions were not significant). That is, in addition to the circadian patterns (Fig. 11a, b), moose tended to use habitats with higher canopy cover when maximum daily temperatures were higher, and lower canopy cover when temperatures were lower. Use of canopy cover by time-of-day in winter was highly correlated with Δt ($r = -0.901$; $P < 0.001$).

In summer, the top-ranked model predicting TPI included both maximum daily temperature and time-of-day, but not their interaction. Accounting for hour-of-day, TPI was related to temperature (TPI = $-2.550 - 0.662 [\pm 0.149 \text{ SE}] \times \text{temperature}$; $t = -4.443$, $P < 0.001$). Use of topographic position appeared to lag a few hours behind the temperature differential associated with TPI (Fig. 11c). We found no correlation between Δt by hour-of-day and topographic position

Table 4. Top ranking model predicting biomass (g/m^2) of *Salix* spp. and *Ceanothus* spp. shrubs from biophysical variables included in top resource selection functions at either 2nd or 3rd order during either season, Cabinet-Salish study area, northwestern Montana, 2013-22. Reference category was dry forest.

	Coefficient	Standard error	<i>z</i>	<i>P</i>
Intercept	-1.957	0.326	-6.004	<0.001
Mesic forest	-1.193	0.912	-1.307	0.191
Pine	-1.176	1.076	-1.092	0.275
Shrubland	-2.188	1.395	-1.569	0.117
Steppe-Grassland	2.061	0.862	2.393	0.017
Wildfire	0.840	0.746	1.126	0.260
Mesic forest \times Wildfire	1.040	1.624	0.640	0.552
Pine \times Wildfire	-1.325	3.284	-0.403	0.687
Shrubland \times Wildfire	3.752	1.823	2.058	0.040
Steppe-Grassland \times Wildfire	-0.821	1.890	-0.434	0.664

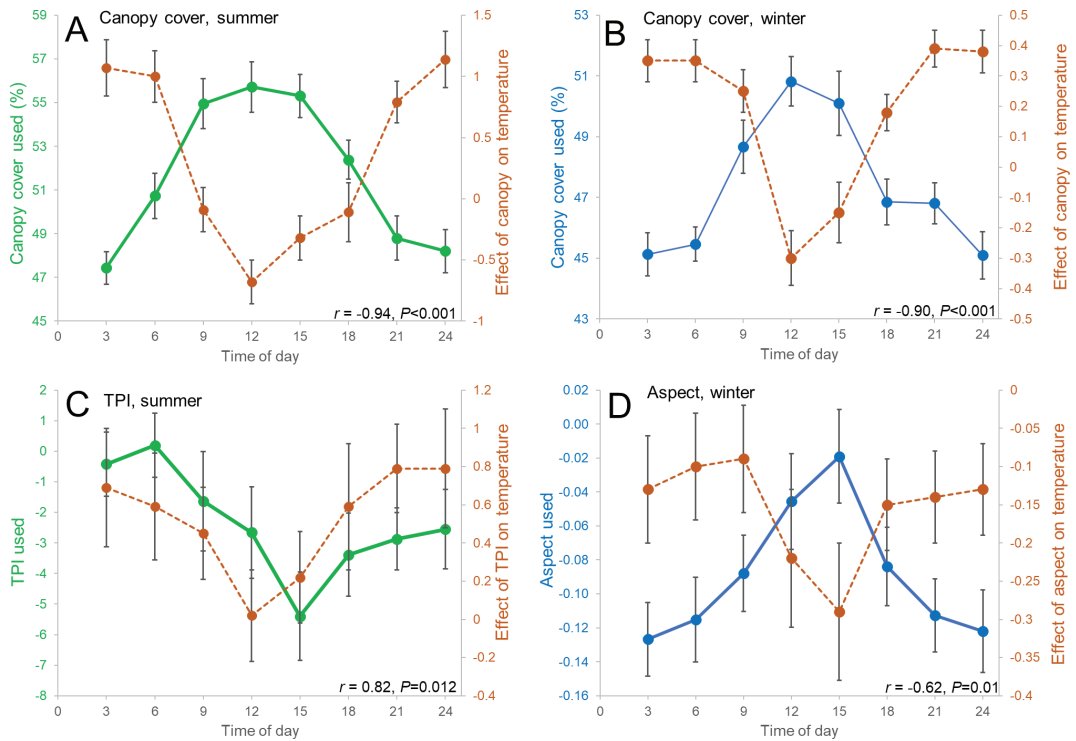


Fig. 11. Mean use of A) canopy cover during summer, B) canopy cover during winter, C) TPI during summer, and D) aspect during winter for moose by time of day and compared with the coefficient relating temperature differential (Δt) to those same environmental covariates (orange, from DeCesare et al. 2023), Cabinet-Salish study area of northwestern Montana, 2013-2022. Error bars represent standard errors.

in summer ($r = 0.373$, $P = 0.362$); however, there was a correlation between Δt by hour-of-day and topographic position that lagged by 3 h ($r = 0.822$, $P = 0.012$). We found no associations between winter use of topographic position and either maximum daily temperature or hour-of-day (all $P > 0.12$).

In summer, neither maximum daily temperature nor time of day predicted how moose used habitats with respect to topographic aspect. In winter, the top-ranked model predicting aspect included maximum daily temperature and time-of-day (accounting for hour-of-day, aspect = $-0.122 + 0.0166 [\pm 0.0026 \text{ SE}] \times \text{temperature}$; $t = 6.4844$, $P < 0.001$). Use of cooler aspects increased slightly during afternoon hours when cooling produced by their orientation relative to

ambient conditions was at its greatest magnitude; the correlation between mean aspect used by hour-of-day and Δt was -0.622 ($P = 0.01$; Fig. 11d).

DISCUSSION

Moose in the Cabinet-Salish mountains of northwestern Montana exhibited varied patterns in habitat use and selection, similar to other studies in which heterogeneity among individuals was examined (Gillingham and Parker 2008, Mabile et al. 2012, McCulley et al 2017). Some variation arose because individuals encountered different resource availability, and in some cases, the existence of specific resources within home ranges. Other variation may have reflected biological differences including individual nutritional

condition, reproductive status, or risk aversion (Bonnot et al. 2015, Walker et al. 2023). That said, some patterns appeared general and were evident in either the RSF analyses, functional responses to resource abundance, or both.

During winter moose selected intermediate elevations where non-vegetated and shrubland types were underrepresented and riparian areas overrepresented in home ranges. At a finer scale of selection, they tended to avoid unvegetated areas and pine-dominated forests. We also identified a modest tendency to select for convex topography (i.e., ridges) over concave topography (i.e., drainages) in winter. Use of vegetation type in winter appeared to be somewhat negatively frequency-dependent (e.g., Mabelle et al. 2012, Hoy et al. 2019), with use exceeding availability when the vegetation type was rare, but selectivity declining with increasing availability. These patterns were generally similar to those among moose living ~ 110 km to the northeast in the North Fork of the Flathead River (Langley 1993).

In summer moose selected intermediate elevations, mesic and spruce-fir forests, and areas with riparian zones to locate their home ranges. Riparian zones were strongly selected, with open areas (vegetated at the forb layer) were also selected (albeit less strongly). Riparian zones were strongly selected, although open areas (vegetated at the forb layer) were also selected (albeit less strongly). Additional support for selective use of riparian zones in summer included selection for concave topography (e.g., drainages) and proximity to water. The switch from use of convex slopes in winter to concave slopes in summer likely related to seasonal differences in the functional form associated with forested foothill ridges that provided ample harvested areas during winter, versus rockier alpine ridges surrounding migratory individuals in summer. Additionally, riparian habitat within drainages was always at a premium,

both on the landscape and within home ranges. However, selection for riparian zones in summer was not saturated even in home ranges with relatively large amounts of riparian habitat (Fig. 5); that is, moose selected riparian habitat regardless of its relative availability. We also observed a weak (non-significant) tendency for moose to use mesic forests more than their relative availability, and dry forests commensurately less. When dry forests (and forests dominated by pine) constituted a substantial proportion of home ranges, moose used them in lower proportion than availability.

In common with other studies in northwestern Montana (Matchett 1985, Langley 1993) and elsewhere (Brown et al. 2018) where dense conifer overstories proliferate in the absence of disturbance, we found that moose generally selected areas in which previous disturbance resulted in an early seral stage with reduced canopy cover. Most moose preferentially used stands that had either been logged or burned previously; however, a few individuals with minimal disturbance within their home range showed no inclination to select for disturbed areas. As in other studies (Matchett 1985, Julianus et al. 2019, Mumma et al. 2021), preference for disturbed forests was non-linear, with essentially no selection in the initial 10-years post-disturbance, high selection the following 2 decades, and gradual abatement thereafter. This pattern of highest selection during the intermediate-aged (~ 10–29 years) disturbance was evident regardless of whether the disturbance was in the form of timber harvest (Fig. 7) or wildfire (Fig. 9). In contrast with Matchett (1985), we found little evidence that even-aged harvesting was more attractive to moose than uneven-aged silvicultural treatments that retained various stages of overstory. If anything, among stands with a history of cutting, moose exhibited slightly greater selection for

multi-storied than single-storied stands (Fig. 2, 6). Although wildfires were rare in the study area and burns were encountered by only a few moose, they tended to be intensively used more than expected. During summer and among areas where wildfire had occurred 10-30 years earlier, selection for burn areas was strong and consistent regardless of the relative abundance of burns within home ranges (Fig. 8).

Timber harvest is often viewed as a surrogate for wildfire in opening the canopy, allowing more sunlight to reach the understory and encouraging growth of early successional, typically deciduous species a few years later (Hunter 1990, Rempel et al. 1997, Strong and Gates 2006). However, we noted substantial differences between timber harvest and wildfire in production of some key shrubs. In particular, *Salix* and *Ceanothus* had significantly higher biomass (unit per area basis) in burns than in harvested and unharvested areas. Both *Salix* spp. (particularly *S. scouleriana*, Bedunah et al. 1999) and *Ceanothus velutinus* are considered fire-adapted species that increase after most burns (Fischer and Bradley 1987, Smith and Fischer 1997). Moose in the nearby Yaak River drainage used *Ceanothus* heavily, and Matchett (1985) recommended that post-harvest burning be employed to favor this shrub because its seed germination is stimulated by heat (Arno et al. 1986, Makela 1990). Given the importance of these species in the diets of moose and the rarity of burns on the landscape, consideration of diet and plant composition further reinforces the potential value of burns to moose in this area.

Because vegetation plots were not distributed randomly across the study area (i.e., plot abundance was not necessarily proportional to the abundance of vegetation types), we lacked a rigorous way to estimate relative abundance of these shrub species within the study area. However, consideration of shrub

biomass within vegetation types (Fig. 10a) in the context of the proportional abundance of vegetation and harvest types makes clear that neither *Ceanothus* spp. nor *Salix* spp. were common. Both species achieved their highest biomass in the steppe-grass type, but this vegetation type constituted only ~ 1.4% of the study area. Neither were abundant or common in the dry or mesic forest types which together constituted ~ 82% of the study area. Conversely, *Salix* and *Ceanothus* were relatively abundant following wildfire (Fig. 10a), but burns constituted < 1.9% of the study area.

Given their dependence on shrubs for forage, it appears counterintuitive that moose selected against the vegetation types we collapsed into the category “shrublands” at the 2nd-order (landscape) level of selection (albeit, not at the 3rd-order of selection in summer, Fig. 2a). Some insight into this seeming contradiction comes from an examination of the vegetation communities categorized as shrubland types by NatureServe (2018) that we collapsed into a single “shrubland” type. Approximately 69.6% of shrublands were located either in recent (< 10 year-old) timber harvests for which moose exhibited no selection (Fig. 7), or in recent burns which our analyses suggested were avoided by moose (Fig. 9). An additional 19.7% of shrublands were located at high elevations above 99% of summer moose locations (1730 m), and associated with avalanche chutes and alpine vegetation. Finally, our analyses of vegetation data found that *Salix* and *Ceanothus* were somewhat (not significantly) less abundant in the shrubland category than in the steppe-grass category (Fig. 10a) and the most abundant dry forest category (Table 4), unless fire had been present. Thus, we interpret the lack of an expected selection for shrublands as reflecting characteristics of the remote sensing-based categorization rather than aversion to or lack of selection for shrubs per se.

DeCesare et al. (2023) showed that, at any given time, the expected temperature varied significantly at sites within the Cabinet-Salish Mountains study area. Summer, canopy cover, elevation, and TPI were all important in predicting the degree to which sites diverged from the average ambient temperature. The amplitude of divergence among sites was quite large, averaging 7.6 °C at any given time, and up to 20.5 °C. Further, the relationships between these habitat characteristics and temperatures varied by time of day. Whether conditions were warmer or cooler than the study area as a whole typically reversed between mid-day and nocturnal hours. However, the DeCesare et al. (2023) study was not designed to determine whether moose responded behaviorally (moved) to access any perceived advantage of these site-specific thermal characteristics.

Our analyses demonstrated that maximum daily temperatures were significant predictors of elevation and topographic positions selected by moose in summer, and of elevation, canopy cover, and aspects selected by moose in winter. In all 5 cases, selection was positive for sites that were likely to be cooler than warmer. Further, our analyses demonstrated that regardless of the maximum temperature on any given day, moose tended to use topographic position (in summer), aspect (in winter), and canopy cover (in both seasons) according to circadian patterns that matched when sites were likely cooler than the average condition in the study area. We acknowledge that, although we know these circadian patterns matched known temperature patterns, they remain correlational whose causes could have resided elsewhere (for example, avoiding predators, Kohl et al. 2018, Johnson-Bice et al. 2023).

Our results on moose responses to temperature have 3 related implications. The first is that all inferences from the RSF maps and functional response curves should be

understood as applying on average, across thermal conditions that influenced moose behavior and location. Underlying all analyses are our findings that moose made different decisions during day and night, and in some cases, during generally warm or cool days. The second implication is that moose in the study area were able to respond to any preference in thermal condition via short-distance movements. We observed diurnal patterns in use of canopy cover, topographic positions, and aspects, but not in elevation. Importantly, the first 3 characteristics vary on a fine geographic scale, but moose would have to travel further distances to realize a substantial difference in elevation. The third implication is that as in most studies where investigated (e.g., Dussault et al. 2004, Melin et al. 2014, Street et al. 2015a, 2016, Borowik et al. 2020, Burkholder et al. 2022), moose habitat use in the Cabinet-Salish area was influenced by fine-scale thermal properties. Although we focused here on examining use of habitat resources quantified by the continuous variables found important (e.g., canopy cover) by DeCesare et al. (2023), these in turn were correlated with the thermal properties of vegetation types in the study area. For example, a post-hoc examination of hourly use of shrublands by collared moose showed the proportion of location in shrublands was high during nocturnal hours and lower in daytime (Fig. S2). In both summer and winter, moose made subtle adjustments in their overall habitat selection to prioritize occupying cooler than warmer sites.

Where supporting moose populations in mesic, coniferous forests such as in northwestern Montana is an objective, forest managers are faced with some complexity. Creating early seral conditions will generally encourage production of shrubs important as moose forage. However, we found that wild-fire was more likely than timber harvests to produce shrubs preferred by moose (i.e., *Salix* and *Ceanothus*), and that moose slightly

preferred uneven-aged more than even-aged harvested stands. Further, managers should not expect an immediate response in moose use as we found no evidence of selection during the initial decade post-disturbance. Ideally, early seral stands would be located proximate to stands providing denser canopy to provide an optimal mix of forage and cover providing thermal relief during seasonally warm periods (summer and winter) and the warmest hours of the day.

ACKNOWLEDGEMENTS

Funding for this project was provided by the general sale of hunting and fishing licenses in Montana, the annual auction of a male Shiras moose hunting license (MCA 87-2-724), Federal Aid in Wildlife Restoration Grants W-154-R and W-157-R1 through W-157-R7, and the Safari Club International Foundation. We thank Stoltze Land & Lumber, Weyerhaeuser, and the many private landowners and area residents who graciously allowed us to conduct captures and ground monitoring on their properties. We thank the anonymous reviewers for helpful reviews of previous versions of the manuscript. We express appreciation to the biologists and pilots who collected data during the study, including J. Coltrane, B. Malo, J. Rahn, J. Ramsey, R. Swisher, , and J. Williams. We thank T. Chilton-Radandt, J. Gude, and N. Anderson, Montana FWP for advice and discussion.

SUPPLEMENTARY MATERIAL

Supplementary data are available with the article at <https://alcesjournal.org/index.php/alces/article/view/1945>.

LITERATURE CITED

- ALSTON, J. M., M. J. JOYCE, J. A. MERKLE, and R. A. MOEN. 2020. Temperature shapes, movement, and habitat selection by a heat-sensitive ungulate. *Landscape Ecology* 35: 1961–1973. <https://doi.org/10.1007/s10980-020-01072-y>.
- ARNO, S. F., D. G. SIMMERMAN, and R. E. KEANE. 1986. Characterizing succession within a forest habitat type – an approach designed for resource managers. Research Note INT-357. U. S. Department of Agriculture Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- BEDUNAH, D. J., M. G. HARRINGTON, and D. M. AYERS. 1999. Antelope bitterbrush and Scouler’s willow response to a forest restoration project. Pages 256–259 in D. E. McArthur, W. K. Ostler, and C. L. Wambolt, compilers. Proceedings RMRS-P-11, Shrubland Ecotones. 12–14 August 1998, Ephraim, Utah. Intermountain Research Station, US Department of Agriculture Forest Service, Ogden, Utah, USA.
- BEYER, H. L., D. T. HAYDON, J. M. MORALES, J. L. FRAIR, M. HEBBLEWHITE, M. MITCHELL, and J. MATTHIOPOULOS. 2010. The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2245–2254.
- BJØRNERAAS, K., I. HERFINDAL, E. J. SOLBERG, B-E SÆTHER, B. VAN MOORTER, and C. M. ROLANDSEN. 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. *Oecologia* 168: 231–243.
- BONNOT, N., H. VERHEYDEN, P. BLANCHARD, J. COTE, L. DEBEFFE, B. CARGNELUTTI, F. Klein, A. M. HEWISON, and N. MORELLET. 2015. Interindividual variability in habitat use: evidence for a risk management syndrome in roe deer? *Behavioral Ecology* 26: 105–114.
- BOROWIK, T., M. RATKIEWICZ, W. MAŚLANKO, N. DUDA, and R. KOWALCZYK. 2020. Too hot to handle: summer space use shift in

- a cold-adapted ungulate at the edge of its range. *Landscape Ecology* 353: 1341–1351. <https://doi.org/10.1007/s10980-020-01018-4>.
- BOWYER, R. T., V. VAN BALLEMBERGHE, and J. G. KIE. 2003. Moose (*Alces alces*). Pages 931–964 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. *Wild Mammals of North America*. 2nd Edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.
- BOYCE, M. S., P. R. VERNIER, S. E. NIELSEN, and F. K. A. SCHMIEGELOW. 2002. Evaluating resource selection functions. *Ecological Modelling* 157: 281–300.
- BROOKS, M. E., K. KRISTENSEN, K. J. VAN BENTHEM, A. MAGNUSSON, C. W. BERG, A. NIELSEN, H. J. SKAUG, M. MAECHLER, and B. M. BOLKER. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9: 378–400. <https://doi.org/10.32614/RJ-2017-066>.
- BROWN, C. L., K. KIELLAND, E. S. EUSKIRCHEN, T. J. BRINKMAN, R. W. RUESS, and K. A. KELLIE. 2018. Fire-mediated patterns of habitat use by male moose (*Alces alces*) in Alaska. *Canadian Journal of Zoology* 96: 183–192.
- BURKHOLDER, B. O., R. B. HARRIS, N. J. DECESARE, S. J. BOCCADORI, and R. A. GARROTT. 2022. Winter habitat selection by female moose in southwestern Montana and effects of snow and temperature. *Wildlife Biology* 2022: e01040.
- BURNHAM, K. P., and D. R. ANDERSON. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd Edition. Springer, New York, New York, USA.
- CALENGE, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197: 516–519
- DECESARE, N. J., R. B. HARRIS, J. R. NEWBY, and C. J. PETERSON. 2023. Spatial and temporal heterogeneity in thermal conditions for wildlife. *Alces* 59: 35–51.
- _____, M. HEBBLEWHITE, F. SCHMIEGELOW, D. HERVIEUX, G. J. MCDERMID, L. NEUFELD, M. BRADLEY, J. WHITTINGTON, K. G. SMITH, L. E. MORGANTINI, M. WHEATLEY, and M. MUSIANI. 2012. Transcending scale dependence in identifying habitat with resource selection functions. *Ecological Applications* 22: 1068–1083.
- _____, C. J. PETERSON, and R. B. HARRIS. 2022. Vital Rates, Limiting Factors, and Monitoring Methods for Moose in Montana. Annual Report, September 2022. Federal Aid in Wildlife Restoration Grant W-157-R-7. Montana Fish, Wildlife and Parks, Helena, Montana, USA.
- _____, T. D. SMUCKER, R. A. GARROTT, and J. A. GUDE. 2014. Moose status and management in Montana. *Alces* 50: 35–51.
- DUSSAULT, C., J-P. OUELLET, R. COURTOIS, J. HUOT, J. BRETON, and J. LAROCHELLE. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. *Ecoscience* 11: 321–328.
- FIEBERG, J., J. MATTHIOPOULOS, M. HEBBLEWHITE, M. S. BOYCE, and J. L. FRAIR. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical Transactions of the Royal Society B* 365: 2233–2244.
- FISCHER, W. C., and A. F. BRADLEY. 1987. *Fire Ecology of Western Montana Forest Habitat Types*. General Technical Report INT-22. USDA Forest Service Intermountain Research Station, Ogden, Utah, USA.
- FRAIR, J. L., J. FIEBERG, M. HEBBLEWHITE, F. CAGNACCI, N. J. DECESARE, and L. PEDROTTI. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2187–2200.
- FRANCIS, A. L., C. PROCTER, G. KUZYK, and J. T. FISHER. 2021. Female moose prioritize

- forage over mortality risk in harvested landscapes. *Journal of Wildlife Management* 85: 156–168.
- GILLINGHAM, M. P., and PARKER, K. L. 2008. The importance of individual variation in defining habitat selection by moose in northern British Columbia. *Alces* 44: 7–20.
- HAYES, T. A., N. J. DECESARE, C. J. PETERSON, C. J. BISHOP, and M. S. MITCHELL. 2022. Trade-offs in forest disturbance management for plant communities and ungulates. *Forest Ecology and Management* 506: 119972.
- HOLBROOK, J. D., L. E. OLSON, N. J. DECESARE, M. HEBBLEWHITE, J. R. SQUIRES, and R. STEENWEG. 2019. Functional responses in habitat selection: clarifying hypotheses and interpretations. *Ecological Applications* 29: 1–15.
- HOY, S. R., J. A. VUCETICH, R. S. LIU, D. L. DEANGELIS, R. O. PETERSON, L. M. VUCETICH, and J. J. HENDERSON. 2019. Negative frequency-dependent foraging behavior in a generalist herbivore *Alces* and its stabilizing influence on food web dynamics. *Journal of Animal Ecology* 88: 1291–1304.
- HUNTER, M. L. Jr. 1990. *Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- JENKINS, K. J., and R. G. WRIGHT. 1988. Resource partitioning and competition among cervids in the northern Rocky Mountains. *Journal of Applied Ecology* 25: 11–24.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65–71.
- JOHNSON-BICE, S., T. D. GABLE, A. T. HOMKES, S. K. WINDELS, J. K. BUMP, and J. G. BRUGGINK. 2023. Logging, linear features and human infrastructure shape the spatial dynamics of wolf predation on an ungulate neonate. *Ecological Applications* 33: e2911.
- JULIANUS, E., T. N. HOLLINGSWORTH, A. D. MCGUIRE, and K. KIELLAND. 2019. Availability and use of moose browse in response to post-fire succession on Kanuti National Wildlife Refuge, Alaska. *Alces* 55: 67–89.
- KIE, J. G., J. MATTHIOPOULOS, J. FIEBERG, R. A. POWELL, F. CAGNACCI, M. S. MITCHELL, J. GAILLARD, and P. R. MOORCROFT. 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2221–2231.
- KNOWLTON, F. F. 1960. Food habits, movements and populations of moose in the Gravelly Mountains, Montana. *Journal of Wildlife Management* 24: 162–170.
- KOHL, M. T., D. R. STAHLER, M. C. METZ, J. D. FORESTER, M. J. KAUFFMAN, N. VARLEY, P. J. WHITE, D. W. SMITH, and D. R. MACNULTY. 2018. Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs* 88: 638–652.
- KUFELD, R. C., and BOWDEN, D. C. 1996. Movements and habitat selection of Shiras moose (*Alces shirasi*) in Colorado. *Alces* 32: 85–99.
- LANDFIRE. 2020. Existing Vegetation Types (EVT) CONUS. <<https://www.landfire.gov/>> (accessed April 2023).
- LANGLEY, M. A. 1993. Habitat selection, mortality and population monitoring of Shiras moose in the North Fork of the Flathead River Valley, Montana. M. S. Thesis. University of Montana, Missoula, Montana, USA.
- LÜDECKE, D., M. S. BEN-SHACHAR, I. PATIL, P. WAGGONER, and D. MAKOWSKI. 2021. Performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software* 6 (60): 3139. 10.21105/joss.03139.
- MABILLE, G., C. DUSSAULT, J-P. OUELLET, and C. LAURIAN. 2012. Linking trade-offs in habitat selection with the occurrence of functional responses for moose living in

- two nearby study areas. *Oecologia* 170: 965–977.
- MAKELA, P. D. 1990. Effects of prescribed burning on the Burdette Creek winter range. M. S. Thesis. University of Montana, Missoula, Montana, USA.
- MANLY, B. F., McDONALD, L., D. THOMAS, T. McDONALD, and W. ERICKSON. 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Second Edition. Kluwer Academic Publishers, Boston, Massachusetts, USA.
- MATCHETT, M. R. 1985. Habitat selection by moose in the Yaak river drainage, northwestern Montana. *Alces* 21: 161–189.
- MCCANN, N. P., R. A. MOEN, and T. R. HARRIS. 2013. Warm-season heat stress in moose *Alces alces*. *Canadian Journal of Zoology* 91: 893–898.
- MCCULLEY, A. M., K. L. PARKER, and M. P. GILLINGHAM. 2017. Yukon moose: I. Seasonal resource selection by males and females in a multi-predator boreal ecosystem. *Alces* 53: 113–136.
- MCCUNE, B., and D. KEON. 2002. Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* 13: 603–606. <https://doi.org/10.1111/j.1654-1103.2002.tb02087.x>.
- MELIN, M., J. MATALA, L. MEHTÄTALO, R. TILIKAINEN, O-P. TAKKANEN, M. MALTAMO, J. PUSENIUS, and P. PACKALEN. 2014. Moose (*Alces alces*) reacts to high summer temperatures by utilizing thermal shelters in boreal forests – an analysis based on airborne laser scanning of the canopy structure at moose locations. *Global Change Biology* 20: 1115–1125.
- MUFF, S., J. SIGNER, J., and J. FIEBERG. 2020. Accounting for individual specific variation in habitat-selection studies: efficient estimation of mixed-effects models using Bayesian or frequentist computation. *Journal of Animal Ecology* 89: 80–92.
- MUMMA, M. A., M. P. GILLINGHAM, S. MARSHALL, C. PROCTER, A. R. BEVINGTON, and M. SCHEIDEMAN. 2021. Regional moose (*Alces alces*) responses to forestry cutblocks are driven by landscape-scale patterns of vegetation composition and regrowth. *Forest Ecology and Management* 481: 118763.
- MURTAUGH, P. A. 2007. Simplicity and complexity in ecological data analysis. *Ecology* 88: 56–62.
- MYSTERUD, A., and R. A. IMS. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* 79: 1435–1441.
- NATURESERVE. 2018. *International Ecological Classification Standard: Terrestrial Ecological Classifications*. NatureServe Central Databases, Arlington, Virginia, USA. (Data current as of 28 August 2018).
- NEWBY, J. R., and DECESARE, N. D. 2020. Multiple nutritional currencies shape pregnancy in a large herbivore. *Canadian Journal of Zoology* 98: 307–315.
- PEEK, J. M. 1998. Habitat relationships. Pages 351-376 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and Management of the North American Moose*. Smithsonian Institution Press, Washington, D. C., USA.
- PETERSON, C. J., N. J. DECESARE, T. A. HAYES, C. J. BISHOP, and M. S. MITCHELL. 2022. Consequences of migratory strategy on habitat selection by mule deer. *Journal of Wildlife Management* 86: e22135.
- PIERCE, D. J., and J. M. PEEK. 1984. Moose habitat use and selection patterns in north central Idaho. *Journal of Wildlife Management* 48: 1335–1343.
- POOLE, K. G., and K. STUART-SMITH. 2005. Fine-scale winter habitat selection by moose in interior montane forests. *Alces* 41: 1–8.
- PROFFITT, K. M., J. DEVOE, K. BARKER, R. DURHAM, T. HAYES, M. HEBBLEWHITE, C. JOURDONNAIS, P. RAMSEY, and J. SHAMHART. 2019. A century of changing fire management alters ungulate forage in a wildfire-dominated landscape. *Forestry* 92: 523–537.

- R CORE TEAM. 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- REMPPEL, R. S., P. C. ELKIE, A. R. RODGERS, and M. J. GLUCK. 1997. Timber-management and natural-disturbance effects on moose habitat: landscape evaluation. *Journal of Wildlife Management* 61: 517–524.
- RENECKER, L. A., and C. C. SCHWARTZ. 1998. Food habits and feeding behaviour. Pages 403–439 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and Management of the North American Moose*. Smithsonian Institution Press, Washington, D.C., USA.
- SCHWAB, F. E., and M. D. PITT. 1991. Moose selection of canopy cover types related to operative temperature, forage and snow depth. *Canadian Journal of Zoology* 69: 3071–3077.
- SHIPLEY, L. 2010. Fifty years of food and foraging in moose: lessons in ecology from a model herbivore. *Alces* 46: 1–13.
- SCHREMPP, T. V., J. L. RACHLOW, T. R. JOHNSON, L. A. SHIPLEY, R. A. LONG, J. L. AYCRIGG, and M. A. HURLEY. 2019. Linking forest management to moose population trends: the role of the nutritional landscape. *PlosOne* 14: e0219128.
- SMITH, J. K., and W. C. FISCHER. 1997. Fire Ecology of the Forest Habitat Types of Northern Idaho. General Technical Report INT-GTR-363. U. S. Department of Agriculture Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- STEPHENSON, T. R., V. VAN BALLEMBERGHE, J. M. PEEK, and J. G. MACCRACKEN. 2006. Spatio-temporal constraints on moose habitat and carrying capacity in coastal Alaska: vegetation succession and climate. *Rangeland Ecology and Management* 59: 359–72.
- STREET, G. M., J. FIEBERG, A. R. RODGERS, M. CARSTENSEN, R. MOEN, S. A. MOORE, S. K. WINDELS, and J. D. FORESTER. 2016. Habitat functional response mitigates reduced foraging opportunity: implications for animal fitness and space use. *Landscape Ecology* 31: 1939–1953.
- _____, A. R. RODGERS, and J. M. FRYXELL. 2015a. Mid-day temperature variation influences seasonal habitat selection by moose. *Journal of Wildlife Management* 79: 505–512.
- _____, L. M. VANDER VENNEN, T. AVGAR, A. MOSSER, M. L. ANDERSON, A. R. RODGERS, and J. M. FRYXELL. 2015b. Habitat selection following recent disturbance: model transferability with implications for management and conservation of moose (*Alces alces*). *Canadian Journal of Zoology* 93: 813–821.
- STRONG, W. L., and C. C. GATES. 2006. Herbicide-induced change to ungulate forage habitat in western Alberta, Canada. *Forest Ecology and Management* 222: 469–475.
- TYERS, D. B. 2003. Winter ecology of moose on the northern Yellowstone winter range. Ph. D. Dissertation. Montana State University, Bozeman, Montana, USA.
- USFS (United States Forest Service). 2023. Timber Harvests. ESRI geodatabase. <<https://data.fs.usda.gov/geodata/edw/datasets.php>> (accessed March 2023).
- USGS (United State Geological Survey). 2019. 3D elevation program 30-meter resolution digital elevation model. <<https://www.usgs.gov/3d-elevation-program>> (accessed March 2023).
- VAN BEEST, F. M., B. VAN MOORTER, and J. M. MILNER. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Animal Behaviour* 84: 723–735.
- VAN DYKE, F. B. L. PROBERT, and G. M. VAN BEEK. 1995. Seasonal habitat use characteristics of moose in south-central Montana. *Alces* 31: 15–26.
- WALKER, R. H., M. C. HUTCHINSON, A. B. POTTER, J. A. BECKER, R. A. LONG and R.

- M. PRINGLE. 2023. Mechanisms of individual variation in large herbivore diets: roles of spatial heterogeneity and state-dependent foraging. *Ecology* 104(2): p.e3921.
- WEISS, A.D. 2001. Topographic Position and Landforms Analysis. Poster Presentation, ESRI User Conference. San Diego, California, USA. <<http://www.jennessent.com/downloads/tpi-poster-tnc>> (accessed March 2023).
- WILSON, A. M., and P. D. MILES. 2000. Forest Resources of the Kootenai National Forest. USDA Forest Service Rocky Mountain Research Station, Ogden, Utah, USA.
- ZEILEIS, A., and T. HOTHORN. 2002. Diagnostic checking in regression relationships. *R News* 2(3): 7–10.
- ZUUR, A., E. IENO, and G. SMITH. 2007. *Analyzing Ecological Data*. 10.1007/978-0-387-45972-1.