

FINE-SCALE WINTER HABITAT SELECTION BY MOOSE IN INTERIOR MONTANE FORESTS

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ABSTRACT: Clarification of animal activity during habitat studies may facilitate understanding of the complexities of habitat selection. Animal activity is difficult to determine with remote monitoring (e.g., GPS collars). We used snow-tracking and vegetation sampling to examine site-level habitat selection by moose (*Alces alces*) within late-winter range in montane forests in southeastern British Columbia. We assessed vegetation characteristics within systematically placed available plots, and moose use plots, divided into foraging and travelling plots. Willow (*Salix* spp.), red-osier dogwood (*Cornus stolonifera*), and saskatoon (*Amelanchier alnifolia*), together termed “moose shrubs”, made up 83% of browse events recorded. Moose foraging plots had greater coverage of total shrub, moose shrub, and willow, lower canopy cover, and fewer trees than available and travelling plots; snow depth did not influence moose foraging activity. Moose foraging areas had 2.4 times more total shrub coverage, 3.8 times more moose shrub coverage, and 4.4 times greater willow coverage than available plots. Moose travelling plots had less snow depth and were located closer to seral edges than available and foraging plots. Multivariate modeling indicated moose selected foraging areas where cover of shrubs was higher; willow coverage alone explained a significant amount of model fit. Moose traveled in areas with shallower snow depth, decreased distance to seral edge, and lower amounts of moose shrub, although these variables explained little of the variation in the data. Managers wishing to provide high quality late-winter moose range in interior montane environments should manage habitats to promote both forage production and reduced travel costs. Only a few key forage species appear to be preferred by moose during late winter in any particular area. These species can be readily identified, and production of these preferred browse species enhanced.

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Maintenance of winter range is an important component of moose (*Alces alces*) conservation in managed forests throughout North America (Peek 1998, Thompson and Stewart 1998). Although considerable research has been conducted on broad-scale habitat selection by moose, comparatively few studies provide field assessment of winter habitat selection at the fine scale, especially within interior mountain ecosystems (Pierce and Peek 1984, Van Dyke 1995, Tyers 2003). Remote assessment of habitat use and selection (e.g., using radiocollars) also generally fails to differentiate animal activity in the selection

process. Clarification of animal activity during habitat studies may facilitate understanding of the complexities of habitat selection and provide further information for moose habitat management (Van Dyke 1995).

Moose habitat guidelines in many areas focus on the retention of sufficient cover within the landscape, generally from mature coniferous forest (Thompson and Stewart 1998). However, there remains considerable controversy over the requirement for mature coniferous habitat for moose (Balsom et al. 1996, Peek 1998). Stands with high crown closure have reduced snow levels compared

to open areas (Pierce and Peek 1984, D'Eon 2004), but also generally have less preferred shade-intolerant shrubs, compromising forage quantity and intake (Peek 1998). During late winter when snow is deep, moose exhibit restricted movements and habitat use (Kelsall 1969, Coady 1974, Thompson and Vukelich 1981, Hundertmark et al. 1990, Peek 1998). We hypothesized that access to forage and cost of locomotion (both affected by snow depth) are key factors influencing use of late-winter range by moose at both broad and fine scales (Peek 1998, Schwartz 1998). Thus, we expect habitats selected by moose within late-winter range would differ depending upon the animal's activity (Van Dyke 1995), with selection for low snow areas for travelling and for more open areas with high shrub coverage for foraging.

Here we examine site-level habitat selection within late-winter range by moose in 3 areas of southeastern British Columbia. We used radio-collared moose to define late-winter range (Poole and Stuart-Smith 2007) and used snow-tracking and vegetation sampling to examine habitat selection within late-winter range.

STUDY AREA

We selected 3 areas within southeastern British Columbia to compare results across geographic areas and snow regimes (Fig. 1). Two areas (Flathead [49°15'N, 114°30'W] and Upper Elk [50°20'N, 114°55'W] valleys) were within the Rocky Mountains, and one was in the Purcell Mountains (Spillimacheen Valley [51°05'N, 117°15'W]). All areas have experienced significant industrial timber harvesting over the past 50 years, utilizing a variety of clear-cutting (in all 3 areas) and selective logging (more in the Spillimacheen) techniques. At the time of the study, moose densities were approximately 450 per 1,000 km² in the Flathead and Upper Elk, and unknown, but likely somewhat lower in the Spillimacheen Valley (BC Ministry of Envi-

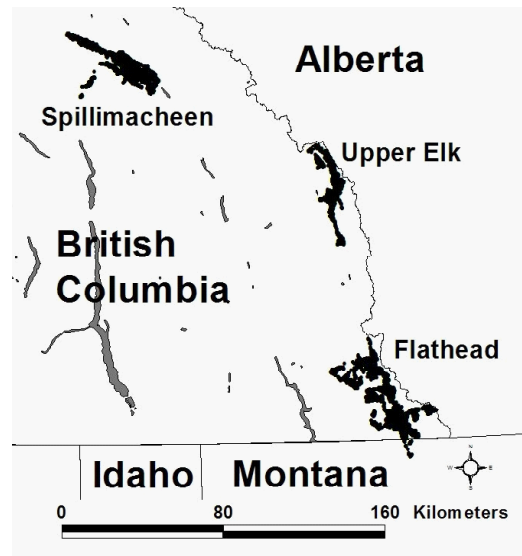


Fig. 1. Locations of 3 study areas (showing collared moose locations) within southeastern British Columbia, Canada, 2001–2003.

ronment, unpublished data). Montane Spruce (MS) and Engelmann Spruce–Subalpine Fir (ESSF) biogeoclimatic zones are predominant in all areas, with some Interior Cedar–Hemlock (ICH) and Interior Douglas–Fir (IDF), especially in the Spillimacheen Valley (Meidinger and Pojar 1991, Braumandl and Curran 1992). The IDF zone occurs in valley bottoms and lower slopes (800–1,200 m asl), and typically has pure Douglas-fir (*Pseudotsuga menziesii*) or mixed seral stands of Douglas-fir, western larch (*Larix occidentalis*), and lodgepole pine (*Pinus contorta*). Trembling aspen (*Populus tremuloides*) are also present. The ICH zone also occurs at 750–1,550 m elevation in wetter areas and includes a wide variety of conifer tree species, with western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) predominating. Several deciduous species – aspen, black cottonwood (*Populus balsamifera*), and paper birch (*Betula papyrifera*) – are also present. The MS zone is found at moderate elevation valley bottoms and slopes (1,200–1,650 m), and commonly has Douglas-fir, western larch, and white spruce (*Picea glauca*), with extensive seral

stands of lodgepole pine due to past wildfires. Aspen, cottonwood, and birch are also present. The ESSF zone occurs at higher elevations (1,650–2,100 m) and is dominated by closed-canopy forests of Engelmann spruce (*P. engelmannii*) and subalpine fir (*Abies lasiocarpa*), and seral lodgepole pine stands. On high mountains, the Alpine Tundra (AT) zone occurs above the ESSF.

July and January mean temperatures in the study area are approximately 17°C and –8°C, respectively, and valley bottom precipitation varied from 500–1,150 mm annually. Snowfall and accumulation vary widely, with deeper accumulation at higher elevations. We obtained snow survey (depth) and snow pillow data (snow water equivalent) from Government of British Columbia weather station data from various stations scattered throughout the study area (21–49 years of data; available at http://wlapwww.gov.bc.ca/rfc/river_forecast/snowp.htm). During winter 2001–2002 southeastern British Columbia experienced average snow accumulation through to early March 2002, and 20–30% above average snow accumulation and a delay of 3–4 weeks in snowmelt through to June. Precipitation and snow accumulation during winter 2002–2003 were 25–35% below station normals through to early March 2003 and 10–15% below normal for the remainder of the winter.

METHODS

Fieldwork

Eight radio-collared moose were available in each area each of winters 2001–2002 and 2002–2003, and we used monthly VHF locations and GPS collar locations obtained 12 times per day from these animals to help identify late-winter range in each area (Poole and Stuart-Smith 2007). Our intent was not to track individual collared moose but simply to conduct sampling in areas considered the heart of late-winter range in each area. We considered all collared moose to be migratory (*sensu* Langley 1993) with seasonally

distinct ranges.

To examine what site-level factors influence moose use of habitat during late winter, we conducted fieldwork in early March 2002 (Spillimacheen and Upper Elk) and 2003 (Flathead), spending 1 week in each area. Following the design of Huggard (1999), transects were laid out perpendicular to road and snowmobile trail access at widely distributed sites in what we considered representative late-winter moose habitat in each of the 3 areas. At 100-m intervals along transects, we conducted a 5.65-m radius (0.01 ha) availability plot, where we recorded snow depth, the species, dbh and total number of large trees (> 7.5 cm dbh), and the species and proportion cover of each shrub (uncovered by snow). We visually estimated distance to nearest seral edge, defined as the edge between stands < 30 years old (early seral, including logged areas) and stands ≥ 30 years old. We estimated canopy cover visually as the percent of the sky obscured by foliage and branches > 3 m above the ground (Huggard 1999). To measure moose use plots, we walked transects until we encountered a moose track. We then followed these tracks up to 1 km in both directions, or until the tracks were lost. At 200-m intervals along moose tracks we conducted a 5.65-m radius use plot as described above for availability plots. The classification of travelling or foraging near each use plot was based on the path taken and the amount of browsing observed leading up to and including the plot (linear paths with little or no browsing indicated travelling, versus convoluted paths with considerable browsing indicated foraging). Number of browse events in the 50 m of tracking leading up to the plot averaged 19.9 for foraging plots and 0.7 for travelling plots ($n = 125$ and 98 , respectively). We recorded all occurrences of browse species selected along the tracks by counting all browse events (bites) by shrub species, defined as each twig or stem freshly bitten.

Statistical Analyses

We used ANOVA and Tukey tests to test for differences in vegetation characteristics and snow depth among plots (PROC GLM, SAS Institute 1997). We used logistic regression to compare vegetation characteristics of moose forage and travelling plots to available plots, and used the logit function and tested assumptions regarding residuals. We tested a priori hypotheses about moose habitat use by selecting variables we felt would index limitations to winter movement (snow depth and canopy closure), forage (we compared 3 measures of shrub cover independently), and security (indexed by distance to the forest edge). We tested for multi-collinearity among variables (using availability plots only; $n = 213$) using Spearman rank correlation analysis in order to avoid including highly correlated variables in the same model ($r > 0.7$; Tabachnick and Fidell 1996). No more than 5 variables were considered in any model. We applied an arcsine transformation to variables measured as percentages to produce more normal frequency distributions. Discrete variables were examined to ensure adequate cell frequencies ($> 5\%$ of observations per cell; Tabachnick and Fidell 1996). We assessed models by comparing R^2 values, and identified significant variables using the Wald test ($P < 0.05$) and odds ratio results (a variable was considered not significant if the odds ratio 95% confidence interval included 1.0; Tabachnick and Fidell 1996). Variables that were not significant were removed one at a time from models (the poorest fitting variables first) such that preferred models contained only variables that made significant contributions to model fit. We did not use a model selection approach based on information theory (e.g., Akaike's Information Criteria [AIC]; Burnham and Anderson 2002) because we used a small number of variables to test a few simple a priori hypotheses. We conducted all statistical analyses using SAS software (SAS Institute 1997).

RESULTS

Sampling effort was roughly equal among the 3 areas, and totalled 213 habitat availability plots, 223 moose use plots, 39.5 km of moose track followed, and 10,935 browse events recorded. Browse species selection was relatively consistent among areas (Fig. 2). Willow (*Salix* spp.), red-osier dogwood (*Cornus stolonifera*), and saskatoon (*Amelanchier alnifolia*), together termed "moose shrubs", made up 83% of browse events recorded, with willow alone comprising 52% of browse events. We did not distinguish willow species in the field, but recognized that there were likely 2–3 prominent species present in each area. Birch (*Betula* spp.), aspen, alder (*Alnus* spp.), soopolallie (*Shepherdia canadensis*), and 2 species of coniferous trees (lodgepole pine and subalpine fir) formed the bulk of remaining browse species.

All but 1 variable (tree dbh) differed significantly among plot types (Table 1). Moose foraging plots had greater coverage of total shrub, moose shrub, and willow, lower canopy cover, and fewer trees than available

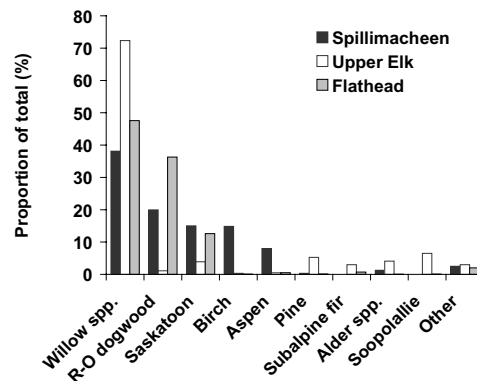


Fig. 2. Browse use (proportion of total browse events in each area) by moose in the Spillimacheen Valley ($n = 3,446$ browse events), the Upper Elk Valley ($n = 3,347$), and the Flathead Valley ($n = 4,142$), East Kootenay, British Columbia, February–March 2002–2003. R-O dogwood = red-osier dogwood, Pine = lodgepole pine. Other includes traces ($< 1.5\%$) of other shrubs and trees.

Table 1. Vegetation characteristics and snow depth (\bar{x} with SE in parentheses) within moose late winter range in southeastern British Columbia for available plots ($n = 213$), foraging plots ($n = 125$), and travelling plots ($n = 98$), March 2002 and 2003. Significance among plot types was examined using ANOVA (PROC GLM; SAS Institute 1997).

Variable	Available	Foraging	Travelling	<i>P</i>
Shrub coverage (%)	9.7 (0.65)	23.3 (1.36)*	8.6 (0.95)	<0.001
Moose shrub coverage (%)	3.5 (0.44)	13.0 (1.22)*	1.7 (0.31)	<0.001
Willow coverage (%)	2.4 (0.40)	10.6 (1.15)*	1.0 (0.25)	<0.001
Canopy cover (%)	22.0 (1.33)	15.4 (1.47)*	22.0 (1.83)	0.002
Number of trees	8.8 (0.57)	5.1 (0.60)*	7.9 (0.77)	<0.001
dbh of trees (cm)	13.6 (0.59)	13.5 (1.04)	15.2 (0.91)	0.32
Distance to seral edge (m)	63 (4.1)	66 (6.8)	45 (4.6)*	0.024
Snow depth (cm)	64.6 (1.36)	65.9 (1.64)	57.9 (1.67)*	0.004

* Differs from all other sites; Tukey's test, $P < 0.05$.

and travelling plots. Moose travelling plots had less snow depth and were located closer to seral edges than available and foraging plots. Moose foraging areas had 2.4 times more total shrub coverage, 3.8 times more moose shrub coverage, and 4.4 times greater willow coverage than available plots. Snow depth was negatively correlated with canopy cover ($r = -0.46$, $P < 0.001$).

We considered 5 variables in multivariate analysis of factors influencing moose use of foraging and travelling areas: shrub (willow, moose shrub, and total shrub cover were considered independently because they were correlated), snow depth, canopy cover, mean dbh of trees, and distance to edge. Canopy cover and number of large trees were correlated ($r = 0.83$, $P < 0.001$), and we removed number of large trees from the analysis, as we believe canopy cover to be a more causative variable. Moose selected foraging areas where cover of moose shrubs was higher ($R^2 = 0.26$, $-2 \log \text{likelihood} = 366.6$, model $\chi^2 = 68.7$, $df = 1$, $P < 0.0001$). Using total shrub coverage slightly increased the explanatory power of the model ($R^2 = 0.30$, $-2 \log \text{likelihood} = 354.8$, model $\chi^2 = 80.5$, $df = 1$, $P < 0.0001$). Willow coverage alone explained a significant amount of model fit ($R^2 = 0.21$, $-2 \log \text{likelihood} = 379.4$, model $\chi^2 = 56.0$, $df = 1$,

$P < 0.0001$). No other variables, including snow depth, canopy cover, mean tree dbh, and distance to seral edge were significant or related to moose forage selection when any shrub cover was included in the regression.

Moose traveled in areas with shallower snow depth, decreased distance to seral edge, and lower amounts of moose shrub, although these variables explained little of the variation in the data ($R^2 = 0.10$, $-2 \log \text{likelihood} = 335.6$, model $\chi^2 = 22.0$, $df = 3$, $P < 0.0001$). Total shrubs, willow, canopy cover, and mean tree dbh were not significant variables.

Snow depths during winter 2002 in the Upper Elk and Spillimacheen (74 ± 2.3 cm and 72 ± 1.8 cm, respectively) were approximately 20 cm greater than depths encountered in the Flathead in 2003 (53 ± 2.0 cm). With the Flathead data removed, modeling outputs for moose foraging areas were not improved, but moose traveled in areas of reduced snow depth with no other variables significant and the final model explaining slightly more variation in the data ($R^2 = 0.12$, $-2 \log \text{likelihood} = 203.3$, model $\chi^2 = 16.6$, $df = 1$, $P < 0.0001$). Thus, in 2002 moose tended to use areas with lower snow depth for travelling, while less snow in 2003 resulted in no selection by moose for areas of lower snow depth for travelling.

DISCUSSION

Our results suggest that shrub cover, especially willow cover, appeared to be the main factor determining moose foraging areas, and areas with lower snow depth and lower moose shrub coverage that were closer to seral edge were weakly selected for travelling. Thus, at the fine-scale level, habitat selection was specific for each activity. Van Dyke (1995) documented a similar differentiation in habitat selection between feeding and travelling activities by moose in south-central Montana.

Snow depth within our sampling areas did not appear to influence moose foraging activity because snow depths were similar to available plots. Snow depth is probably the primary causative factor influencing late-winter range distribution of moose (Peek 1998) and many other ungulates in temperate climates (Boyce 1991, Mackie et al. 1998). Snow depths > 50–70 cm are thought to impede moose movement and may be a critical threshold for the timing of movement from early to late-winter range; movements are thought to be restricted at depths 70–90 cm, and depths > 90 cm are considered critical for moose survival (Kelsall 1969, Coady 1974, Welsh et al. 1980, Thompson and Vukelich 1981, Sweanor and Sandegren 1989, Hundertmark et al. 1990), although both snow depth and density influence moose movements and habitat use patterns (Pierce and Peek 1984, Matchett 1985). Thus, the snow depths encountered in this study within late-winter range appeared to be insufficient to affect fine-scale selection of foraging sites. These results support Peek's (1998:369) assertion that moose select habitat primarily based on available forage. Other studies have confirmed the importance of browse availability in the winter distribution of moose (e.g., Pierce and Peek 1984, Telfer 1988, Westworth et al. 1989). In south-central Montana, Van Dyke (1995) found that moose foraging sites had higher shrub coverage and reduced canopy closure compared to other areas within the home range, but no measures

of snow depth were presented.

Three species comprised the bulk of moose diet in the areas we sampled. Despite the wide breadth of plants eaten by moose in their holarctic distribution, generally only a few species are eaten in large quantities in any area (Renecker and Schwartz 1998). Snow tracking suggested willow was the key forage for moose during late winter in all areas; similar results have been found across North America (Renecker and Schwartz 1998). Pierce and Peek (1984) found willow to be 1 of 2 preferred winter forage species in north-central Idaho. In addition to riparian valley bottoms, we also found extensive willow coverage in early seral cutblocks, and scattered in patches in mid-seral to older pine and fir stands in mesic habitats. Red-osier dogwood generally had greatest coverage in mature pine-fir and spruce stands in riparian areas and smaller moist pockets. Saskatoon was found on drier early seral and older, open pine-fir stands.

Energetics appears to be the main factor driving selection of feeding areas (higher abundance of preferred forage) and travelling areas (slightly lower snow depths and resulting lower costs of locomotion) during late winter. Peek (1998:369) suggested that low snow habitats that favour conservation of energy are the ones most prominently used; these typically include closed canopy conifer stands that reduce snow depths and locomotion costs, and stands with the tallest and densest shrub cover to maximize forage intake. Our field studies agree with this general premise, although we saw limited selection for closed stands, possibly because snow depths were insufficient to influence the cost of locomotion.

MANAGEMENT IMPLICATIONS

Managers wishing to provide high quality late-winter moose range in interior montane environments should manage habitats to promote both forage production and reduced travel costs. Forage habitats should include low overstory canopy cover to maximize

production of preferred shrub species. Travel areas should be interspersed within late-winter range, and should retain sufficient canopy closure to reduce snow depths. In areas or winters of greater snow depth, moose may prefer to forage closer to cover and areas of reduced costs of movement (Thompson and Vukelich 1981).

Few key forage species appear to be used by moose during late winter in any particular area; these species can be readily identified by tracking or simple vegetation plot comparisons (use versus available), but generally include willow and dogwood, and, in our area, saskatoon. Once identified, production of these preferred browse species could be enhanced. Core forage areas should be located in moister areas or riparian habitats, for the greatest growth of preferred shrub species. Riparian floodplains often make up comparatively small proportions of the landscape, and should be managed to provide continual forage habitat.

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