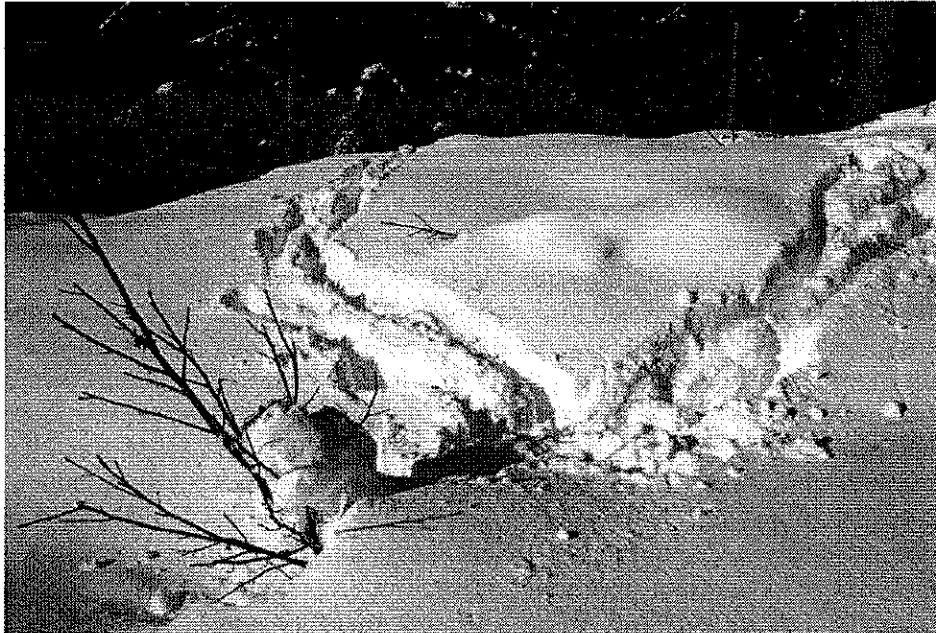


**Moose habitat selection in relation to forest harvesting in a
deep snow zone of British Columbia**
Winter 2002



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SUMMARY

Ungulate winter range (UWR) management in southeast British Columbia is premised on the application of habitat management guidelines within defined winter range zones. Existing guidelines and UWR boundaries are currently under review and will be finalized and legislated by 2003. It is the explicit objective of the West Kootenay UWR Committee to use all available empirical data on wintering ungulates in the review of current guidelines and boundaries.

This document reports a study of moose habitat use and distribution in the Lake Revelstoke Valley during February and March 2002. General objectives were to determine moose habitat preferences and gain an understanding of moose habitat ecology in the study area. Specific objectives were to determine the relative importance of forest openings and closed-canopy areas to moose, determine an upper elevational limit of moose use, and how moose are affected by increasing snow depth with increasing elevation. Our ultimate goal in these investigations was to contribute empirical data to the delineation of UWR zones and the establishment of habitat management guidelines.

During February and March 2002, we surveyed 49.9 km along 28 straight-line transects in a study area extending along the west and east sides of the Lake Revelstoke reservoir from Downie Creek to Encampment Creek. At each occurrence of moose tracks we performed habitat plots where we recorded GPS location, slope gradient, aspect, snow depth, canopy cover, tree species composition, habitat type, structural stage, browse availability, and evidence of browsing. To measure habitat availability within the landscape, we performed similar habitat plots along transects at 100-m intervals.

Moose showed increasing selection for decreasing elevation, decreasing slope, and decreasing direct solar radiation. Ninety-five percent of moose use was below 1000 m elevation. Approximately 11% of moose use was above the current moose management line, which is at a mean elevation of 906 m. The greatest use of direct solar radiation was at intermediate values, but those values were also the most abundant in the study area. Logging roads were the most selected habitat type, followed by clearcuts. Moose used clearcuts more than 50% of the time. Logging roads and clearcuts accounted for more than 65% of moose use. Western redcedar/hemlock and Engelmann spruce/subalpine fir stands were avoided. Douglas-fir dominant stands were used in proportion to their availability. Structural stages 3 (herb/shrub) and 4 (pole/sapling) were selected. Selection dropped off consistently from structural stages 5-7 (young forest, mature forest, and old forest, respectively). Moose displayed preference for low canopy cover, avoidance of intermediate cover, and neutral selection of high cover. Seventy-eight percent of moose use occurred in habitats with $\leq 40\%$ canopy cover.

Highest selection for browse occurred in plots that had 21-30% browse cover. Plots with $<10\%$ browse cover were avoided, as were plots with $>30\%$ cover. Willow and black cottonwood were the most preferred browse species. Western redcedar was also preferred, and it was the most abundant browse cover available to moose.

Habitat models that were based solely on capability variables (static topographic variables) did not deserve any consideration relative to models based solely on suitability variables (dynamic vegetation-based variables; evidence ratio [ER] $\sim 50,000:1$). Similarly, models that were mappable (mappable variables are those readily available in digital format) did not deserve any consideration, compared to models that included

variables that were only possible to collect from the ground (e.g., shrub species, snow depth, fine-scale road use; ER=15,236:1). When willow presence was removed from the “best” model, the resulting model was only 527 times as likely to represent the system. The “best” mappable model included elevation, slope, structural stage, and Douglas-fir overstory cover. Removing elevation from this model made the resultant model 1.2 times as likely, meaning that a model without elevation also deserves consideration.

From these findings, we suggest that moose in this system were governed more by food availability, particularly willow, than by forest cover. Snow depth was not a driving variable, nor was mature forest cover. As a result, our findings do not support a current tendency towards the retention of denser forests to encourage refuges of lower snow depths. Moose selected stands that had little or no forest cover, even during the period of deepest snow accumulation. Conversely, 89% of moose tracks were observed below the current upper boundary, almost exactly matching the West Kootenay UWR Committee’s target of 90%. On this basis we support the location of the current UWR boundary.

Snow depths experienced during our study were about average, and therefore provide a degree of validity to our results. However, we recognize the limitations of 1 winter of data collection, and therefore recommend additional work to confirm the findings reported here. Additional work should also focus on the establishment of stand-level guidelines including patch size and retention guidelines.

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INTRODUCTION

Forest managers are no longer charged merely with sustained yield timber management. As non-timber values have gained prominence, diverse and sometimes competing objectives have necessitated scientific studies to ensure the long-term maintenance of a wider range of values, including wildlife. Management of ungulates during the winter, particularly in deep snow zones, can sometimes compete with timber values. Mule deer (*Odocoileus hemionus*), and especially caribou (*Rangifer tarandus*), have shown preference for older stands of trees (Armleder et al. 1994, Apps et al. 2001), stands that also provide valuable timber.

Relative to other ungulates, however, moose (*Alces alces*) appear to be more resilient to forest management activities. Several studies have indicated a preference for clearcuts (Tomm et al. 1981, Rempel et al. 1997), even in winter (Poole and Mowat 2002), provided there is little harassment from humans or predators (Tomm et al. 1981, Rempel et al. 1997). Despite these findings, uncertainty remains as to whether these patterns are consistent in areas of very deep snow, such as the northern Columbia Mountains of British Columbia (BC), where valley bottom snow depths often exceed 1 m.

Snow can affect ungulates in at least 2 ways – firstly, it increases energy expenditure associated with locomotion. For example, deer require roughly 6 times the energy to walk through 50 cm of snow when compared to bare ground (Parker et al. 1984). Secondly, snow covers understory vegetation, reducing the availability of food sources (Hovey 1987). By modelling net energy balances of deer and elk, some researchers have suggested that the latter is of greater consequence (e.g., Wickstrom 1984). This may also be true of moose, which are adapted to eating very abundant and rapidly growing food sources such as willow and alder (Oldemeyer et al. 1977), and are predicted to be less affected by snow depth due in part to their large bodies.

The effects of deep snow can be mediated somewhat by the presence of certain mature tree species, particularly Douglas-fir (*Pseudotsuga menziesii*), western redcedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) (Pauley et al. 1993, D'Eon 2001). Although mature stands tend to contain less food, they can provide security from predators, bedding sites, and easier movement. Very old stands have also been shown to provide a good interspersed of both cover and forage (Armleder et al. 1984).

In this study, we determined the relative importance to moose of forest openings that provide food, and more closed forest areas that provide relief from deep snow. We also estimated the upper elevation boundary of moose during late winter, and investigated how they react to increasing snow depths with elevation. These objectives were of particular importance because the delineation of ungulate winter range boundaries, and the management guidelines within those boundaries, become legally binding in BC in 2003. To date, many of the decisions regarding moose management in southeastern BC have been based on expert opinion and limited empirical data, and have yet to be tested with independent data. This study is an attempt to do so, using track encounter transects during late winter.

Review of moose literature in the study area

Since European settlement, moose have not been known to be abundant in the area north of Revelstoke, and are believed to have expanded their range into this area as a consequence of forest clearing that provided abundant food (Simpson et al. 1988). There are few published documents on moose ecology in southeast BC or areas with similar habitat conditions. This is perhaps due to their recent expansion into this area. The vast majority of moose literature pertains to areas outside southeast BC and is concentrated on the ecology of moose in boreal habitat. As a result, little is known about the ecology of moose in the mountainous regions of BC, especially in the unusually deep snow conditions of the north Columbia Mountains.

However, notable exceptions exist and provide a basis for a study design in the area north of Revelstoke (Bonar 1983, 1985, Simpson et al. 1988). Bonar (1983) studied population levels in the Columbia Basin from Mica Dam to Revelstoke prior to flooding in 1983. The impetus for this study was concern over anticipated loss of moose habitat, mainly riparian areas, because of imminent large-scale flooding for hydroelectric development. He stated that from 1977 to 1983 population levels were stable at 250 to 270 moose. Prior to flooding the majority of moose winter habitat was in valley-bottom, riparian locations.

In a winter food study after flooding of the Columbia system, Bonar (1985) stated that moose winter habitat was confined to areas below 1000 m. He found that spatial distribution of moose was explained by a combination of food palatability and availability. He found very definite food preferences that shifted with food availability based on snow depths. In early winter (November/December), when snow depths were not restrictive, moose preferred deciduous shrub species such as dogwood (*Cornus stolonifera*) and willow (*Salix spp.*). As late winter (January to March) snow depths buried vegetation and restricted movement, moose retreated to denser coniferous forests with shallower associated snow depths. Late winter food preferences then shifted to available species such as yew (*Taxus brevifolia*) and western redcedar.

Simpson et al. (1988) provided a comprehensive review of moose ecology in the Columbia River drainage from Mica Dam to the northeast arm of Arrow Lake and associated tributaries. They suggested that moose in this area demonstrate a general winter pattern of occupying valley bottom areas dominated by mature forests associated with riparian areas. Using telemetry data from 1983/84, they found that during low snow-depth seasons moose used early successional habitat extensively, presumably to feed on abundant preferred browse. These areas included clearcuts, recent burns, riparian areas, wetlands, and avalanche chutes. Use of early successional habitat dropped dramatically as snow depths increased. Mature forests made up 78% of March telemetry locations, suggesting that moose sought shallower snow depths during this period.

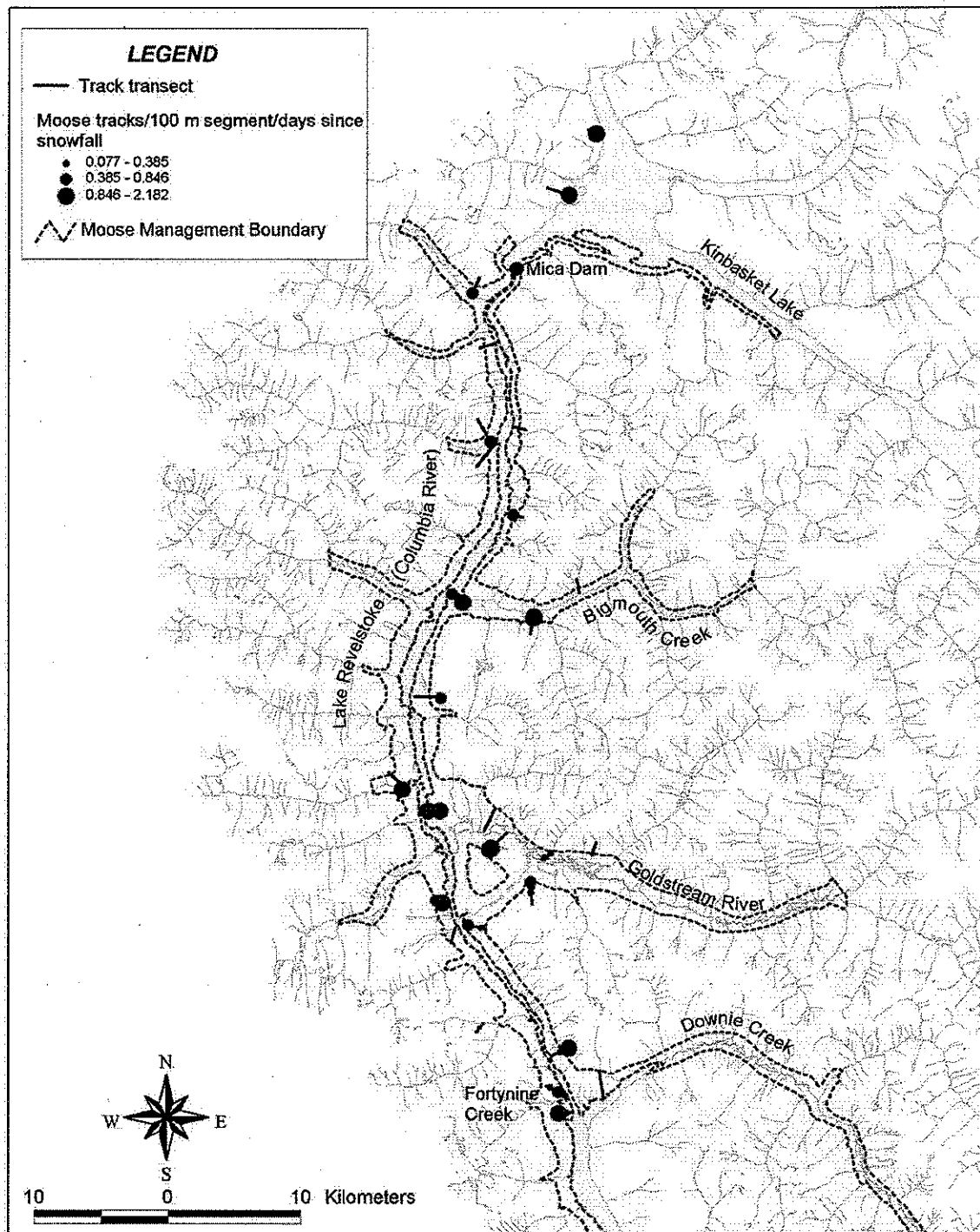


Figure 1. Lake Revelstoke Valley moose winter range study area and the 28 snow track transects surveyed in February and March 2002. Also shown are the number of moose tracks recorded/100 m segment/days since snowfall, and the current moose management boundary.

STUDY AREA

The study area was located in the northern Columbia Mountains along the shores of Lake Revelstoke and its tributaries from Encampment Creek in the north to Downie Creek in the south (Figure 1). The centre of the study area is 85 km N of Revelstoke, BC, within the Columbia Forest District, Nelson Region. Valley bottom elevation is approximately 570 m asl, and surrounding ridges and mountain peaks range from 2,000 – 3,000 m. The valley is bisected by the Lake Revelstoke reservoir, created by damming a portion of the Columbia River in 1983. The reservoir varies in width from 250 m – 1,400 m, but is usually about 700 m wide. On the east side of the reservoir, there is a 2-lane highway that parallels the shoreline, usually within 100 m, that was built to service Mica Dam and is now also used by recreationists and logging trucks. In contrast, the west side of the reservoir is accessible only by boat or small ferry, except at its northern tip. The main forest operators in the area were Downie Timber Ltd., Evans Forests Products, and Revelstoke Community Forests Corporation. There was also 6,000 ha of private land, located on both sides of the reservoir from 10 km north of Bigmouth creek to just south of the Goldstream River. Forest harvesting also occurs on this private land, but no forest cover data were available. Using our transects as an estimate of habitat type, 70.6% (60 of 85 availability plots) of the private land was in a clearcut state (i.e., logged and ≤ 20 yr old), compared to 24.7% for the remainder of the study area.

The dominant biogeoclimatic subzone and variants in the study area are Interior Cedar-Hemlock wet-cool (ICHwk1), very wet-cool (ICHvk1) and to a small extent moist-warm (ICHmw3), at lower elevations (Braumandl and Curran 1992). Upper elevation areas are dominated by Engelmann spruce-Subalpine fir very wet-cold (ESSFvc). The transition between the ICH and ESSF zones occur at approximately 1,280-1,400 m, depending on the subzone-variant and aspect.

Dominant tree species in these ICH subzones are western redcedar, western hemlock and to a smaller extent Douglas-fir. At higher elevations, where the ESSF replaces the ICH, large tracts of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) occur.

METHODS

Study area stratification

Simpson et al. (1988) suggested that early winter range extends to 1,219 m and late winter range is restricted to < 914 m. We therefore sampled up to 1,300 m to attempt to capture all possible late winter habitat. To ensure sufficient sampling among ecological strata, we stratified this range by low elevation (< 700 m) and high elevation (700-1,300 m) zones. As well, we stratified the study area by aspect using the 4 cardinal direction classes. We then allocated transects based on equal representation among all 8 strata. Within strata, we randomly chose transect start locations.

Since our sampling area was large (~50,000 ha), we chose to survey a maximum number of transects once, rather than surveying half that number twice at different times within the late winter season. Although this sacrificed the precision of parameter estimates, it was more likely to capture a broader range of ecological conditions, which was likely to improve model accuracy. We intentionally dispersed field crews throughout the study area to minimize spatial and temporal biases. We confined all sampling to late winter (February and March) since this was the time of year that was most constraining to ungulate distributions.

Field methods

From start locations we established straight-line transects oriented perpendicular to contour lines (refer to D'Eon 2001 for review of methods). Briefly, we recorded the number and location of all ungulate tracks (by species) encountered along transects. We could not distinguish white-tail deer (*O. virginianus*) from mule deer because their tracks are very similar (Murie 1974). We also recorded wolf (*Canis lupus*), cougar (*Felis concolor*), wolverine (*Gulo gulo*), and marten (*Martes americana*) tracks, but formal analyses were restricted to ungulates. A single track was defined as a transect that intersected a single set of tracks. If a transect intersected a trail so that the number of individuals could not be distinguished, it was recorded as a trail (Thompson et al. 1989). We termed these track locations "use" plots and collected the following habitat and biophysical data: Global Positioning System (GPS) location, three snow depths, 4 estimates of canopy cover¹, visual estimates of tree species composition within a 20 m radius, general habitat type (riparian/wetland, clearcut [within 20 yr], logging road, deciduous leading, Cedar/Hemlock leading, Douglas-fir leading, and Engelmann spruce/subalpine fir leading), and structural stage (1=sparse bryoid, 2=herb, 3=herb/shrub, 4=pole/sapling, 5=young forest, 6=mature forest, 7=old forest; for complete description see FMDTE 1998). As well, within a 5.65 m circular plot we estimated available browse cover and recorded browse sign. Available browse cover was defined as the percent cover of shrubs (without leaves present) or tree branches within 2 m from the surface of the snowpack. If there were > 1 tracks within a 10 m portion of a transect, all tracks were recorded, but only 1 use plot was done. To measure habitat availability within the landscape, we performed similar habitat plots along all transects at 100-m intervals. We also recorded when tracking conditions did not permit track detection to distinguish these instances from a zero value. To increase the chance of encountering tracks, we waited a minimum of 24 hours between the end of a snowfall and a subsequent sampling session. We recorded the amount of time since the previous snowfall to permit the application of correction factors (Thompson et al. 1989).

¹ Note that "canopy cover" differs from the term "crown closure" that is sometimes used by foresters. Canopy cover is the percent of sky that is obscured by branches or foliage, whereas crown closure fills in the gaps between the branches.

Data management and analysis

We imported the Universal Transverse Mercator coordinates of each GPS location into Arcview, a Geographic Information System package. For each location we extracted elevation, percent slope, aspect in degrees, and solar radiation. Elevation was obtained from a digital elevation model, which was created from 1:20,000 scale Terrain Resource Inventory Mapping (TRIM). Slope and aspect were derived from the DEM, at a resolution of 25 m pixels. Two models of solar radiation were created: solar "duration" and solar "direct" (Kumar et al. 1997). Duration measures the hours of sunlight that hits each pixel, and as such accounts for shading from adjacent mountains. Direct measures the solar radiation that hits each pixel in kW/m^2 , and may incorporate the effect of slope, although it is difficult to tell from Kumar et al. (1997). Each pixel represented the mean measurements that were taken once every 2 hours for a 24-hour period each week from 11 January to 31 March (Mowat et al. 2002a). Because this model was created for the entire west Kootenays, the resolution was coarser (50 m pixels) than other topographic variables to save computing time. Solar radiation was considered a surrogate for aspect because of its high correlation with aspect class ($r = 0.834$, R. D'Eon unpublished data). As well, solar radiation may be an improvement over aspect, because it can be analysed as a continuous variable in multivariate statistical procedures.

For non-topographic variables (i.e., forest cover), we based our analyses solely on ground-based data because 17% of our transects occurred on private land, where no digital forest cover information was available. This forced us to use structural stage estimates (FMDTE 1998) as an approximation of stand age. However, using ground-based variables also permitted us to evaluate fine-scale habitat selection, such as the potential use of roads or individual shrub species, which would not have been possible using remotely sensed data. To examine the effect of overstory tree species, we multiplied percent composition by the amount of canopy cover. This was to avoid situations where there were 1 or 2 trees in the area, making up 100% of the crown composition, yet accounted for very little overstory biomass.

We began our analyses by making univariate comparisons of the proportion of used habitat to what was available. We converted "trail" to 5 tracks, and converted tracks to number of tracks/days since snowfall to correct for the amount of time that elapsed since the last snowfall (note that this would not matter for multivariate analyses since data were converted to presence/absence). Proportional use was calculated by dividing the number of tracks within the category of a variable by the total number of tracks. The same was done with the 100-m-interval availability plots. We placed less emphasis on the statistical significance of these comparisons because we were more interested in the magnitude of the differences (Johnson 1999), and the selection trends across the range of the habitat variable. We summarized 4 TRIM-based remotely sensed variables: slope, aspect, elevation, and direct solar radiation. We also summarized 4 ground-based variables: habitat type, structural stage, snow depth, and canopy cover. We used the results of the univariate analyses, as well as results from other studies, to formulate candidate multivariate models (Burnham and Anderson 1998).

In our analyses we differentiate between use and selection. Use was treated as the proportion of a habitat category that was used, whereas selection indicates use that was disproportionate to what was available in the study area. For example, a habitat category

that was used 90% of the time, but was also available in 90% of the area, was not selected. By contrast, a habitat type that was used 30% of the time, but occurred in 15% of the study area, was selected at a 2:1 ratio. To help gauge selection, we calculated Ivlev's electivity index (Krebs 1989). This is simply proportional use minus proportional availability divided by the sum of proportional use and availability. Values can range from -1 to +1. Positive values indicate preference and negative values indicate avoidance. In the above examples, Ivlev's index would be 0 and 0.33, respectively. One drawback of Ivlev's index is that values are sensitive to low sample sizes such that 1% available and 0% use produces a value of -1, however, we present proportional bar graphs so that this problem can be evaluated.

Multivariate analyses were done using logistic regression, by converting moose track data to presence/absence and modelling the probability of detecting a moose. In other words, presence was defined as each use plot that was conducted. This differed slightly from D'Eon's (2001) coarser-scale method where use was attributed to an entire 100 m interval of a transect. We used an information-theoretic approach to guide the selection of competing multivariate models (Burnham and Anderson 1998). This approach ensured that results were robust to model selection uncertainty, providing reliable inferences by accounting for model overparameterization (Burnham and Anderson 1998, Anderson et al. 2000). We developed an a-priori set of first-order candidate models to explain moose habitat selection. We selected the "best" candidate model(s) using Akaike Information Criteria (AIC) (Anderson et al. 2000), and tested for overdispersion (Anderson et al. 1994). AIC units are a relative indication of model parsimony, which is a compromise between bias (under-parameterization) and variance (over-parameterization). We used Akaike weights to gauge the relative importance of different factors affecting habitat selection (Burnham and Anderson 1998), and took the ratio of the AIC weights for different candidate models as the weight of evidence that a given model was better than another (Burnham and Anderson 1998). As suggested by Anderson and Burnham, (2002), for each model we presented AIC values, the maximized log likelihood (Log L), the number of parameters (k) and AIC weights (AIC_w), and only reported model fit statistics for the global models. We also provided evidence ratios relative to the "best" model. Evidence ratios are simply the ratio between AIC_w of any 2 models, and are a means of gauging the relative support of one model over another.

We used 2 modelling approaches. The first was more heuristic in nature because it included consideration of all variables, including those that were not mappable, such as presence of individual shrub species or snow depth. Also, variables that were too fine-scaled to be detectable using remote sensing, such as specific use on a logging road, could be examined. We hypothesized that including non-mappable variables would reveal more about moose ecology than using strictly remotely-sensed variables. We also differentiated between "capability" variables and "suitability" variables. We defined the former as temporally static whereas the latter are temporally dynamic. We were interested in comparing the predictive ability of those 2 sets of variables, because deer and elk selection can be well explained by slope, elevation, and aspect or some measure of solar radiation (D'Eon 2001), whereas the same may not be true of moose. We also gauged the relative importance of different food sources such as willow or western redcedar by removing those variables from the top model set.

Since part of this exercise was predictive in nature for management purposes, our second approach to modelling used only mappable variables. Anderson and Burnham (2002) argue that for predictive modelling, model averaging should be considered. Model averaging is appropriate when there are >1 models in the top model set. We considered all models within 0-4 AIC as the top model set, and incorporated model selection uncertainty by deriving parameter estimates from this top model set (Burnham and Anderson 1998: pp 139). Model averaging was done by using the AIC_w of the top model set, scaling them to one, and multiplying those new weights by the parameter estimate. In other words, a weighted average of the parameter estimates was obtained.

RESULTS

We surveyed a total of 49.9 km across 28 transects, yielding a mean transect length of 1.78 km (range 0.8 – 2.6 km), and 499 availability plots. There was a 3 week gap between when the first 22 transects were surveyed (February 5-28) and the remaining 6 (March 22-24). We recorded 124 moose tracks and 1 moose trail distributed across 63 moose use plots. One wolverine trail, 1 set of caribou tracks, and 142 marten tracks were also counted. We also found 81 deer tracks concentrated in 7 plots. With one exception, the deer tracks were localized near Fortynine Creek, in the SW portion of the study area. With only 7 plots, no formal analyses were possible for deer. The spatial distribution of moose tracks is presented in Figure 1.

Snow pillow data near the study area (Mt. Revelstoke and Molson Creek) indicated that snow depths were about 18% above normal, but these automated stations were above 1,800 m elevation. Snow survey measurements at Downie Slide, which is located at 980 m elevation, indicated that depths were 15% below normal on March 1 but by April 1 they had reached normal levels (MSRM 2002).

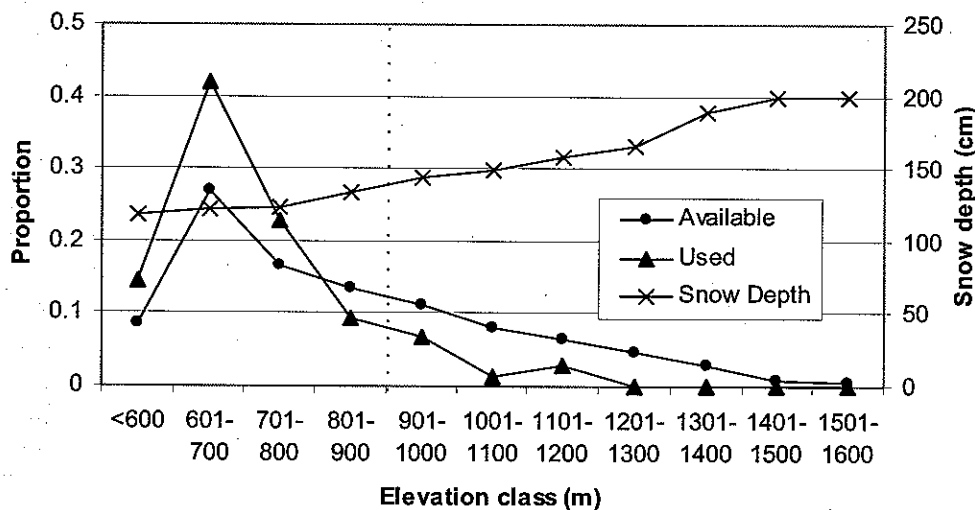


Figure 2. Snow depth and proportions of available area and moose tracks (corrected for days since snowfall) by 100-m elevation class in the Lake Revelstoke Valley, February/March 2002. Dashed vertical line represents the mean elevation of the current moose winter range boundary (Revelstoke Minister's Advisory Committee).

Univariate analyses

Topographic variables

Moose showed increasing selection for decreasing elevation, decreasing slope, and decreasing direct solar radiation (Figs. 2, 3). Ninety-five percent of moose use was below 1,000 m elevation. Approximately 11% of moose use was above the current moose management line, which is at a mean elevation of 906 m. The greatest use of direct solar radiation was at intermediate values ($\sim 70,000 \text{ kW/m}^2$), but those values were also the most abundant in the study area. Unlike solar radiation, there were no consistent trends from cold to hot aspects (Fig. 3c). There were no differences in the number of tracks (/km/days since snow) between the east and west sides of the Revelstoke reservoir (East: $\bar{x} = 0.0068$, $SE=0.0023$, $n=13$ transects, West: $\bar{x} = 0.0057$, $SE=0.0017$, $n=15$ transects). The east and west sides were assumed to have high and low human use, respectively.

Non-topographic variables

Logging roads were the most selected habitat type, followed by clearcuts (Fig. 4a). More than 50% of moose tracks were detected in clearcuts. Logging roads and clearcuts accounted for more than 65% of moose use. Deciduous stands and riparian/wetland habitats were very rare so the reliability of selection patterns is tenuous. Western redcedar/western hemlock and Engelmann spruce/subalpine fir stands were avoided, although the latter occurs in deeper snow at higher elevation. Douglas-fir dominant stands were used in proportion to their availability (Fig. 4a). These patterns were consistent between the 2 sampling sessions (Appendix 1), even though snow depths increased by 18% during this 3 week gap. The selection pattern among structural stages was not linear, although sample sizes were low for stages 1 (sparse/bryoid) and 2 (herb; Fig. 4b). Most of the area in structural stage 1 was actually road. Structural stages 3 (herb/shrub) and 4 (pole/sapling) were selected. The highest proportional use occurred in the herb/shrub stage. Selection dropped off consistently from structural stages 5 to 7 (young forest, mature forest, and old forest, respectively). Canopy cover displayed a U-shaped selection pattern, with highest use and selection for low values, and neutral selection of high values (Fig. 4c). Seventy-eight percent of moose use occurred in habitats with $\leq 40\%$ canopy cover.

Selection of browse cover displayed a mild inverted U-shaped distribution (Fig. 5a). The highest selection for browse occurred in plots that had 21-30% browse cover. Plots with $<20\%$ browse cover were not selected, as were plots with $>30\%$ cover. Willow and black cottonwood (*Populus balsamifera*) were the most preferred browse species (Fig. 5b). Western redcedar was also preferred, and it was the most abundant browse cover available to moose.

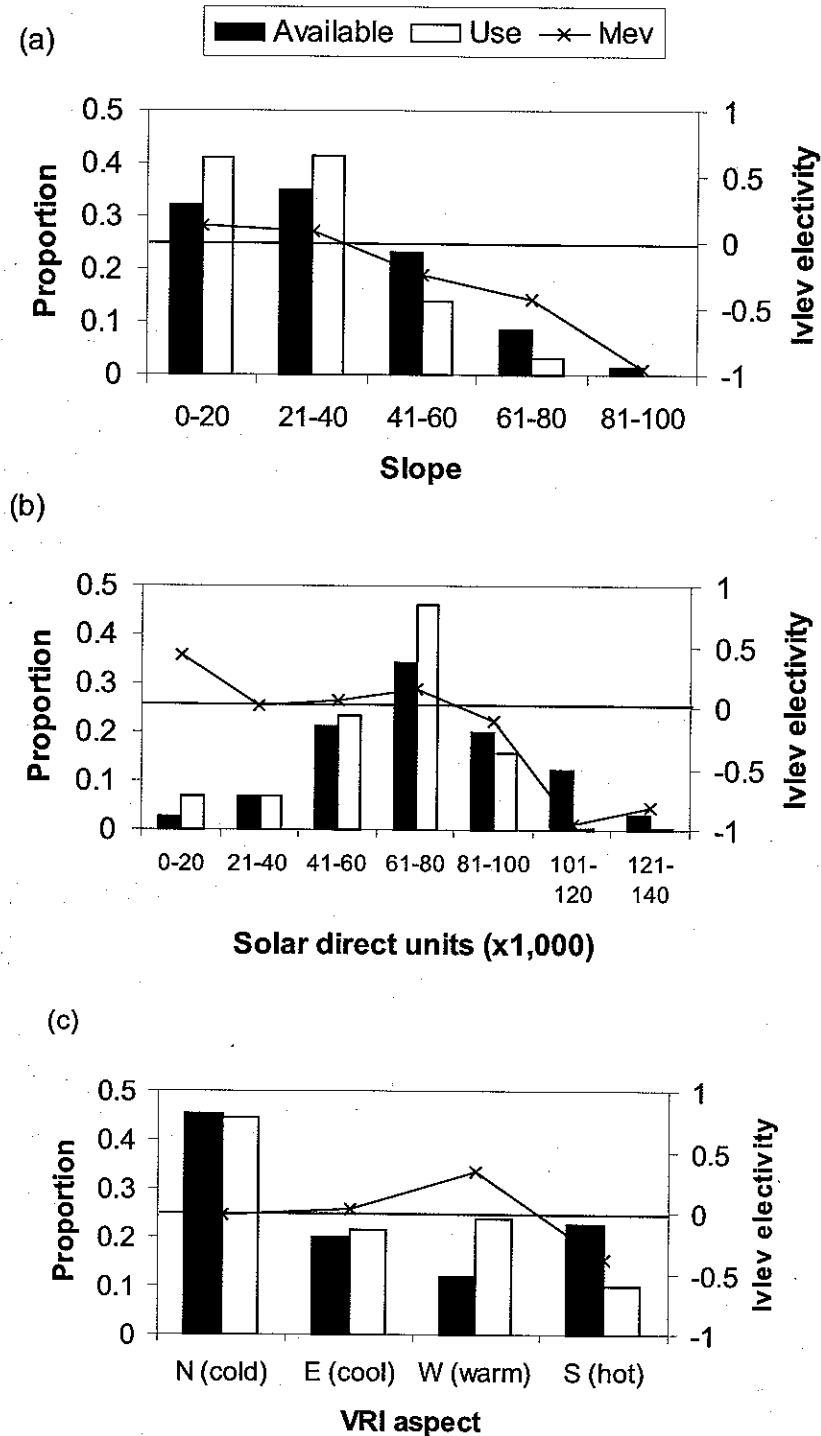


Figure 3. Proportional moose use, availability, and Ivlev's electivity index for % slope (a), direct solar radiation (kW/m^2) (b), and vegetation resource inventory (VRI) aspect classes (c) (N = north ($286-59^\circ$), E = east ($60-153^\circ$), S = south ($136-240^\circ$), W = west ($241-285^\circ$)) during a winter track study in the Lake Revelstoke Valley, British Columbia, February-March 2002. Available and use distributions are not significantly different for any of the variables (G-test, $p > 0.05$).

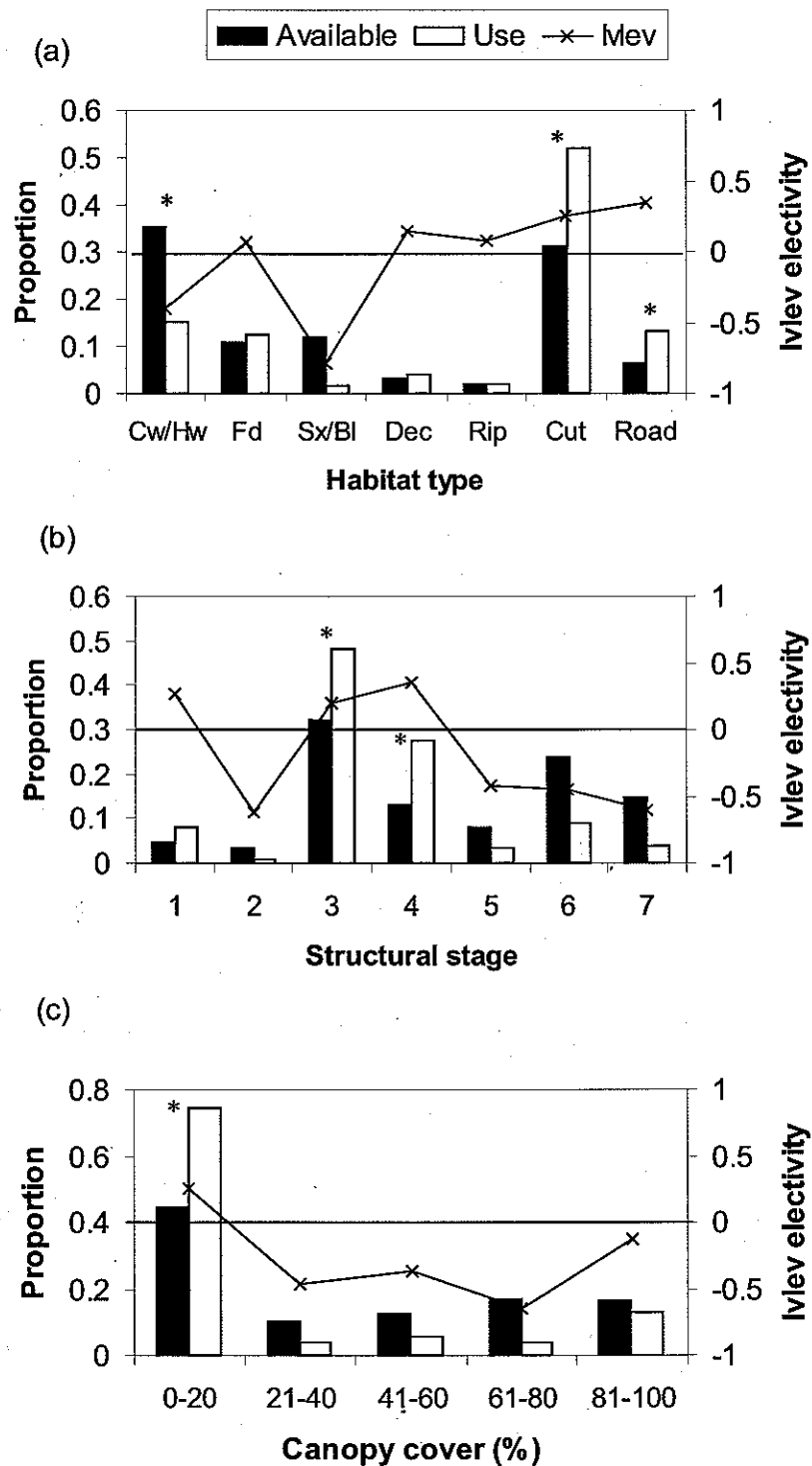


Figure 4. Proportional moose use, availability, and Ivlev's electivity index for habitat type (a), structural stage (b), and canopy cover (c), during a winter track study in the Lake Revelstoke Valley, British Columbia, February-March 2002. See text for categorical descriptions of (a) and (b). Available and use distributions were significantly different for all 3 variables (G_{adj} test, $p < 0.05$). Significant G_{adj} -test result indicated (*) at $\alpha = 0.05$.

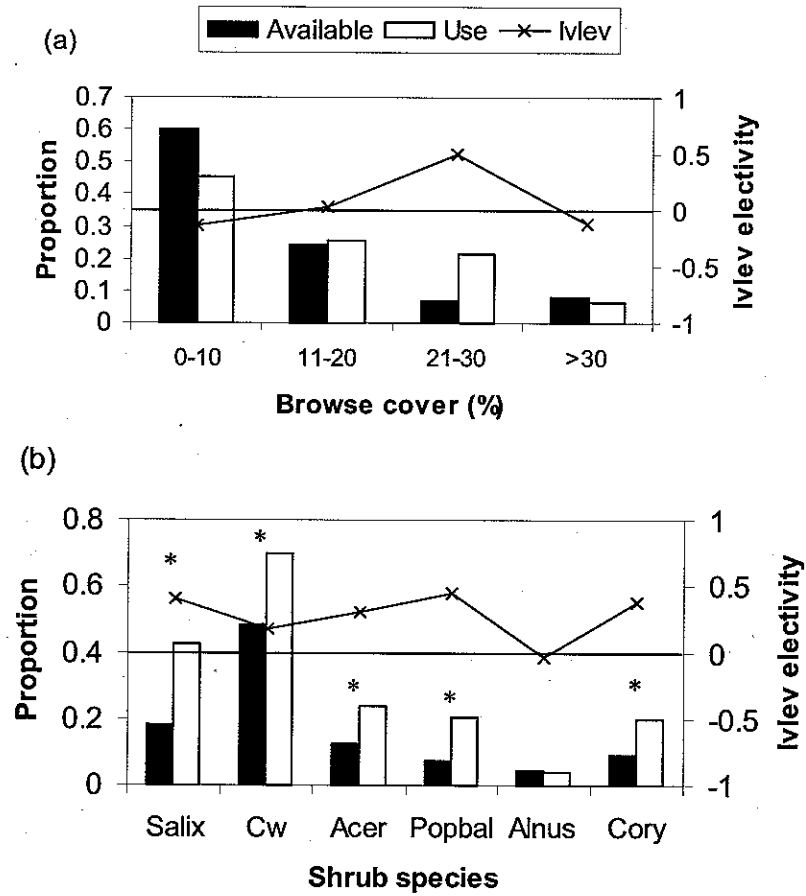


Figure 5. Proportional moose use and availability of browse cover (a), and browse species presence in used vs. available plots (b) in the Lake Revelstoke Valley, February 2002. Also presented is Ivlev's electivity index. For browse species, use was defined as presence in use plots. Proportions do not equal 100% because they were calculated for each species. Only the 6 most abundant species on transects were presented. Acer = *Acer glabrum*, Alnus = *Alnus spp.*, Cory = *Corylus cornuta*, Cw = *Thuja plicata* (< 2m), Popbal = *Populus balsamifera*, Sal = *Salix spp.* Significant G_{adj} -test result indicated (*) at $\alpha = 0.05$. No differences occurred between used and available distributions for (a).

Multivariate analyses

Neither of the global models (the most parameterized models) showed signs of overdispersion. The ratio of the deviance to the degrees of freedom was 0.73 for the heuristic global model and 0.79 for the predictive global model. Ratios much greater than one indicate overdispersion (SAS 1999).

Heuristic models

The most parsimonious ("best") model included slope, direct radiation, logging road, structural stage, salix browse presence, cedar browse presence, and Douglas-fir overstory. Models that were based solely on capability variables did not deserve any consideration relative to models based solely on suitability variables (e.g., $AIC\omega_{14/17} \sim 50,000$; Table 1). Similarly, models that were mappable did not deserve any consideration compared to models that included variables that were only possible to collect from the ground (e.g., shrub species, snow depth, fine-scale road use; $AIC\omega_{1/16} = 15,236$; Table 1). When the presence of willow, a preferred food item, was removed from the best model, the resulting model was only 527 times as likely to represent the system ($AIC\omega_{1/15}$; Table 1). When the same was done with western redcedar browse presence, the resulting model was 3.64 times as likely ($AIC\omega_{1/5}$; Table 1). When Douglas-fir overstory biomass was removed from the best model, the resulting model was 3.71 times as likely ($AIC\omega_{1/6}$; Table 1). Replacing snow depth with elevation model did not substantially change the evidence of one model over another ($AIC\omega_{2/3} = 1.31$). We did not include canopy cover in our candidate models, because it was highly correlated with structural stage ($R=0.74$).

Predictive models

We included structural stage as a mappable variable because we could convert this to age, based on approximate age ranges. We did not include roads in our mappable model set because, for management purposes, it would provide little benefit to pick out thin, linear features on a map. Also, we visually inspected digital orthophotos in the study area and overlaid different road types, and found numerous instances where the TRIM roads could not be corroborated by the orthophotos. We did however, find good corroboration between clearcuts in the digital forest cover data (activity code = L, age ≤ 20) and the orthophotos.

The best mappable model included elevation, slope, structural stage, and Douglas-fir overstory. Removing elevation from this model made the resultant model 1.2 times as likely, meaning that a model without elevation also deserves consideration. Solar direct consistently performed better than duration at explaining the moose data. We only present one example, but the best predictive model had an evidence ratio of 4.68 relative to the same model with solar duration substituted for direct ($AIC\omega_{1/4}$; Table 2). Solar duration was not included in the global model because of the high correlation between direct and duration ($R=0.70$).

Unlike the previous set of models (see above, Table 1), the global model was included in the top model set ($\Delta AIC = 2$), suggesting that it was not overparameterized. The top 3 models should all be given consideration using this information-theoretic approach. To use this information as a predictive tool, we used the model averaging technique to incorporate inference from the top 3 models. Model parameter estimates are given in Appendix 2.

Table 1. Models used to predict the probability of detecting a moose in the Lake Revelstoke Valley, BC, using logistic regression equations. Variables included are both mappable (readily available in digital format) and non-mappable. AIC values are a relative indication of model parsimony (lower values indicate more parsimony), k is the number of parameters in the model (including the intercept), Log L is the maximized log-likelihood, ΔAIC is the difference in AIC values between the any model and the most parsimonious model, AIC ω_i is the relative influence of each model, and the evidence ratio is ratio of AIC ω_i relative to the best model. R^2 for the global model (no. 13) = 0.21, and classification success was 0.79. Direction of parameter (+ve or -ve) is given in brackets for the global model. Sample size was 562.

no.	Model structure ^{1,2}	AIC	k	Log L	ΔAIC	AIC ω_i	Evidence ratio
1	slope + sol_dir + road + stru_stag + salix_bro + cw_bro + fd_bio	349.70	8	-166.85	0.00	0.256	1.00
2	slope + sol_dir + road + stru_stag + salix_bro + cw_bro + fd_bio + sno_dep	350.66	9	-166.33	0.96	0.159	1.62
3	elev + slope + sol_dir + road + stru_stag + salix_bro + cw_bro + fd_bio	351.20	9	-166.60	1.50	0.121	2.11
4	slope + sol_dir + road + salix_bro + fd_bio	352.01	6	-170.00	2.31	0.081	3.17
5	slope + sol_dir + road + stru_stag + salix_bro + fd_bio	352.29	8	-168.14	2.58	0.070	3.64
6	slope + sol_dir + road + stru_stag + salix_bro + cw_bro	352.32	7	-169.16	2.62	0.069	3.71
7	elev + slope + sol_dir + road + stru_stag + salix_bro + cw_bro + fd_bio + sno_dep	352.45	10	-166.22	2.75	0.065	3.95
8	slope + sol_dir + log_20 + road + salix_bro + fd_bio + sno_dep	352.63	8	-168.31	2.93	0.059	4.32
9	slope + sol_dir + road + salix_bro	353.88	5	-171.94	4.18	0.032	8.07
10	elev + slope + sol_dir + log + 20 + road + salix_bro + cw_bro + fd_bio + sno_avsnodep	353.91	10	-166.95	4.21	0.031	8.20
11	slope + sol_dir + road + salix_bro + sno_dep	354.05	6	-171.02	4.34	0.029	8.78
12	log_20 + road + stru_stag + salix_bro + cw_bro + fd_bio + sno_dep	355.79	8	-169.89	6.09	0.012	20.99
13	elev(-) + slope(-) + sol_dir(-) + log_20(+) + road(+) + stru_stag(-) + salix_bro(+) + cw_bro(+) + fd_bio(+) + cwhw_bio(-) + sno_dep(-)	356.25	12	-166.13	6.55	0.010	26.48
14	log_20 + road + stru_stag + salix_bro + cw_bro + fd_bio + cwhw_bio + sno_dep	357.79	9	-169.89	8.09	0.004	57.05
15	slope + sol_dir + road + stru_stag + cw_bro + fd_bio	362.24	7	-174.12	12.54	4.9E-04	527.69
16	elev + slope + sol_dir + stru_stag + fd_bio	368.96	6	-178.48	19.26	1.7E-05	15,237.27
17	elev + slope + sol_dir	379.46	4	-185.73	29.76	8.8E-08	2,896,460.41
18	slope + sol_dir	379.96	3	-186.98	30.26	6.9E-08	3,722,849.77
19	Null	396.39	1	-197.20	46.69	1.9E-11	Billions

¹ Variables are elev=elevation; slope=% slope; sol_dir=direct solar radiation; log_20=areas that were logged within 20 years; road=logging road; stru_stag=structural stage; salix_bro and cw_bro=the presence of salix or western redcedar browse, respectively; fd_bro and cwhw_bro=an index of overstory biomass of Douglas-fir and western redcedar and western hemlock, respectively; sno_dep=snow depth.

² Variables in bold were derived from remotely sensed TRIM data; other were measured on the ground.

Table 2. Predictive models used to determine the probability of detecting a moose in the Lake Revelstoke Valley, BC, using logistic regression equations. Variables included have the potential to be mapped based on available digital data. AIC values are an indication of model parsimony (lower values indicate more parsimony), k is the number of parameters in the model (including the intercept), Log L is the maximized log-likelihood, ΔAIC is the difference in AIC values between any model and the most parsimonious model, AIC ω_i is the relative influence of each model, and the evidence ratio is ratio of AIC ω_i , relative to the best model. A lower evidence ratio indicates similar evidence among models. R^2 for the global model (no. 3) = 0.21, and classification success was 0.79. Direction of parameter (+ve or -ve) is given in brackets for the global model. Sample size was 562.

no.	Model structure ^{1,2}	AIC	k	Log L	ΔAIC	AIC ω_i	Evidence ratio
1	elev + slope + sol_dir + stru_stag + fd_bio	368.96	6	-178.48	0.00	0.388	1.00
2	slope + sol_dir + stru_stag + fd_bio	369.33	5	-179.66	0.36	0.324	1.20
3	elev(-) + Slope(-) + Sol_dir(-) + log_20(-) + stru_stag(-) + Fd_bio(+)	370.96	7	-178.48	2.00	0.143	2.72
4	elev + slope + Sol_dur + stru_stag + Fd_bio	372.05	6	-180.03	3.09	0.083	4.68
5	elev + slope + Sol_dir + stru_stag	372.83	5	-181.42	3.87	0.056	6.91
6	slope + sol_dir + log_20 + Fd_bio	378.16	5	-184.08	9.19	0.004	99.24
7	elev + slope + sol_dir	379.46	4	-185.73	10.50	0.002	190.09

¹ Variables are elev=elevation; slope=% slope; sol_dir=direct solar radiation; log_20=areas that were logged within 20 years; stru_stag=structural stage; Fd_bio=an index of overstory biomass of Douglas-fir.

² Variables in bold were derived from remotely sensed TRIM data; other were measured on the ground

DISCUSSION

Current guidelines in the "Revelstoke Minister's Advisory Committee Land-Use Recommendations" call for 34-40% forest cover retention composed of ≥ 100 -120 year old trees, and crown closure within those forested units must be $\geq 70\%$. These recommendations are in place so that "Dense, mature stands with interlocking crowns provide the required attributes to facilitate foraging and movement opportunities". The results from our one year of study generally do not support these recommendations. Moose selected stands that had little or no forest cover, even during the period of deepest snow accumulation. They also preferred younger seral stages, particularly open shrub-dominated habitats. These results also differ from those found by Simpson et al. (1988) in the same study area. In their limited telemetry dataset, they found that moose used burns and cut areas less than 5% in February and March, compared to roughly 65% in our study. However, the availability of clearcuts has likely increased greatly since Simpson et al.'s (1988) study, and they did not report availability, so comparing selection between the 2 studies was not possible. Simpson et al. (1988) did find that moose used clearcuts and burns more than 30% from November through January. One aspect of the current moose guidelines that appears accurate is the elevation of the upper management boundary (Fig 2). This upper line fits within the West Kootenay Ungulate Winter Range Management Committee's objective to manage for 90% of ungulate population levels across 90% of their range (Mowat et al. 2002b). Approximately 89% of moose use was to the left (i.e., below) the dashed line in Figure 2, which represents the current moose management boundary. However, the relevance of this boundary is not abundantly clear given that moose responded much more to dynamic variables such as vegetation, rather than to static variables such as elevation (Table 1). In fact, it is possible that as logging progresses to higher elevations, winter moose use will as well, up to a point where snow depth buries food, or palatable browse no longer occurs naturally.

Our modelling indicated that food, particularly willow, was the single most important parameter influencing moose habitat selection. This occurred even though the study took place in an area with very deep, soft snow, where some might suggest that snow depth or elevation would be more influential. We discount the possibility that we did not sample a broad enough range of elevation or snow depths, because 35% of our sampling occurred above 900 m, and only 11% of moose use occurred there (of course, sampling up to 3,000 m would have likely yielded different results, but defining such a large "availability" would be biologically suspect). Note that including snow depth or elevation did not substantially change the evidence of the top models, but when willow was removed from the best model, the resulting model was only 528 times as likely to represent the system. It follows that if an animal has sufficient food, then the energy expenditures associated with locomotion become secondary. We suspect this to be the case in our study area. Sinking depths were often >70 cm and anecdotal observations of moose noted slow, labouring movements, with snow at or exceeding brisket height (Serrouya et al., pers. observations). However, the abundant supply of open, willow-producing habitats likely outweighed the costs of locomotion in deep snow. We predict that for moose, snow depths should become limiting when the threshold of food burial is reached, rather than the threshold of snow depth that limits movement.

Moose tracks were frequently found on logging roads, even though they only accounted for 6% of the study area. Moose may be selecting roads for at least 2 reasons: first, we hypothesize that moose used these relatively flat, continuous features to access higher elevation clearcuts. Moose preferred flatter slopes in both univariate and multivariate analyses. Roads used frequently by snowmobiles would further facilitate movement because of the effect they have on snow compaction, but we did not record the presence or proximity of snowmobile tracks. Secondly, moose may be targeting roads because they frequently occur on, or create, habitat edges. Habitat edges are known to have greater productivity, which could benefit willow abundance.

We found decreasing selection for increasing solar radiation. Mowat and Poole (2002) also found that moose had a negative relationship with solar radiation (in their case, solar duration). They postulated that this was more related to the avoidance of deer and elk forage areas, rather than a topographic influence. This could not have been the case in our area, because those ungulates were almost completely absent. Hurd (1999) also found that moose preferred cooler (north) aspects, although he also attributed this to resource partitioning with elk. Given the apparent consistency of moose selection for areas with less solar influence, we do not discount the possibility that a thermal mechanism is occurring that benefits moose in some way, either by influencing snow conditions or moose thermoregulation.

The presence of Douglas-fir overstory biomass in the multivariate models was difficult to explain because moose did not select for overstory cover. Removing Douglas-fir from the predictive models yielded a model that was not in the top model set, suggesting that this variable was important. In contrast, removing Douglas-fir from the heuristic models yielded a model that was within 2 AIC units of the top model set, meaning the model without Douglas-fir should not be discounted. Douglas-fir was more important in the predictive models, presumably because other ground-based vegetation features could not be included to explain moose use (however, we found no strong correlation between Douglas-fir and any of the other vegetative variables that were considered). Upon closer examination of the data, we discovered that as the presence of Douglas-fir increased in the overstory, moose decreased their avoidance of structural stages 5 and 6 (Fig. 6). The pattern was clearest for structural stage 5 – when no Douglas-fir was present in the canopy, this stage was completely avoided, but when Douglas-fir made up more than 40% of the canopy, it was used in proportion to what was available (note that this manipulation had little effect on structural stages 3 and 4, because moose are not in those stands for overstory cover). Some evidence of Douglas-fir canopy selection can also be noted in the analysis of habitat types. There was an avoidance of western redcedar/western hemlock and Engelmann spruce/subalpine fir stands, and neutral use of Douglas-fir stands (Fig 4a). But when we re-examined these habitat types filtering for greater than 40% canopy cover, we found that Douglas-fir stands were used in greater proportions (29% use vs. 20% available) relative to when the data included the complete range of canopy cover (12% use vs. 11% available; Fig 4a). Taken together, we interpret this to mean that when moose infrequently used cover, they preferred Douglas-fir over other stand types. We believe that the strong selection for open stands was overshadowing the subtle selection for Douglas-fir, when moose were in cover.

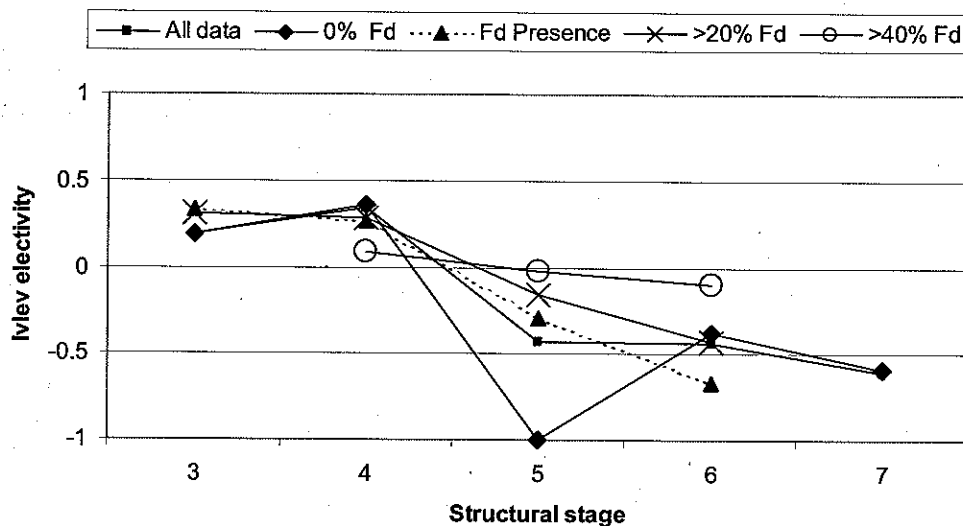


Figure 6. Moose selection for structural stage. Iterations included using the complete data set (All Data; $n=499$ availability (A), 63 use (U) plots), removing Douglas-fir from the data (0% Fd; $n=405$ A, 46 U), including only stands that had Douglas-fir present (Fd presence; $n=85$ A, 26 U), including stands where Douglas-fir was $\geq 20\%$ (20% Fd; $n=58$ A, 16 U), and including stands where Douglas-fir was $\geq 40\%$ (40% Fd; $n=29$ A, 9 U). Positive value indicates selection, negative value indicates avoidance.

Many authors recognize the importance of abundant forage to moose (Tomm et al. 1981, Pierce and Peek 1984, Moen et al. 1997). Of greater dispute is the need for cover. Our results differ from some (e.g., Pierce and Peek 1984, Huggard and Klenner 1997) who suggest that during deep snow periods, mature forest is important. However, Van Dyke et al. (1995) found that moose selected for shrub dominated wetlands and aspen stands in winter, and either avoided or did not select for evergreen cover. Their study was conducted in south-central Montana, where annual snowfall was 386 cm, and mean winter elevation use was 1807 m (winter defined as December through February). In their review, Balsom et al. (1996) found repeated reports of moose using mature forest cover in winter, but they found no evidence that cover was "critical". They correctly noted that management experiments would be required to address this issue. In our study, even though moose did not select for cover $> 20\%$, very dense stands were used in proportion to what was available. This U-shaped distribution (Fig. 4c) suggests that dense canopies, although not preferred, should not be completely discounted in moose management guidelines. This supposition is reinforced by the high use of cover reported by Simpson et al. (1988) in their preliminary study of moose in the same area.

Our current study was designed to determine dominant habitat selection factors by capturing as much biophysical variation as possible. It was, however, based only on 1 year's data. Hence, variability associated with climate, winter severity, snow quantity and quality, and population levels were not captured. Both winter severity and overall population levels can have strong effects on ungulate habitat selection (Boulanger et al.

2000). As well, the ideal-free distribution theory predicts that as population levels rise, a higher proportion of individuals occupy suboptimal habitats (but fitness is predicted to be equal in each habitat; Fretwell and Lucas 1970). Some evidence of this exists for other ungulates (Borkowski 2000, Boulanger et al. 2000). Snow survey data suggest that 2001-2002 was at near average levels, but population levels were likely higher than "typical" levels. This could potentially influence the patterns observed in this study because tracks could have been detected in habitats of lower habitat quality that would otherwise not have been used.

MANAGEMENT RECOMMENDATIONS

Our recommendations are based on the assumption that the long-term management of moose is a desired objective. We realize that moose are currently considered pests by some, because of the damage to cedar plantations. This issue is being addressed in part by a different study (D'Eon et al. 2002).

The clearest pattern that emerged in our study was that moose preferred food, and habitats that promote food growth such as willow in clearcuts. In the wet, productive areas that dominate the northern Columbia Mountains, willow grows rapidly following clearcuts, so detailed stand management guidelines to initiate willow production are probably not required. On the other hand, estimating the exact amount of cover required is not possible from this study. Such a question is best dealt with through landscape and stand-level experimentation (e.g., see Huggard and Klenner 1997 and Armleder et al. 1998). However, the fact that closed habitats (>40% cover) were used 22% leads us to conclude that cover should be included in management guidelines. The uncertainty surrounding questions of "how much? and where?" should be dealt with by leaving varying amounts, in various spatial arrangements, so that one prescription is not applied everywhere, because the consequences of being wrong would be much more serious.

Of greater concern, however, is the long term supply of habitat attributes that moose require. Such issues are best dealt with using timber supply and habitat projection tools such as ATLAS and SIMFOR or SELES, respectively. However, even a cursory review of the data provides some useful insight. In approximately 25-40 years, 45% of the landscape will be in structural stages, which, according to our current data, are avoided by moose. With the loss of riparian habitat due to flooding, moose have come to rely on early seral stands as a major food supply. Because of current seral stage distributions, these stands are expected to become less abundant over the next 25-40 years, particularly under 1,200 m elevation. To mitigate this, harvesting younger-than-optimal stands could be considered when there is an anticipated early-seral deficit. A more refined approach would be to zone areas with the intention of relaxing silvicultural practices that promote tree growth at the expense of prolonging shrub seral stages. Managers should avoid the temptation to harvest reserve areas because this would likely conflict with more difficult-to-manage attributes, such as the long term supply of coarse woody debris, snags or lichen that are required by a much broader range of organisms (Huggard 2000).

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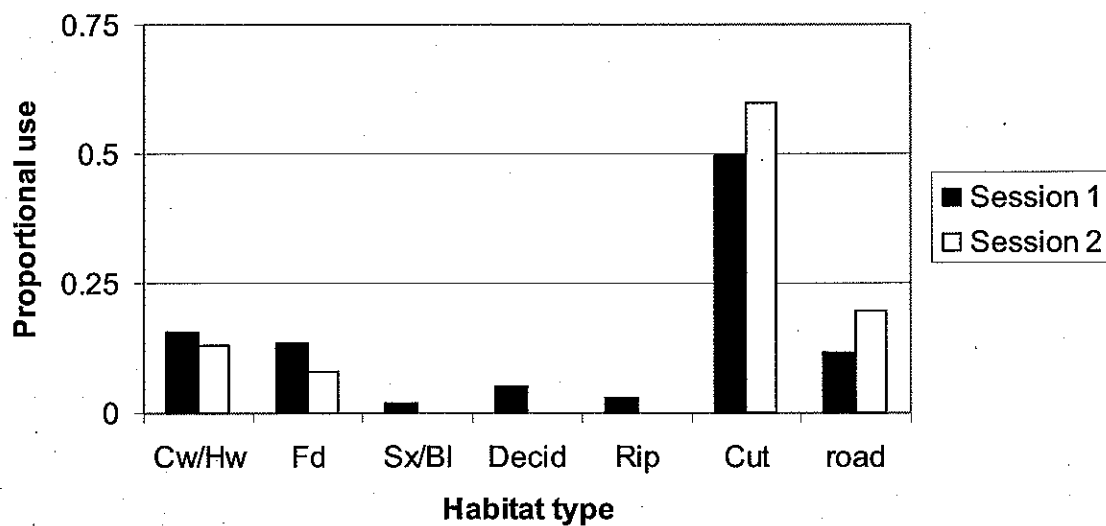
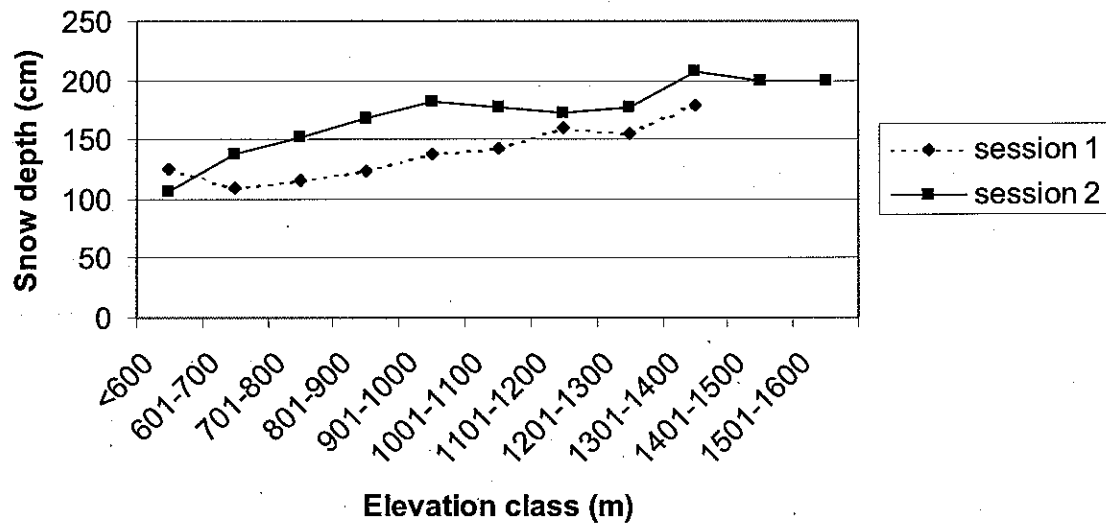
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APPENDIX 1. Snow depths and use of habitat types between the 2 sampling sessions.

The first figure illustrates mean snow depths by elevation for the first sampling session (February 5 to 28; n=22 transects; session 1) and the second sampling session (March 22-24; n=6 transects; session 2). Snow was 18% deeper the second sampling session. The second figure compares use of habitat types between the 2 sampling sessions. The patterns were similar between the 2 sampling sessions. In fact, use of open habitats was slightly greater the second session, despite deeper snow.



APPENDIX 2. Predictive model parameter estimates

Parameter ¹	DF	Estimate	Error
Intercept	1	1.341234	0.9273
ELEV	1	-0.00086	0.000948
SLOPE	1	-0.02184	0.0103
SOL_DIR	1	-0.00002	7.45E-06
Log_20	1	-0.00069	0.3057
Struc_stag	1	-0.29559	0.0984
Fdbio	1	0.022452	0.000088

¹ elev=elevation; slope=% slope; sol_dir=direct solar radiation; log_20=areas that were logged within 20 years; struc_stag=structural stage; Fdbio=an index of Douglas-fir overstory biomass.