Winter habitat selection by female moose in western interior montane forests

Kim G. Poole and Kari Stuart-Smith

Abstract: Winter range has been identified as an important component of moose (*Alces alces* (L., 1758)) conservation in managed forests, yet there have been few studies on habitat associations in montane ecosystems. We investigated habitat selection by moose at landscape and stand scales during late winter in southeastern British Columbia using global positioning system (GPS) collars on 24 adult moose cows in each of two winters. The strongest determinant of late-winter range at the landscape scale was decreasing elevation, which is probably the primary causative factor influencing late-winter distribution of moose. Within late-winter range, topographic variables had little influence on moose habitat selection. Lower crown closure was the strongest determinant of stand-scale selection, although the resultant model was weak. We found no disproportionate selection for stands with high crown closure, and there was little evidence for greater use of cover stands with increasing snow as winter progressed. Within late-winter range, moose selected forage habitats (42% use vs. 30% availability) over cover habitats (22% use vs. 37% availability). The delineation of late-winter moose range can be based on snow depth, or elevation as its surrogate.

Résumé : Chez les orignaux (*Alces alces* (L., 1758)), l’aire vitale en hiver est reconnue comme une composante importante de leur conservation dans les forêts aménagées; il y a cependant peu d’étude des associations d’habitat dans les écosystèmes de montagne. Nous avons étudié la sélection de l’habitat chez l’original à l’échelle du paysage et du boisé à la fin de l’hiver dans le sud-est de la Colombie-Britannique chez 24 femelles adultes porteuses de colliers munis de systèmes de positionnement géographique (GPS) durant chacun de deux hivers. L’altitude décroissante est le facteur déterminant le plus important de l’aire vitale en fin d’hiver à l’échelle du paysage, alors que les orignaux choisissent aussi les pentes plus douces et l’insolation plus forte. L’altitude est vraisemblablement une variable de remplacement pour l’épaisseur de la neige qui est probablement le facteur causal principal à affecter la répartition des orignaux en fin d’hiver. Au sein de l’aire vitale de fin d’hiver, les variables topographiques ont peu d’influence sur la sélection d’habitat chez l’original. À l’échelle du boisé, une fermeture plus basse de la couverture des arbres est le facteur déterminant le plus fort de la sélection, mais le modèle obtenu est faible. Il n’y a pas de sélection disproportionnée pour les habitats possédant une fermeture de canopée élevée et il y a peu d’indications que les orignaux utilisent les boisés qui possèdent une couverture arborecente en fonction de l’accumulation de la neige au cours de l’hiver. Dans l’aire vitale de fin d’hiver, les orignaux choisissent de préférence les habitats à cause de l’alimentation (42% d’usage contre 30% de disponibilité) qu’à cause de la couverture (22% d’usage contre 37% de disponibilité). La délimitation de l’aire vitale de fin d’hui de l’original peut se faire en fonction de la profondeur de la neige ou en fonction de l’altitude qui en est une variable de remplacement.

Introduction

Winter range has been identified as an important component of moose (*Alces alces* (L., 1758)) conservation in managed forests throughout North America (Peek 1997; Thompson and Stewart 1997). Moose exhibit the most restrictive movements and habitat use during winter, particularly during the late-winter deep-snow period (Kelsall 1969; Coady 1974; Thompson and Vukelich 1981; Hundertmark et al. 1990; Peek 1997). Furthermore, moose lose body mass during winter (Schwartz 1997), and experience the greatest proportion of adult starvation and predator-related mortality at this time, which is often related to winter severity (Ballard et al. 1991; Van Ballenberghe and Ballard 1997).

Management guidelines for moose winter range in many areas of North America focus on the retention of sufficient coniferous cover within the landscape, ostensibly to provide interlocking crowns for snow interception cover to facilitate movement and foraging on shade-tolerant shrubs (Thompson and Stewart 1997). In montane ecosystems of the northern Rocky Mountains, there is a strong emphasis on providing high amounts of closed-canopy coniferous cover (Thompson and Stewart 1997), based on several studies showing high use and selection for closed-canopy conifer stands for shelter and feeding in late winter (Pierce and Peek 1984; Matchett 1985; Langley 1993). Tyers (2003) found that northern Yellowstone moose used willow stands in early winter, but shifted into mature, closed-canopy forests during mid-winter and late winter. However, other studies in the region showed high use of shrub-dominated wetlands and riparian areas during winter (van Dyke et al. 1995; Table 26, which cites
five older studies from Montana and Wyoming, on p. 355 of Peek 1997). Furthermore, small sample sizes (Pierce and Peek 1984; Matchett 1985) or simplicity of analysis (Langley 1993) limited the few studies that have been conducted in the region. Thus, there is conflicting information about moose habitat use in the region in winter, in particular the degree of use and importance of mature coniferous cover (cf. Balsom et al. 1996; Peek 1997).

Here we examine late-winter habitat selection by moose cows in three areas of southeastern British Columbia. Our overall goal was to provide information on moose habitat selection in interior montane ecosystems during late winter to help forest managers identify winter-range areas and develop management guidelines. We chose to monitor adult cows because they are the most reproductively important age and sex class, and, especially when accompanied by calves, may make greater use of cover than males during winter (Miquelle et al. 1992; p. 372 of Peek 1997). Our specific objectives were to (i) examine broad-scale habitat selection and provide guidance for an empirically based boundary for moose late-winter range, (ii) define cover and forage habitats in this environment for moose in terms of stand age and type, and (iii) determine the relative proportion of forage and cover habitats used by moose within the winter range. We hypothesized that energy balance is the key factor influencing overwinter survival of moose, and that access to forage and cost of locomotion (both affected by snow depth) are likely ultimate factors influencing use of late-winter range (Peek 1997; Schwartz 1997).

Materials and methods

Study area

We selected three areas within southeastern British Columbia to sample the range of ecosystems where moose are abundant (Fig. 1). Two areas (Flathead and Upper Elk valleys) were within the Rocky Mountains and one was in the Purcell Mountains (Spillimacheen Valley). Moose densities were approximately 450 per 1000 km² in Flathead and Upper Elk, and unknown in the Spillimacheen Valley (British Columbia Ministry of Environment, unpublished data). Montane spruce (MS) and Engelmann spruce–subalpine fir (ESSF) biogeoclimatic zones predominate 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 (800–1200 m above sea level (a.s.l.)), and typically has pure Douglas-fir (Pseudotsuga menziesii (Mirbel) Franco) or mixed stands of Douglas-fir, western larch (Larix occidentalis Nutt.), and lodgepole pine (Pinus contorta Dougl. ex Loud.). The ICH zone occurs at 750–1550 m a.s.l. in wetter areas and contains a wide variety of conifer tree species, including western hemlock (Tsuga heterophylla (Raf.) Sarg.) and western redcedar (Thuja plicata Donn ex D. Don), as well as Douglas-fir, western larch, and lodgepole pine. The MS zone is found at moderate elevation valley bottoms and slopes (1200–1650 m a.s.l.), and commonly has white spruce, western larch, and Douglas-fir, with extensive seral stands of lodgepole pine owing to past wildfires. The ESSF occurs at higher elevations (1650–2100 m a.s.l.) and is dominated by closed-canopy forests of spruce and subalpine fir, and seral lodgepole pine stands. On high mountains, the alpine tundra (AT) zone occurs above the ESSF. Quaking aspen (Populus tremuloides Michx.), black cottonwood (Populus balsamifera ssp. trichocarpa (Torr. & Gray ex Hook.) Brayshaw), and paper birch (Betula papyrifera Marsh.) occur in small amounts primarily in the IDF, MS, and ICH. All three areas have experienced significant industrial timber harvesting over the past 40 years.

July and January mean temperatures at lower elevations in the study area are approximately 17 and −8 °C, respectively. Snowfall and accumulation vary widely, with deeper accum-
mulation at higher elevations (Fig. 2). We obtained snow survey (depth) and snow pillow data (snow water equivalent) from Environment Canada weather station data from various stations scattered throughout the region. 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 normal through to early March 2003 and 10%–15% below normal for the remainder of the winter.

Capture

We captured 48 adult female moose by helicopter netgunning (Carpenter and Innes 1995), 8 in each area in late December 2001 and early January 2003. We attempted to spread capture effort evenly throughout each area. Capture and handling protocol followed the principles and guidelines of the Canadian Council on Animal Care (1993). We fitted a global positioning system (GPS) collar (model G2000; Advanced Telemetry Systems, Isanta, Minnesota) on each moose, programmed to obtain a fix every 2 h from deployment to 30 April, and every 4 h from 1 May through to retrieval in August–September. Collars were released remotely from the animals, recovered, and data downloaded.

Habitat use

We examined habitat use both at the landscape scale (late-winter range within the landscape; 2nd-order selection; Johnson 1980) and at the stand scale (moose locations within late-winter range; 3rd-order selection). We were more interested in population-level responses to habitat variation than variation among individuals; therefore we pooled data from individual moose (White and Garrott 1990; Aeabischer et al. 1993; Manly et al. 2002). Numbers of late-winter locations were roughly equal among all GPS-collared moose, providing equal weighting for each animal. We retained all locations in our analysis. This follows the advice of researchers who argue that obtaining a representative sample of tagged animals, especially for those that migrate, and sampling locations systematically through time are more important than ensuring that successive observations are statistically independent (McNay et al. 1994; Otis and White 1999; Millsbaugh and Marzluff 2001).

We obtained digital 1:20000 scale topographic files (Geographic Data, B.C. 1992) and current forest inventory planning files (Forest Cover; Resources Inventory Branch 1995), and 1:50000 scale B.C. Watershed Atlas files (British Columbia Ministry of Sustainable Resource Management), and conducted analyses using ArcInfo® version 8.0 (Environmental Systems Research Institute, Inc. 1999) geographic information system (GIS) and wildlife based extensions (Rodgers and Carr 1998; Hooge and Eichenlaub 2000). Forest-cover maps delineate relatively homogeneous forest stands or forest-cover types based on the interpretation of aerial photographs and ground-truthing information, with a minimum resolution of about 2 ha. These maps commonly include information on tree species, age, and crown closure, and are widely used in British Columbia for forest management.

We stratified data into seasons according to seasonal education shifts made by each individual. We classified late winter generally as from mid- to late January to mid- to late March. At the landscape scale, we compared random locations from within the 90% fixed kernel polygon delineating the late-winter range of each animal with random locations placed within the areas (defined by a 100% minimum convex polygon surrounding all moose radio locations in each area over both years). We used 10,000 random locations within each area and combined all three areas for analysis. We excluded the USA locations from one moose in the Flathead that made a 9-day excursion into Montana in mid-January 2003 prior to late winter. At the stand scale within late-winter range, we examined moose locations compared with random locations from within the 90% fixed kernel polygon encompassing individual moose late-winter range. Within each late-winter-range polygon, we placed the same numbers of late-winter locations as were obtained for each moose. Locations without complete digital data sets were deleted from the analyses.

For each moose use and random location, we determined elevation and slope. In lieu of aspect, we used solar duration, which is the number of hours per day that the sun illuminates a pixel based on latitude and the shading effects of nearby topography (Kumar et al. 1997). We calculated means for solar duration for 1 January – 31 March to match work completed elsewhere in the region (Poole and Mowat 2005). We determined distance to all but the smallest permanent streams. We determined main tree species, percent species composition, crown closure, and stand age for moose locations and random points. We used species composition, stand structure, and logging history to assign nine cover types: (1) open (primarily open stands with no overstory data; mainly brush dominated, meadows, and rocky areas), (2) deciduous — leading, (3) recently logged (≤10 years old), (4) older logged (10–40 years old), (5) lodgepole pine — leading, (6) Douglas-fir — leading, (7) riparian (generally open floodplains and shrub flats along valley bottoms, and swamps), (8) spruce — leading, and (9) subalpine (upper elevation spruce–balsam stands, alpine forest and alpine; mainly >1800 m).

Based on the relationship between shrub coverage and crown closure observed in field studies (Peek et al. 2001) and published literature on minimum requirements for snow interception cover (e.g., Jenkins and Wright 1988; Schwab and Pitt 1991), we defined forage habitat from digital sources as stands with ≤20% “evergreen crown closure” and <30 years age, and cover habitat as stands with ≥60 years of age and ≥40% evergreen crown closure. Habitat that fell between these two definitions was designated mid-seral. “Evergreen crown closure” was used to index snow depth under the canopy, and was defined as total stand crown closure minus 50% of the proportion of western larch and 80% of the proportion of deciduous trees. Analysis of the digital database suggested that mean crown closure increased rapidly with stand age then levelled off in stands >30–35 years of age, and decreased slightly as stands aged (Poole and Stuart-Smith 2004). We included stand age in our habitat definitions to increase the accuracy of interpretation of the digital database (Dussault et al. 2001). We determined the proportion of forage and cover habitats available to and used by each moose within the late-winter
range. We further examined use of cover habitat over half-month periods each winter to determine whether moose increased use of cover as snow depth increased (Balsom et al. 1996). We also examined the influence of time of day on use of different cover types and the number of successful GPS moose locations. We hypothesized that moose would occupy heavier cover and that the GPS collars would record fewer moose locations during daylight hours because crown closure (and tree spacing and height) is negatively correlated with GPS observation rate (Rempel et al. 1995; Moen et al. 1996b; Dussault et al. 1999).

Statistical analyses
We used resource selection functions (RSF) to quantify the relationship between moose habitat selection and topography and overstory vegetation for moose location data at landscape and stand scales. We began by identifying variables that were useful for differentiating used locations from availability locations, and that we believed were biologically justified and relevant at the scale being considered. We considered an a priori set of candidate models based on the literature and field observations. Following suggestions by Burnham and Anderson (2002), we assessed the strength of competing models using Akaike’s information criterion values corrected for small sample sizes ($\Delta AIC_c$), differences in $AIC_c$ values ($\Delta AIC_c$), and Akaike weights ($w_i$). We tested for multi-collinearity among variables using Spearman’s rank correlation analysis to avoid including highly correlated variables in the same model ($r_s > 0.7$). We excluded stand age from the analyses because crown closure and stand age were highly correlated at the landscape scale ($r = 0.80$) and we considered crown closure to be a more causative factor influencing snow depth and forage cover. Models that failed to converge were removed from analysis. We examined likelihood ratio $\chi^2$ statistics for assessment of goodness-of-fit for the most highly parameterized model within each analysis. We used 95% confidence intervals (CI) to assess the strength of the effect of each predictor covariate on the dependent variable, and used the Wald $\chi^2$ statistic to compare the relative importance among variables. Poor power and inconclusive statistical inference are expected from co-

Results

Capture and GPS collars
We obtained 79,578 locations from the 48 GPS-collared moose; 32,191 of these from the late-winter period. No moose died prior to the end of winter. All GPS-collared moose were considered migratory (sensu Langley 1993) with seasonally distinct ranges. Several moose in each area undertook seasonal movements of 30–65 km. GPS-collar data quality was high during late winter (88% location success and 79% three-dimensional fixes).

Late-winter habitat selection

Landscape scale
Late-winter range occupied approximately 10%–19% of each area. Compared with the combined ranges of the study animals, late-winter range was located in areas of lower elevation and slope, higher solar insolation, less distance to water, lower age, and higher crown closure (Tables 1, 2). Absolute differences in elevation existed among areas (Table 1), but in each area the lowest available elevations were selected and selection tapered off significantly at higher elevations (Fig. 3). Late-winter range was mostly pine, spruce, and logged forest; older logged areas, pine, and riparian areas were used more than available, whereas subalpine was used less (Table 2).

We chose four habitat variables for inclusion in the logistic regression modelling process at the landscape scale — elevation, slope, solar insolation, and crown closure. We did not consider distance to water as an explanatory variable because we could see no biological basis for this. The full model consisting of the variables for elevation, slope, solar insolation, and crown closure was the most parsimonious (Table 3). This model was statistically significant ($\chi^2_5 = 18.657, P < 0.0001$) and explained 35% of the total deviance. Late-winter range was located in areas of lower elevation and slope, and higher solar insolation and crown closure. Confidence intervals for all variables did not overlap 0 (Table 4). Elevation was a factor in all five top models and had the highest Wald $\chi^2$ statistic among variables (Table 4). Crown closure had a low Wald $\chi^2$ statistic and made a relatively small contribution to the change in $\Delta AIC_c$ between the two top models.

Stand scale
Compared with habitats available within the late-winter range, moose used areas with slightly lower elevation, slope, and distance to water, slightly higher solar insolation, lower crown closure, and younger age stands (Tables 1, 2). Lodgepole pine and older (>10 years) logged stands were the cover types used to the greatest extent by moose (Table 2). Open, older logged stands, and riparian stands were used more than available, whereas pine stands were used less.

We considered five variables for inclusion in logistic regression modelling at this scale — crown closure, elevation, slope, solar insolation, and distance to water. The full model consisting of all five variables was the most parsimonious (Table 3) and was statistically significant ($\chi^2_5 = 38.23, P < 0.0001$), but explained only 5% of the variation in the data. Within late-winter range, moose used areas of higher elevation, lower slope, solar insolation, and crown closure, and greater distance to water. Confidence intervals for all variables did not overlap 0, but values for elevation and distance to water approached 0 (Table 4). Crown closure was a factor in all six top models and had the highest Wald $\chi^2$ statistic among variables (Table 4). Distance to water had a low Wald $\chi^2$ statistic and made a comparatively small contribution to the change in $\Delta AIC_c$ between the two top models.

Use of forage and cover habitats
Overall, 42% ± 3.0% (mean ± SE) of moose locations were in forage habitats and 22% ± 2.6% were in cover habitats. When related to the amount of forage and cover habitats available within late-winter range, moose showed proportionately less selection for cover (22% ± 2.8% use.
Use of cover habitat by moose did not increase with increasing snow depths as winter progressed except in late March 2002 (Fig. 4). The proportion of cover and forage used by moose during late winter varied during the day, with 29% greater use of cover and 19% less use of forage habitats in the hours of 1201–1600 compared with the hours of 0001–0400 (Fig. 5). The number of GPS locations (a surrogate for observation rate given equal numbers of location attempts among time periods) was also lowest in the hours of 1201–1600 and closely paralleled the proportion of cover used by moose.

**Discussion**

**Landscape-scale habitat selection**

Our analyses indicated that decreasing elevation was the single strongest determinant of moose late-winter range at the landscape scale. A similar pattern has been described for other interior mountainous areas, where moose tend to descend to lower elevation valley bottoms during winter (Pierce and Peek 1984; Matchett 1985; Langley 1993; van Dyke et al. 1995). We suggest that elevation acts as a primary surrogate for snow depth, which is probably the primary causative factor influencing late-winter-range distribution of moose (Peek 1997) and many other ungulates in temperate climes (Boyce 1991; Mackie et al. 1998). D’Eon (2004) showed that elevation was the most important bio-

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**Table 1.** Characteristics of continuous variables (units and acronyms in parentheses) for random study-area locations (n = 29 075), random late-winter-range locations (n = 32 179), and locations used by 48 moose cows within late-winter range (n = 32 191) in southeastern British Columbia, Canada, 2001–2003.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Random study area</th>
<th>Random late-winter range</th>
<th>Late-winter moose use</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation (m; elev.)</td>
<td>Overall</td>
<td>1775±404</td>
<td>1401±249</td>
</tr>
<tr>
<td></td>
<td>Spillimacheen</td>
<td>1703±523</td>
<td>1131±163</td>
</tr>
<tr>
<td></td>
<td>Flathead</td>
<td>1746±276</td>
<td>1416±169</td>
</tr>
<tr>
<td></td>
<td>Upper Elk</td>
<td>1888±339</td>
<td>1600±170</td>
</tr>
<tr>
<td>Slope (°)</td>
<td>Overall</td>
<td>19.3±60.1</td>
<td>10.2±56.6</td>
</tr>
<tr>
<td></td>
<td>Spillimacheen</td>
<td>536±157</td>
<td>611±96</td>
</tr>
<tr>
<td></td>
<td>Flathead</td>
<td>386±328</td>
<td>285±277</td>
</tr>
<tr>
<td></td>
<td>Upper Elk</td>
<td>24±24.5</td>
<td>33±25.2</td>
</tr>
<tr>
<td>Age (year)</td>
<td>Overall</td>
<td>63±74.8</td>
<td>61±51.9</td>
</tr>
</tbody>
</table>

Note: Values are means ± SD. All comparisons of variables between random study area and random late-winter range (landscape scale), and random late-winter range and moose use locations (stand scale) are significant (Student’s t tests; all P < 0.001, except for the slope at the stand scale (P = 0.034)).

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**Table 2.** Characteristics of cover-type variables for random study-area locations (n = 29 075), random late-winter-range locations (n = 32 179), and locations used by 48 moose cows within late-winter range (n = 32 191) in southeastern British Columbia, 2001–2003.

<table>
<thead>
<tr>
<th>Cover type</th>
<th>Random study area (%)</th>
<th>Random late-winter range (%)</th>
<th>Late-winter moose use (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open</td>
<td>8</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>Deciduous</td>
<td>1</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Logged recent (&lt;10 years)</td>
<td>3</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Logged older (10–40 years)</td>
<td>7</td>
<td>15</td>
<td>24</td>
</tr>
<tr>
<td>Pine</td>
<td>25</td>
<td>42</td>
<td>29</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>4</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Riparian</td>
<td>2</td>
<td>7</td>
<td>11</td>
</tr>
<tr>
<td>Spruce</td>
<td>13</td>
<td>12</td>
<td>11</td>
</tr>
<tr>
<td>Subalpine</td>
<td>37</td>
<td>3</td>
<td>2</td>
</tr>
</tbody>
</table>

Note: Definitions of cover types provided in the text.

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**Fig. 3.** Selection (w ± 95% CI) of elevation classes by 48 moose at the landscape scale in three areas during late winter in southeastern British Columbia, 2001–2003. Sample sizes are 8935, 11 215, and 12 011 for the Spillimacheen, Upper Elk, and Flathead areas, respectively.

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vs. 37% ± 2.8% available) and greater selection of forage habitats (42% ± 1.9% vs. 30% ± 1.9%).

Use of cover habitat by moose did not increase with increasing snow depths as winter progressed except in late
physical or habitat attribute in predicting snow depth in the adjacent mountainous and wetter West Kootenay region, followed by aspect, canopy cover (at low elevations only), and slope, in order of importance.

The range of elevations used within late-winter range was generally greater than previously shown from studies in this region (Matchett 1985; Langley 1993). However, the mean use of elevation varied among areas, likely driven by differences in available elevations and snow depth among areas. Slope also influenced the location of late-winter range. Little use of slopes >30% have been reported elsewhere (Matchett 1985; Langley 1993). Our data suggest solar insolation had some influence on late-winter-range location; selection for south- and west-facing slopes has been observed elsewhere (Matchett 1985; Langley 1993). Crown closure was very weakly related to landscape-scale selection of late-winter range, emphasizing the central importance of snow depth in determining the extent of winter range and the importance of elevation in determining life-history strategies and movements of this species in mountainous environments.

### Stand-scale habitat selection

Our results suggest that once moose moved to late-winter range, both topographic variables and overstory (crown closure), as determined using digital databases, had little influence on habitat selection. Among variables, decreased crown closure was the strongest determinant of stand-scale selection. Fieldwork in all three areas showed that shrub coverage had the greatest influence on fine-scale late-winter habitat use by moose, with willow (*Salix spp.*) coverage contributing a majority of model fit (Poole and Stuart-Smith 2001–2003). Cover defined as stands with ≥60 years age and ≥40% evergreen crown closure.

### Table 3. Variables, number of parameters (*K*), ΔAICc, and Akaike weights (*w*<sub>i</sub>) for the top candidate models considered in describing moose late-winter range at the landscape scale (top 5 of 8 models) and stand scale (top 6 of 11 models), southeastern British Columbia, 2001–2003.

<table>
<thead>
<tr>
<th>Variables in the models</th>
<th><em>K</em></th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th><em>w</em>&lt;sub&gt;i&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Landscape</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elev. (–), slope (–), solar (+), CC (+)</td>
<td>5</td>
<td>0.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Elev., slope, solar</td>
<td>4</td>
<td>48.9</td>
<td>0.0</td>
</tr>
<tr>
<td>Elev., solar, CC</td>
<td>4</td>
<td>515.2</td>
<td>0.0</td>
</tr>
<tr>
<td>Elev., slope, CC</td>
<td>4</td>
<td>848.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Elev., CC</td>
<td>3</td>
<td>1891.3</td>
<td>0.0</td>
</tr>
<tr>
<td><strong>Stand</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elev. (+), slope (–), solar (–), CC (–), distwater (+)</td>
<td>6</td>
<td>0.0</td>
<td>0.99</td>
</tr>
<tr>
<td>Elev., slope, solar, CC</td>
<td>5</td>
<td>9.7</td>
<td>0.01</td>
</tr>
<tr>
<td>Slope, solar, CC</td>
<td>5</td>
<td>100.8</td>
<td>0.0</td>
</tr>
<tr>
<td>Slope, CC</td>
<td>4</td>
<td>112.7</td>
<td>0.0</td>
</tr>
<tr>
<td>Elev., slope, CC</td>
<td>5</td>
<td>153.9</td>
<td>0.0</td>
</tr>
<tr>
<td>Elev., solar, CC, distwater (-)</td>
<td>5</td>
<td>215.9</td>
<td>0.0</td>
</tr>
</tbody>
</table>

**Note:** The plus and minus indicate the direction of the relationship of independent variables. Variable descriptions are provided in Table 1.

### Table 4. Coefficients, 95% CI, and Wald χ² of the most parsimonious models for selection by moose of winter range at the landscape and stand scales in southeastern British Columbia, 2001–2003.

<table>
<thead>
<tr>
<th>Variable</th>
<th>β coefficient</th>
<th>±95% CI</th>
<th>Wald χ²</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Landscape</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elev.</td>
<td>-0.00274</td>
<td>-0.00281, -0.00267</td>
<td>5785</td>
</tr>
<tr>
<td>Slope</td>
<td>-0.02240</td>
<td>-0.02430, -0.02040</td>
<td>513</td>
</tr>
<tr>
<td>Solar</td>
<td>0.00268</td>
<td>0.00250, 0.00287</td>
<td>805</td>
</tr>
<tr>
<td>CC</td>
<td>0.00274</td>
<td>0.00199, 0.00349</td>
<td>51</td>
</tr>
<tr>
<td><strong>Stand</strong></td>
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</tr>
<tr>
<td>Elev.</td>
<td>0.00030</td>
<td>0.00024, 0.00035</td>
<td>103</td>
</tr>
<tr>
<td>Slope</td>
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<td>Solar</td>
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<td>Distwater</td>
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<td>0.00004, 0.00014</td>
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</table>

**Note:** Variable descriptions are provided in Table 1.
We found an inverse relationship between canopy closure and shrub coverage (Poole and Stuart-Smith 2004), and conclude that crown closure is the primary digitally derived variable which we can use as a surrogate for forage abundance. However, the resolution in the digital databases used here may not have been fine enough to show strong selection. In south-central Montana, van Dyke (1995) also found that moose feeding sites had higher shrub coverage and reduced canopy closure.

Results presented in Poole and Stuart-Smith (2005) support Peek’s (1997: 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). Among forage categories, study moose selected most strongly for riparian, open, and brush-dominated areas, and older logged stands. Forage values, and hence use by moose, tend to peak on burns and cutovers at 11–30 years post disturbance (Thompson and Vukelich 1981; Matchett 1985; Thompson and Stewart 1997), but clearcuts are avoided if little browse is present (Kufeld and Bowden 1996).

Although digital mapping of riparian habitats within southeastern British Columbia was poor, it was evident that these areas were used extensively where available. Shrub lands along the Flathead and Upper Elk rivers contained abundant and thick shrub fields up to 3–4 m high. Given this height, large amounts of forage would remain unburied and available to moose even with snow depths >1 m. Extensive use of willow flats in riparian areas has been documented in other studies (Risenhoover 1989; Ballard et al. 1991; van Dyke et al. 1995; Kufeld and Bowden 1996; Peek 1997: 355), emphasizing the importance of this habitat.

We found no selection for stands with high crown closure. The evidence for a shift to greater use of cover stands with increasing snow as winter progressed was weak and was evident only during late March in 2002. These results are in contrast with those found in other studies within the region, which documented high use and often selection of closed-canopy closure stands (Pierce and Peek 1984; Matchett 1985; Langley 1993). In northwestern Montana and central Idaho, dense conifer stands were used for shelter and feeding (Matchett 1985), and old growth grand fir (Abies grandis (Dougl. ex D. Don) Lindl.) and Pacific yew (Taxus brevifolia Nutt.) were used extensively during periods of deep snow (Pierce and Peek 1984). Our higher elevation conifer stands did not contain Pacific yew. There is also some evidence in the literature that moose select mature coniferous habitat with increasing snow depth (summarized in Balsom et al. 1996). However, both Pierce and Peek (1984) and Schwab and Pitt (1991) found no changes in habitat-use patterns from early to late winter. The apparent dichotomy in late-winter habitat selection may be related to the available habitats, snow depth, and shrub availability within the areas of research. Peek (1997) suggested that moose may primarily occupy mature coniferous forest where riparian habitats are less extensive. A table summarizing studies from the western States during the 1960s through mid-1980s demonstrated that percent winter habitat use of closed conifer habitats by Shiras’ moose (Alces alces shirasi Nelson, 1914) varied from 0% to 100%, with the lowest use (<27%) of conifers in riparian and floodplain riparian habitats and the highest use of conifers in areas with little shrub and open habitat (Peek 1997). In Pierce and Peek’s (1984) study, only 3% of the habitat was open. Peek (1997) suggested that these mature conifer forests support moose during winter because of their greater diversity of forage species compared with higher elevation ranges.

The conclusion that moose require large amounts of mature conifer during winter may depend upon the literature reviewed or the areas selected. Balsom et al. (1996) cited 14 studies indicating increased use of dense cover with increased snow depth, but argued that although preference for these sites has often been shown, whether mature coniferous habitat is critical in limiting moose survival and reproduction has not been demonstrated. Studies from Ontario suggest that scale of analysis is important; even when moose select closed canopies at the stand scale, more logging (and hence shrub production) at the landscape scale supports higher populations of moose (Forbes and Theberge 1993).

**Study limitations**

Our findings were based on data from two winters, which may have not been severe enough (with deep, unconsolidated snow) to “force” moose to greater use of cover habitats. The results of this study should be taken in the greater context and compared with data obtained in other studies and during different years. In the North Fork of the Flathead River in Montana, an unusually deep-snow winter caused moose to make less use of hydric shrub communities and greater use of even-aged seral lodgepole pine stands (46% overstory cover), and corresponding greater use of coniferous browse over deciduous shrubs in the diet (Jenkins and Wright 1988). In some areas moose decreased use of deciduous and cut areas during high-snow winters (Hundertmark et al. 1990), but in others moose habitat-use patterns did not differ among winters of dramatically different severity (Pierce and Peek 1984).

The GPS collars missed only 12% of fixes during late winter. Modelling from test data collected over the range of crown closures present in late-winter range suggests that fix success decreases 0.8% for every 10% increase in digital crown closure, resulting in a 3%–6% bias against cover habitats (assuming 40%–70% crown closure in cover stands) (Poole and Stuart-Smith 2004). Although we could apply this correction for missed locations to management guidelines derived from this work, modelling by D’Eon (2003) and Frair et al. (2004) suggest that little if any correction to the data are required when there is loss of comparatively small amounts of data (<10%) and a short GPS-sampling interval. According to modelling by these authors, the resultant changes between corrected and uncorrected data would not influence conclusions about habitat-selection analysis. Topography (slope to horizon) appeared to be responsible for about 25% of the bias in fix success in our studies (Poole and Stuart-Smith 2004), but this bias would presumably vary independent of crown closure. In addition, an unknown proportion of the missed fixes are likely related to animal behaviour, collar orientation, and other variables that would likely have a random impact on habitat-selection analyses. We therefore did not add a correction factor to our crown-closure results to account for missed GPS locations.
We found differences in GPS-collar location success and crown closure use among periods of the day, likely a result of changes in moose behaviour (Moen et al. 1996a), with greater use of cover during the day (presumably more bedding) and with more use of open habitats during crepuscular periods and at night (presumably for foraging). Using GPS collars, Dussault et al. (1999) found that fix success in summer was less during the day than during the night, attributing this to moose using dense forest cover during the heat of the day. One implication of these findings is to put into perspective the results of studies primarily based on daylight relocations of collared animals. We found up to 29% greater use of cover habitats during midday compared with during the night, which could result in higher recommendations for moose cover requirements than actually used on a 24 h basis.

Conclusions

Results of this study suggest that elevation, which is likely a surrogate for snow depth, is the most important factor influencing location of late-winter range and thus can be used to delineate moose winter range in montane ecosystems in the northern Rockies. However, upper elevational cutoffs will vary among areas based on local climatic conditions, even within the same climax ecosystems. For example, late-winter range was located much lower in the Spillimacheen than in the Flathead or the Upper Elk, despite similar vegetation in each area. In all areas, greater emphasis should be placed on management of valley bottoms and adjacent areas because these areas receive disproportionate utilization by moose. However, the fit of our landscape model suggested that other factors influence the choice of winter range, hence simple lines based on elevation will map areas that are little used. Slope and solar insolation contributed to predicting winter range. Given that our research was conducted during two winters of average or below average snow depth, our results may be skewed towards higher elevations and should be considered conservative; moose may make greater use of lower elevation areas during winters of deeper snow (Ballard et al. 1991).

In our study, moose selected open-forage habitats more than cover habitats during late winter. We therefore suggest that managers wishing to provide high-quality winter range within southeastern British Columbia and similar ecosystems focus on providing forage habitats, in addition to providing some cover habitats. Based on use of forage and cover habitats, we suggest rough guidelines for the approximate proportions of each habitat type within late-winter range as 40%–45% forage and 20%–25% cover. Since we monitored the component of the population with likely the most restrictive requirements for cover (Miquelle et al. 1992; Peek 1997), these guidelines should be seen as conservative requirements for cover for the population as a whole. Forage habitat should have low overstory crown closure to maximize production of shrubs. Core forage areas should be located in more moist areas or riparian habitats for the greatest growth of preferred shrub species (Poole and Stuart-Smith 2005). Riparian floodplains often make up comparatively small proportions of the landscape and should be managed to provide continual forage habitat. If hiding cover is not available within these floodplains (either through vegetation or topography), we suggest some forest should be retained in adjacent areas.

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References


