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# Comparison of seasonal habitat selection between threatened woodland caribou ecotypes in central British Columbia

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*Abstract:* Woodland caribou (*Rangifer tarandus caribou*) in British Columbia have been classified into ecotypes based on differences in use of habitat in winter. Although recovery planning focuses on ecotypes, habitat use and selection varies within ecotypes. Our objectives were to compare habitat use and selection among previously identified woodland caribou herds at the transition zone between northern (Moberly, Quintette, and Kennedy herds) and mountain (Parsnip herd) ecotypes in central British Columbia. We developed selection models for each herd in spring, calving, summer/fall, early and late winter. Topographic models best predicted selection by most herds in most seasons, but importance of vegetation-cover was highlighted by disproportionate use of specific vegetation-cover types by all caribou herds (e.g., in early winter, 75% of Kennedy locations were in pine-leading stands, 84% of Parsnip locations were in fir and fir-leading stands, and 87 and 96% of locations were in alpine for the Moberly and Quintette herds, respectively). Using a combination of GPS and VHF radio-collar locations, we documented some spatial overlap among herds within the year, but use of vegetation-cover types and selection of elevations, aspects, and vegetation-cover types differed among herds and within ecotypes in all seasons. Habitat use and selection were most similar between the two northern-ecotype herds residing on the eastern side of the Rocky Mountains. This research indicates that habitat use and selection by caribou herds in all seasons is more variable than ecotype classifications suggest and demonstrates the value of undertaking herd-specific mapping of critical habitat for woodland caribou.

**Key words:** GPS, herd, model, *Rangifer tarandus*, resource, use, vegetation.

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## Introduction

Habitat selection by large ungulates is believed to be related to the amount and availability of food and minerals, insect disturbance, weather and predator avoidance (Skogland, 1980; Bergerud *et al*., 1984; Bowyer, 1986; Barten *et al*., 2001). Variation in habitat selection by large ungulates is likely because one or a combination of these factors is more pronounced in different regions at different times of the year. Research that quantifies variables that influence seasonal habitat selection of large ungulates across a diverse landscape is essential to resource management and species-conservation strategies.

Woodland caribou (*Rangifer tarandus caribou*) display considerable variation in seasonal habitat use within British Columbia (Cichowski, 1993; Terry *et al*., 1996; Poole *et al*., 2000; Apps *et al*., 2001; Johnson *et al*., 2001). Differences in use of habitat and forage (ground versus arboreal lichens) by woodland caribou in winter have led to the categorization of woodland caribou into ecotypes (Bergerud, 1978; Stevenson & Hatler, 1985). Two ecotypes of woodland caribou have been identified in central British Columbia: northern and mountain (Heard & Vagt, 1998). In winter, northern caribou primarily forage on ground lichens in alpine or low-elevation pine forests, whereas mountain caribou forage on arboreal lichens in old-growth subalpine forests (Stevenson & Hatler, 1985; Heard & Vagt, 1998). Differences between woodland caribou ecotypes are likely due to varying climate and topography across woodland caribou range that acts to influence forage distribution, abundance and snow conditions (Bergerud, 1978).

Differences between northern and mountain caribou, particularly in winter, have been made evident by studies examining habitat use and selection for one ecotype of woodland caribou during winter (Cichowski, 1993; Terry *et al*., 1996; Apps *et al*., 2001; Johnson *et al*., 2001). Variation in habitat use and selection by caribou in winter has also been observed within an ecotype (Cichowski, 1993; Terry *et al*., 1996; Gustine *et al*., 2006b), and among individuals in the same herd (Seip, 1992b; Johnson *et al*., 2001; Gustine *et al*., 2006b). Examination of habitat selection among adjacent caribou herds or individuals, however, has received little attention (Rettie & Messier, 2000; Mosnier *et al*., 2003; Saher & Schmiegelow, 2005; Gustine *et al*., 2006b), and differences in use and selection (in all seasons) between northern and mountain caribou herds have not been concurrently examined.

In British Columbia, mountain caribou are listed as endangered and northern caribou are of special concern (Hatter, 2002). Woodland caribou herds in our study area have been nationally designated as "threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2002), and subsequently have been listed as "threatened" under the federal Species at Risk Act (SARA). SARA requires that recovery planning occurs for threatened species. Although recovery planning for woodland caribou in British Columbia focuses on ecotypes, variation within ecotypes of woodland caribou suggests the need to determine whether it is appropriate to apply broad land-management strategies based on ecotype delineation or suitable land-management strategies to specific herds.

We compared habitat use (specifically use of different vegetation-cover types) and developed habitat selection models for four woodland caribou herds at the transition zone from northern to mountain ecotype during spring, calving, combined summer and fall (hereafter termed summer/fall), early and late winter in order to determine whether previously identified herds (Seip, 2002) were spatially and/or ecologically distinct. Our objectives were to: 1) determine whether seasonal range overlap occurred among herds and between ecotypes; and 2) compare seasonal habitat use and selection among herds and between ecotypes. We hypothesized that herds and ecotypes would be spatially separated during each season and that northern-ecotype herds (Kennedy, Moberly and Quintette) would show similar patterns in use and selection and differ from the mountain-ecotype herd (Parsnip), particularly during winter. As habitat selection by woodland caribou may be related to climatic variation, we expected the northern-ecotype herds that inhabited the eastern side of the Rocky Mountains (Quintette and Moberly) to show the most similar patterns in selection.

## Study area

The study area is approximately 8000 km$^2$ and is located in the Rocky Mountains of central British Columbia (Fig. 1). This area is characterized by mountains and rolling hills with variable terrain, ranging from lodgepole pine (*Pinus contorta*) and hybrid white-spruce (*Picea glauca x engelmannii*) forests at 650 m to alpine summits at 2520 m. Four biogeoclimatic zones occur within the study area (Meidinger & Pojar, 1991): Sub-Boreal Spruce (SBS), Boreal White and Black Spruce (BWBS), Engelmann Spruce-Subalpine Fir (ESSF), and Alpine Tundra (AT).

The SBS zone occurs in the valley bottoms up to elevations of approximately 1100 m. This zone is dominated by hybrid white spruce and subalpine fir (*Abies lasiocarpa*), with occasional occurrences of lodgepole pine in drier areas and black spruce (*Picea mariana*) in wetter regions (Meidinger & Pojar, 1991). The BWBS zone occurs on the eastern side of the Rocky Mountains, ranges in elevation from 650 to 1050 m, and is typically colder and drier than the SBS zone. Dominant tree species include white spruce (*Picea glauca*), black spruce and lodgepole pine. Fire is common in this zone and early-seral stands containing trembling aspen (*Populus tremuloides*) and cottonwood (*Populus balsamifera*) are numerous (Meidinger & Pojar, 1991). The ESSF zone occurs above the SBS and BWBS zones to elevations up to 1700 m (Meidinger & Pojar, 1991). The dominant tree species within the ESSF zone are Engelmann spruce (*Picea engelmannii*) and subalpine fir. As elevation increases in the ESSF zone, subalpine fir dominates and the forest becomes more open, eventually turning into parkland where stunted subalpine fir grows in clumps interspersed with alpine meadows (Meidinger & Pojar, 1991). The AT zone occurs above the ESSF zone and is usually treeless. This zone is dominated by permanent ice and snow, rock, dwarf shrubs, forbs, mosses, grasses, sedge and ground lichens.

Prevailing westerly winds typically stall over the central Rocky Mountains resulting in high precipitation on the western side of the Rockies (Demarchi, 1996). The climate in the eastern portion of the study area is drier than in the western portion. The ESSF

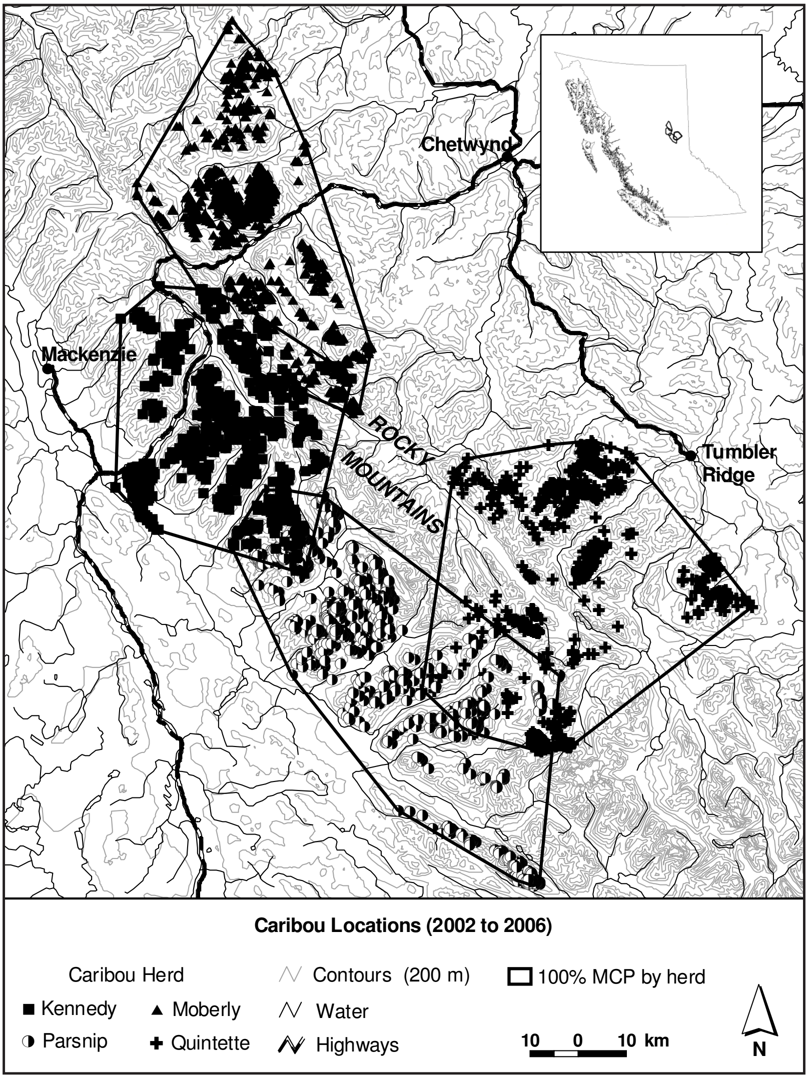

**Fig. 1.** Study area and caribou locations from May 2002 to January 2006 for woodland caribou in central British Columbia. The study area is depicted by a 100% minimum convex polygon (MCP) around all caribou locations for each herd.

zone on the west side of the Rockies has an annual precipitation of approximately 1530 mm compared with approximately 780 mm on the east side (Delong, 1994). The Parsnip (mountain ecotype) and Kennedy (northern ecotype) herds occur in the western portion of the study area whereas the Moberly and Quintette (northern ecotype) herds typically occupy the eastern side of the Rocky Mountains (Fig. 1). A major highway intersects both the Kennedy and Moberly herds, and a railway intersects all four of the herds. Logging has occurred and continues in the valley bottoms and low-elevation subalpine forests throughout the majority of the study area. The Quintette area is more developed than the Parsnip, Kennedy and Moberly areas from a combination of logging, oil and gas exploration and mining.

## Materials and methods

*Caribou locations and location accuracy*

We captured 46 caribou within the four herds (Kennedy = 11, Moberly = 10, Quintette = 15, and Parsnip = 10) by net-gunning from a helicopter between April 2002 and December 2005. Herd sizes ranged from approximately 100 to 200 animals (Seip, 2002), so collared caribou represented from five to 10% of each herd. Caribou were fitted with either VHF (Lotek Fish and Wildlife Monitoring, 115 Pony

Drive, Newmarket, Ontario, Canada L3Y 7B5, Model LMRT-4) or GPS (Televilt, TVP Positioning AB, Bandygatan 2, SE-71134 Lindesberg, Sweden, Model GPS-VHF remote download) collars. Televilt GPS collars were programmed to take fixes every 4 h. All 12 Televilt collars failed to function as programmed; nine collars did not download following the first download period, and five collars stopped emitting a VHF signal and were lost. Seven of the original Televilt GPS-collared caribou were recaptured and collars were replaced with either a VHF or GPS (Advanced Telemetry Systems, 470 First Ave. No., Box 398 Isanti, Minnesota, USA 55040, Model: GPS Remote-Release Collar) collar. Locations were obtained from eight of the Televilt GPS collars during the first download period and from three recovered collars. Ten caribou were fitted with ATS GPS collars. ATS GPS collars were programmed to take fixes every 20 h and data were recovered successfully from collars on each caribou, nine on 18 April 2005, and one following its death in October 2004.

We located both VHF- and GPS-collared caribou (unless the VHF beacon had failed) using radio telemetry from a fixed-wing aircraft using the VHF beacon of both types of collars. We flew weekly in winter and spring, and bimonthly in summer and fall, weather permitting. We recorded caribou locations obtained by aerial telemetry using both a handheld GPS unit and the internal GPS unit in the aircraft to ensure that locations were recorded accurately. We believe that telemetry locations captured in this manner were accurate to within 150 m, and 59% (1143 of 1953) of the VHF locations were confirmed visually. We obtained 1953 aerial-telemetry (hereafter termed VHF) locations between 2 May 2002 and 29 January 2006: Kennedy = 491 ($n$ = 11 individuals), Moberly = 565 ($n$ = 10), Quintette = 422 ($n$ = 15), and Parsnip = 475 ($n$ = 10).

We obtained 7687 locations from 10 caribou throughout all seasons with ATS GPS collars ($n$ = 2, Quintette and Kennedy; $n$ = 3, Moberly and Parsnip), three of which also had data from Televilt GPS collars. We also used data from five individual caribou with Televilt GPS collars in late winter, one of which also recorded locations in early winter. As Televilt GPS collars were programmed to record data every 4 h, we ensured that these collars were consistent with the 20-h ATS GPS-collar fix rate by using only every fifth location. Data from each GPS collar were examined for atypical locations (Spatial Viewer, unpublished program by M. P. Gillingham) and one questionable location was removed. Because dilution of precision (DOP) values and the number of satellites used to obtain a location (2D or 3D) have been related to location error, we removed DOP values >25 for 3D locations ($n$ = 6) and >10 for 2D locations ($n$ = 46) (Rempel & Rodgers, 1997; Dussault *et al.*, 2001). Fix rates of all GPS collars combined exceeded 75% in all seasons with the exception of summer/fall when the fix rate was 63%. After generating 20-h fix locations from the Televilt collars, removing potentially erroneous 2D and 3D fixes, and excluding locations that fell into areas where vegetation-cover data did not exist ($n$ = 5), 5243 GPS-collar locations were used to model seasonal habitat selection of woodland caribou: Kennedy = 1031 ($n$ = 2 individuals, all seasons; $n$ = 3 individuals, late winter), Moberly = 1749 ($n$ = 3, all seasons; $n$ = 4, early and late winter), Quintette = 1173 ($n$ = 2, all seasons; $n$ = 5, late winter), and Parsnip = 1290 ($n$ = 3, all seasons).

### *Herd and seasonal definitions*

We initially grouped radio-collared caribou into one of four previously identified herds (Seip, 2002) based on the capture location of each collared caribou, but some capture locations fell outside of the previously identified herd boundaries. Because ecotypes are distinguished by differences in habitat use during winter (Stevenson & Hatler, 1985), we evaluated herd assignments based on habitat use (VHF data) by individual caribou in early winter. Differences in use of vegetation-cover type (e.g., alpine, fir-leading, pine-leading) among individual caribou were more discernable than other variables that also describe habitat use by caribou (e.g., elevation, slope, aspect). Consequently, we checked original herd assignments and assigned outlying individuals to previously identified herds based on use of vegetation-cover types by individual caribou.

We categorized location data from caribou into five seasons based on migration patterns, biology and snow conditions recorded during telemetry flights, and while conducting fieldwork within the study area: spring (1 April to 14 May), calving (15 May to 14 June), summer/fall (15 June to 31 October), early winter (1 November to 14 January), and late winter (15 January to 31 March). Spring corresponded with the melting of snow and emerging green vegetation on south-facing slopes. Calving encompassed the typical calving period for woodland caribou (Bergerud *et al.*, 1984; Bergerud & Page, 1987; Gustine *et al.*, 2006a). Summer/fall began when the majority of snow had melted from the mountainous areas. Early winter began when snowfall remained on the ground in the mountainous areas and typically coincided with the movement of Kennedy caribou to the low-elevation pine stand at Kennedy Siding. Late winter began when snow depth on the west side of the mountains typically exceeded 1 m and the snowpack had settled and hardened.

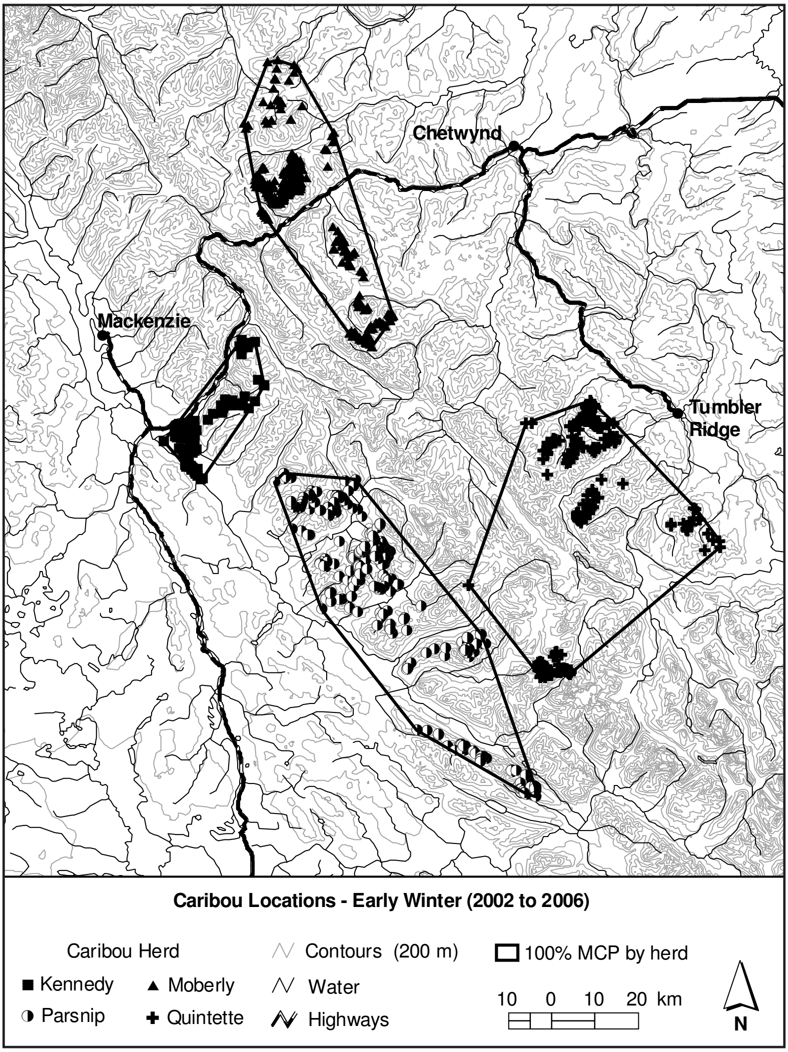

**Fig. 2.** Early winter locations of caribou (2002 to 2006), by herd, showing lack of spatial overlap during this season for woodland caribou in central British Columbia.

*Defining availability*

We examined availability at the scale of an approximate daily movement capability of caribou using the 95th percentile movement distance (Arthur *et al.*, 1996) between consecutive 20-h fixes calculated for each herd during each season. We selected the 95th percentile movement distance after examining frequency distributions by herd and season to identify the distance that a caribou was capable of moving in a 20-h period with the exception of movements that were not typical and may have been provoked by rare human or other disturbance. This distance was applied as a radius around each used caribou location to define the area available to an individual caribou. For each caribou location we generated five random locations within the defined available area. We chose to use movement distance to define availability as opposed to a seasonal home-range estimator as using movement distance allowed the sampled area available to an individual caribou to correspond to each use location for that individual (Compton *et al.*, 2002).

Because available areas may have been underestimated (caribou could have moved farther in 40 h than in 20 h) for locations occurring after a mixed fix (i.e., 40-hr time interval between two fixes), we analyzed the used/available locations as unmatched, in that comparison between used and available locations was across an entire season, as opposed to comparing use and availability for each location. This method allowed us to relate availability to use locations as is appropriate for animals with large home ranges (Compton *et al.*, 2002).

*Model development*

We developed a set of biologically plausible *a priori* candidate models (Table 1) to examine the influence of topographic variables, vegetation-cover type and distance to nearest road on habitat selection of woodland caribou herds in each season using the GPS-location data. Elevation, slope and aspect at each caribou location were obtained from a Digital Elevation Model (DEM) (British Columbia Ministry of Sustainable Resource Management, Base Mapping and Geomatic Services Branch, 2005). Elevation and slope were modeled as continuous variables and we used five categorical variables to model aspect: north (316 to 45 degrees), east (46 to 135 degrees), south (136 to 225 degrees), west (226 to 315 degrees), and no aspect (slope = 0).

Land cover was obtained from digitized 1:20 000 Vegetation Resource Inventory (VRI) data (British Columbia Ministry of Sustainable Resource Management, Land and Resource Data Warehouse, 2005b). We defined 11 vegetation-cover types using a combination of land-cover variables and elevation (Jones, unpubl. data): alpine, parkland, fir, fir-leading, spruce-leading, pine-leading, coniferous-unknown, young-coniferous, deciduous/shrub, open-nonvegetated and open-vegetated. We defined 'fir' as a stand containing only fir trees, whereas 'fir-leading' was a stand dominated by fir but also containing other tree species. The 'young-coniferous' cover type included all coniferous-cover types $\leq$ 40 years, thus all other coniferous classes were >40-years old. As collar locations (GPS and VHF) were not all obtained during the same year as the VRI, we calculated the age of coniferous-cover types specific to the year of each caribou location using the updated-age variable of leading-tree species in the VRI (British Columbia Ministry of Forests and Range, 2005).

Road locations were obtained from Terrestrial Resource Inventory Mapping (TRIM) data (British Columbia Ministry of Sustainable Resource Management, Land and Resource Data Warehouse, 2005a). Distance to nearest road (any type) was modeled as a continuous variable and was calculated using the Spatial Analyst extension in ArcMAP (version 8.3, ESRI, 2003). All vector data were rasterized with a 25-m output resolution using the Spatial Analyst extension in ArcMAP. Variable attributes for each used and available caribou location were obtained from final raster layers using PCI Imageworks (version 9.1, PCI Geomatics, 2003).

Categorical variables (vegetation-cover type and aspect) were modeled with deviation coding using DESMAT (Hendrickx, 2001), and classes that were rarely or never used by caribou ($n < 4$) were excluded from analysis to avoid issues of perfect or near-perfect separation (Menard, 2002). We chose to eliminate categorical variables where $n < 4$ because standard errors (SEs) of variables normalized only when $n \geq 4$. Collinearity of continuous variables in the model set was examined by herd and season and all tolerance scores exceeded the acceptable level of 0.2 (Menard, 2002). To ensure that elevation and vegetation-cover type, were not highly collinear we examined overlap in range of elevations among vegetation-cover types, and used a Kruskal-Wallis test (StataCorp, 2005) to determine whether there were differences in elevation among vegetation-cover types. Although alpine and pine-leading stands differed in elevation, there was considerable overlap (range of elevations and non-significant differences) among the remaining vegetation-cover classes. We concluded that elevation and vegetation-cover type were not inherently collinear.

Prior to modeling, we used logistic regression (Hosmer & Lemeshow, 2000) to evaluate whether selection for elevation was linear (elevation) or quadratic (elevation + elevation$^2$), for each herd in each season by comparing Akaike's Information Criterion for small sample sizes ($AIC_c$) for both the linear and quadratic elevation models (Burnham & Anderson, 2002). The elevation model with the lowest $AIC_c$

**Table 1.** Suite of ecologically plausible models, determined *a priori*, to describe selection for woodland caribou in central British Columbia.

| Model Name | Model Variables |
|---|---|
| Topo Model 1 | Elevation[a] + Aspect + Slope |
| Topo Model 2 | Elevation[a] + Aspect |
| Vegetation - Topo Model 1 | Elevation[a] + Aspect + Vegetation Cover Type |
| Vegetation - Topo Model 2 | Elevation[a] + Vegetation Cover Type |
| Vegetation Model | Vegetation Cover Type |
| Vegetation - DTR Model | Elevation[a] + Vegetation Cover Type + Distance to Road |
| Topo - DTR Model | Elevation[a] + Aspect + Distance to Road |
| DTR Model | Distance to Road |

[a] Elevation was modeled as either a linear or quadratic relationship depending on best fit (see methods and results).

score (typically the quadratic model) was used in the model set (Table 1).

We initially attempted to model selection (using logistic regression) for individual caribou, but small sample sizes resulted in large SEs of variables and the receiver operating characteristic (ROC) curves typically showed less than acceptable (<0.70) discrimination (Manel *et al.*, 2001). Because sample sizes precluded examining selection for individual caribou, we pooled GPS locations by herd and season and used logistic regression to determine the coefficients of selection ($\beta_i$) for each variable and the Huber-White sandwich estimator to obtain robust estimates of variance for these coefficients (Boyce *et al.*, 2002). All logistic-regression analyses were conducted using STATA (version 8.0, StataCorp, 2005).

We considered all models for which Akaike weights ($w_i$) summed to ≥0.95 to be competing models, indicating that given the entire set of models, these models explained over 95% of the variation (Burnham & Anderson, 2002); we use the term 'top' model to refer to those instances where one model explained ≥0.95 of the variation. To evaluate the predictive ability of the top model or competing models for each herd in each season, we used k-fold cross validation (Boyce *et al.*, 2002) to obtain the mean Spearman's rank correlation ($\bar{r}_s$) from five random subsets of the used/available data. Models were considered to be valid if the mean Spearman's rank correlation was significant ($P < 0.5$). We averaged validated competing models (Burnham & Anderson, 2002) to obtain a final model for each herd in each season. Significance of selection coefficients ($\beta_i$) was determined using the Wald statistic (Menard, 2002) for top models, and inferred when the confidence intervals (CIs) did not encompass zero for an averaged final model. Selection was inferred when $\beta_i > 0$ for significant variables.

Of the selection attributes we measured, only vegetation-cover type and roads can be manipulated by managers. Because the addition of topographic variables may have influenced the statistical significance of selection for vegetation-cover types, we also examined selection coefficients from the vegetation-cover type model in the absence of other variables to quantify selection or avoidance of vegetation-cover types by woodland caribou herds.

## Results

*Spatial separation and use of vegetation-cover types*

We considered herds to be spatially separated if the 100% MCP (minimum convex polygon) around seasonal locations for a herd did not overlap with the seasonal MCP of another herd. Using those criteria, evidence of some geographical overlap among herds and ecotypes was apparent in spring, calving, summer/fall, and late winter, but not in early winter (Fig. 2). The northern-ecotype herds on the eastern side of the Rockies (Quintette and Moberly) were spatially separated during all seasons. Some spatial overlap occurred between the Parsnip and Quintette herds and the Kennedy and Moberly herds in all seasons but early winter, and the Parsnip and Kennedy herds in all seasons but early and late winter. Spatial separation may exist within the Moberly herd as collared caribou did not cross the highway (Highway 97) intersecting that herd. Perhaps these groups (north and south) should be considered separate herds, but because individuals had similar habitat-use patterns and sample size ($n$ = 10 individuals) may not have been sufficient to determine that none of the Moberly caribou cross the highway, we modeled them as the same herd.

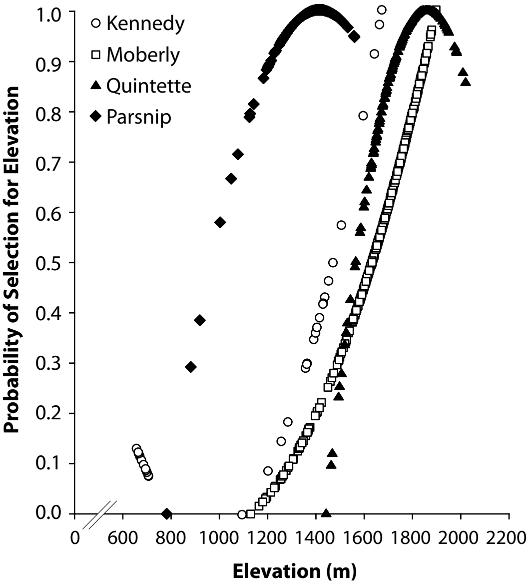

Fig. 3. Probability of selection for elevation in early winter from the top or averaged selection model, by herd, for woodland caribou in central British Columbia. The elevation function was determined by holding other variables in the model constant and calculating the sum of $\beta_{i(elevation)}$ x elevation and $\beta_{i(elevation^2)}$ x elevation$^2$ (scaled between 0-1) at use locations of woodland caribou for that season. Elevation and elevation$^2$ were significant ($P$ < 0.05) for each herd.

Use of vegetation-cover types by GPS-collared caribou varied among herds and seasons (Table 2), but some patterns were evident. The northern-ecotype herds that inhabited the eastern side of the Rockies (Moberly and Quintette) were predominately located

**Table 2.** Percent of total number of used and available GPS (VHF in brackets) locations in vegetation-cover types, by season and herd, for woodland caribou in central British Columbia. Total number of used and available locations (*n*) for each herd is included.

| | Kennedy | | Moberly | | Quintette | | Parsnip | |
|---|---|---|---|---|---|---|---|---|
| **Spring** | Used | Available | Used | Available | Used | Available | Used | Available |
| *n* | 141 (48) | 705 (240) | 217 (54) | 1075 (270) | 152 (48) | 760 (240) | 201 (50) | 1005 (255) |
| Alpine | 36 (63) | 16 (19) | 98 (81) | 40 (35) | 91 (94) | 43 (33) | 12 (6) | 7 (2) |
| Parkland | 15 (8) | 10 (15) | [a] | 10 (9) | [a] | 4 (6) | [a] | |
| Fir | 23 (10) | 17 (10) | [a] (6) | 4 (6) | 5 | 3 (6) | 42 (22) | 21 (16) |
| Fir-leading | 9 (6) | 26 (27) | [a] (2) | 24 (22) | 3 (4) | 18 (17) | 29 (32) | 28 (20) |
| Spruce-leading | [a] | 17 (19) | [a] (6) | 13 (17) | [a] (2) | 19 (23) | 4 (8) | 26 (24) |
| Pine-leading | [a] (4) | (4) | [a] (2) | 4 (7) | [a] | 3 (4) | [a] | |
| Conif.-unknown | [a] | | [a] | | [a] | | 4 (20) | 5 (25) |
| Young-conif. | [a] | 1 (2) | [a] | 2 | [a] | 4 (2) | [a] | |
| Decid./shrub | 11 (2) | 13 (4) | [a] | 2 (2) | [a] | 5 (6) | 7 (10) | 8 (8) |
| Open-nonveg. | [a] (4) | | [a] | | [a] | 1 | [a] | 1 (4) |
| Open-veg. | 6 (2) | 1 | 2 (4) | 1 (2) | [a] | 1 (2) | [a] (2) | 2 (2) |
| **Calving** | | | | | | | | |
| *n* | 64 (30) | 325 (140) | 82 (35) | 415 (175) | 58 (32) | 285 (150) | 110 (34) | 555 (160) |
| Alpine | 36 (23) | 14 (21) | 40 (43) | 19 (26) | 45 (38) | 26 (27) | [a] | 9 (6) |
| Parkland | [a] (10) | 5 (11) | 32 (9) | 11 (9) | [a] (16) | 2 (10) | [a] | |
| Fir | 31 (10) | 12 (18) | 4 (6) | 1 (6) | 2 | 9 | 36 (29) | 21 (22) |
| Fir-leading | 9 (30) | 22 (25) | 11 (23) | 27 (26) | 41 (16) | 28 (13) | 45 (50) | 28 (28) |
| Spruce-leading | 22 (17) | 34 (18) | 10 (17) | 30 (23) | 12 (25) | 28 (30) | 13 (9) | 27 (19) |
| Pine-leading | [a] | | [a] (3) | 2 (3) | [a] | 2 (3) | [a] | |
| Conif.-unknown | [a] (3) | 2 | [a] | | [a] | | 3 (12) | 3 (16) |
| Young-conif. | [a] | 2 | [a] | | [a] | (3) | [a] | 1 |
| Decid./shrub | 2 (7) | 8 (4) | 2 | 6 (6) | [a] | 4 (10) | 3 | 9 (9) |
| Open-nonveg. | [a] | 2 | [a] | 2 | [a] (3) | (3) | [a] | 1 |
| Open-veg. | [a] | 2 (4) | 1 | 1 (3) | [a] (3) | 2 | [a] | 2 |
| **Summer/Fall** | | | | | | | | |
| *n* | 237 (141) | 1185 (705) | 354 (165) | 1760 (840) | 216 (132) | 1075 (660) | 348 (136) | 1745 (675) |
| Alpine | 8 (5) | 9 (10) | 55 (32) | 26 (23) | 53 (33) | 33 (20) | 2 (1) | 8 (4) |
| Parkland | 5 (6) | 5 (6) | 15 (15) | 12 (11) | 2 (8) | 1 (7) | [a] | |
| Fir | 32 (30) | 16 (16) | 1 (3) | 4 (4) | 9 (8) | 9 (9) | 21 (19) | 25 (23) |
| Fir-leading | 28 (35) | 29 (32) | 16 (32) | 29 (25) | 28 (25) | 28 (23) | 69 (60) | 38 (38) |
| Spruce-leading | 12 (11) | 24 (21) | 8 (15) | 20 (21) | 4 (21) | 16 (30) | 4 (8) | 21 (17) |
| Pine-leading | 9 (4) | 4 (2) | [a] (1) | 1 (4) | 2 (3) | 2 (4) | [a] | |
| Conif.-unknown | [a] (1) | | [a] | (2) | [a] | | 2 (10) | 1 (13) |
| Young-conif. | [a] (1) | 1 (1) | [a] | 2 (1) | 1 | 1 (2) | [a] | |
| Decid./shrub | 3 (4) | 9 (9) | [a] | 3 (6) | [a] (2) | 6 (4) | 1 (3) | 4 (4) |
| Open-nonveg. | [a] (1) | 2 (2) | [a] | 1 (1) | [a] | 1 (1) | 1 | 1 |
| Open-veg. | 2 (3) | 1 (1) | 4 (2) | 3 (3) | 1 | 2 (2) | [a] | 1 (1) |

[a] Vegetation-cover type removed from models when use locations <4.

**Table 2.** Continued.

| | Kennedy | | Moberly | | Quintette | | Parsnip | |
|---|---|---|---|---|---|---|---|---|
| **Early Winter** | Used | Available | Used | Available | Used | Available | Used | Available |
| *n* | 248 (106) | 1225 (525) | 472 (112) | 2335 (555) | 238 (81) | 1205 (400) | 237 (97) | 1175 (480) |
| Alpine | 2 | | 87 (67) | 33 (34) | 96 (75) | 40 (35) | [a] | 3 (1) |
| Parkland | 1 (1) | 1 (1) | 4 (8) | 15 (9) | [a] (2) | 1 (5) | [a] | |
| Fir | 3 | 2 (1) | 1 (1) | 4 (3) | 4 (1) | 6 (3) | 30 (28) | 19 (16) |
| Fir-leading | 4 (3) | 6 (5) | 6 (11) | 24 (28) | [a] (5) | 20 (18) | 54 (35) | 36 (29) |
| Spruce-leading | 1 (1) | 19 (20) | 1 (7) | 13 (17) | [a] (11) | 17 (21) | 5 (6) | 24 (15) |
| Pine-leading | 75 (67) | 34 (35) | [a] (4) | 3 (5) | [a] (4) | 3 (13) | [a] | |
| Conif.-unknown | [a] | | [a] | | [a] | | 9 (30) | 9 (30) |
| Young-conif. | 13 (24) | 7 (9) | [a] | 2 (1) | [a] | 2 (3) | [a] | |
| Decid./shrub | [a] (2) | 23 (23) | [a] (2) | 2 (2) | [a] | 7 (3) | 1 (1) | 8 (7) |
| Open-nonveg. | [a] (2) | 6 (7) | [a] | 1 | [a] | 1 | [a] | (1) |
| Open-veg. | [a] (1) | 1 | 1 (1) | 2 (1) | [a] (1) | 2 (1) | [a] | 1 (1) |
| | | | | | | | | |
| **Late Winter** | | | | | | | | |
| *n* | 341 (164) | 1705 (820) | 623 (196) | 3115 (980) | 505 (129) | 2535 (640) | 394 (157) | 1975 (785) |
| Alpine | 23 (21) | 12 (12) | 85 (65) | 49 (39) | 90 (78) | 54 (44) | 2 (2) | 5 (4) |
| Parkland | 12 (7) | 11 (10) | 6 (7) | 13 (10) | [a] (3) | 3 (5) | [a] | |
| Fir | 18 (21) | 11 (10) | 5 (3) | 4 (4) | 5 (2) | 7 (5) | 45 (40) | 30 (22) |
| Fir-leading | 19 (18) | 25 (26) | 1 (7) | 15 (21) | 4 (6) | 20 (19) | 43 (32) | 34 (28) |
| Spruce-leading | 3 (5) | 17 (15) | 1 (10) | 12 (15) | [a] (4) | 9 (16) | 3 (2) | 15 (16) |
| Pine-leading | 17 (6) | 9 (10) | [a] (7) | 3 (7) | [a] (6) | 1 (8) | [a] | |
| Conif.-unknown | [a] | | [a] | | [a] | | [a] (21) | 2 (20) |
| Young-conif. | 3 (12) | 2 (5) | [a] | 1 (1) | [a] | (1) | [a] | |
| Decid./shrub | 3 (5) | 9 (9) | 1 | 2 (2) | [a] (1) | 4 (2) | 6 (1) | 10 (8) |
| Open-nonveg. | [a] (3) | 2 (2) | [a] | 1 (1) | [a] | | [a] | 1 (1) |
| Open-veg. | 2 (1) | 3 (3) | 2 (2) | 1 (1) | [a] | 1 (1) | 1 (2) | 3 (1) |

[a] Vegetation-cover type removed from models when use locations <4.

in alpine in all seasons. In contrast, the northern-ecotype herd on the western side of the Rockies (Kennedy) used five to 10 different vegetation-cover types that varied in percentage of use across seasons. The mountain-ecotype herd (Parsnip) primarily used fir and fir-leading stands in all seasons. Differences in use of vegetation-cover types were most apparent within and among ecotypes in early winter. Seventy-five percent of Kennedy locations were in pine-leading stands, 87 and 96% of locations were in alpine for the Moberly and Quintette herds, respectively, and 84% of Parsnip locations were in fir and fir-leading stands.

The VHF data were generally consistent with the patterns observed from the GPS locations (Table 2). Although we did not statistically test for differences between the GPS and VHF data, the VHF data suggested greater use of fir, fir-leading and spruce-leading stands by the northern-ecotype herds than GPS data, particularly during summer/fall. We attempted to model habitat selection using the VHF data, but small sample sizes resulted in models that we were unable to validate (using k-fold cross validation).

Up to nine vegetation-cover types were removed from selection models due to rare occurrences of use (Table 2). Specifically, spruce-leading, pine-leading, deciduous/shrub, young-coniferous, and open-vegetation classes were often removed for many herds in all seasons, with the exception of the Kennedy herd, which commonly used pine-leading and to a lesser extent young-coniferous stands in early and late winter.

*Selection models*

The model containing all topographic variables (Topo Model 1, Table 3) was the top model during spring, summer/fall, early winter and late winter with the exception of the Kennedy herd during summer/fall and late winter, and the Parsnip herd during summer/fall. This result indicates that vegetation-cover type or distance to nearest road did not contribute to explaining selection by these herds during these seasons and that the combination of elevation, slope and aspect best predicted selection by caribou. The predictive ability of the topographic model ranged from a mean $r_s$ (using k-fold cross validation) of 0.787 in early winter to 0.970 in late winter (all $P < 0.01$). During calving, the model containing vegetation-cover type, elevation and aspect (Table 3) often explained the majority of variation in selection. In two instances (Moberly Topo Model 1 in spring, and Parsnip Topo Model 1 in late winter), mean $r_s$ could not be calculated (using k-fold cross validation) because the combination of elevation + elevation$^2$ predicted the dependent variable perfectly.

Vegetation-cover type or distance to nearest road typically entered into the competing model set only when use of varying elevations by caribou was more common, and the selection coefficient for distance to nearest road was only significant for the Parsnip herd during summer/fall. The DTR Model (containing only the distance to nearest road variable) and the Vegetation Model (containing only the vegetation-cover type variable) never entered into the competing model set (Table 3).

### *Elevation*

Differences in selection patterns for elevation by caribou herds were most apparent in early winter (Fig. 3), but selection for elevation varied among herds in all other seasons. Although elevation was typically modeled as a quadratic ($AIC_c$ scores were lower for the quadratic model than the linear model, for all herds in all seasons, except Quintette in spring and calving), selection for elevation commonly showed a more linear pattern for northern-ecotype herds until elevation exceeded 1600 m (e.g., Quintette herd, Fig. 3). In contrast, selection for elevation by the mountain-ecotype herd was distinctly quadratic in all seasons (e.g., Parsnip herd, Figure 3), showing selection for mid-elevations. An inverse quadratic pattern occurred for the Kennedy herd in early and late winter as these caribou were commonly located in low-elevation pine forests during this period (e.g., Kennedy herd, Fig. 3).

The northern-ecotype caribou on the eastern side of the Rockies (Quintette and Moberly) showed the most similar patterns of use and selection for elevation. These herds were rarely located below 1200 m (range of use: Moberly, 1175 to 2005 m; Quintette, 1250 to 2035 m) and selected elevations above 1600 m in all seasons. Seasonal differences in selection patterns for elevation were still apparent between these two herds, as the Quintette caribou selected for lower elevations (>1600 m) in summer/fall and the highest elevations in late winter (>1900 m), whereas the Moberly caribou selected for lower elevations in late winter (>1600 m), and highest elevations in summer/fall and early winter (>1800 m). Elevation was not significant for the Moberly herd during calving.

The northern-ecotype herd on the west side of the Rockies (Kennedy) selected for elevations similar to the eastern herds during calving (>1800 m), but selected for lower elevations than these herds in summer/fall (>1400 m) and early winter (>1600 m). Elevation was not significant for the Kennedy herd during spring and late winter. Caribou in the Kennedy herd were located at elevations below 1200 m in all seasons except calving, and use of elevations between 700 and 800 m was common in early and late winter (range of use: Kennedy, 710 to 2010 m).

The Parsnip herd was rarely located below 1100 m (range of use: Parsnip, 835 to 1835 m) and showed selection for elevations between 1150 to 1800 m across all seasons. During spring, Parsnip caribou selected the largest range of elevations (1300 to 1800 m), and slightly lower elevations during calving and summer/fall (1250 to 1600 m). The lowest elevations were selected during early winter (1150 to 1600 m) and were similar to elevations selected in late winter (1200 to 1600 m). The Parsnip herd was notably absent from elevations outside of the selected range (only 10 locations < 1100 m), whereas the northern ecotypes were commonly located at lower elevations than selection indicates.

### *Slope and aspect*

Selection for slopes with the lowest gradients was common among all herds in spring, early winter and late winter with the exception of the Kennedy herd where slope was not significant in late winter. Slope was not significant for any of the herds during calving or for the Kennedy and Parsnip herds during summer/fall. The Moberly and Quintette herds both avoided steeper slopes in summer/fall.

The northern-ecotype herds on the eastern side of the Rockies avoided eastern aspects in all seasons and selected for western aspects in all seasons with the exception of the Moberly herd in spring, where western aspects were not significant. Both herds selected for southern aspects in spring and the Quintette herd avoided northern aspects in spring and early winter. Both herds avoided northern aspects in late winter.

Aspect was significant for Kennedy caribou during spring, summer/fall and late winter. Similar to the Quintette herd, the Kennedy caribou selected for southern and western aspects in spring and avoided northern aspects in spring and eastern aspects in late

**Table 3.** Top or competing models, by season and herd, for woodland caribou in central British Columbia. Model variables are presented in Table 2. Competing models are sorted by Akaike model weights ($w_i$). Statistics also include the number of parameters used in each model (K), number of locations (*n*), receiver operating characteristic (ROC), log-likelihood (LL), Akaike's information criteria for small sample sizes (AIC$_c$), and Spearman's rank correlation ($\bar{r}_s$) using *k*-fold cross validation. All $\bar{r}_s$ from five k-fold runs were significant ($P < 0.01$).

| Season | Herd | Model | K | *n* | ROC | LL | AIC$_c$ | $w_i$ | $\bar{r}_s$ |
|---|---|---|---|---|---|---|---|---|---|
| Spring | Kennedy | Topo Model 1 | 7 | 720 | 0.805 | -282.346 | 578.809 | 0.999 | 0.830 |
| | Moberly | Topo Model 1 | 7 | 655 | 0.888 | -257.417 | 528.964 | 1.000 | [a] |
| | Quintette | Topo Model 1 | 6 | 634 | 0.825 | -247.527 | 507.149 | 1.000 | 0.801 |
| | Parsnip | Topo Model 1 | 7 | 1162 | 0.869 | -375.652 | 765.378 | 1.000 | 0.863 |
| Calving | Kennedy | Vegetation - Topo Model 1 | 9 | 325 | 0.898 | -99.207 | 216.872 | 0.427 | 0.791 |
| | Kennedy | Vegetation - Topo Model 2 | 6 | 325 | 0.888 | -102.596 | 217.380 | 0.331 | 0.837 |
| | Kennedy | Vegetation - DTR Model | 7 | 325 | 0.889 | -101.879 | 218.024 | 0.240 | 0.779 |
| | Moberly | Vegetation - Topo Model 1 | 9 | 438 | 0.807 | -161.125 | 340.587 | 0.771 | 0.813 |
| | Moberly | Topo Model 2 | 6 | 438 | 0.792 | -166.274 | 344.687 | 0.099 | 0.797 |
| | Moberly | Topo Model 1 | 7 | 438 | 0.787 | -165.466 | 345.127 | 0.080 | 0.863 |
| | Quintette | Topo - DTR Model | 6 | 292 | 0.789 | -119.261 | 250.732 | 0.456 | 0.644 |
| | Quintette | Vegetation - Topo Model 1 | 7 | 292 | 0.787 | -118.882 | 252.061 | 0.235 | 0.768 |
| | Parsnip | Vegetation - Topo Model 1 | 8 | 521 | 0.799 | -204.677 | 425.573 | 0.354 | 0.851 |
| | Parsnip | Topo Model 2 | 6 | 521 | 0.790 | -207.227 | 426.570 | 0.215 | 0.862 |
| | Parsnip | Vegetation - Topo Model 2 | 5 | 521 | 0.782 | -208.667 | 427.412 | 0.141 | 0.874 |
| | Parsnip | Topo Model 1 | 7 | 521 | 0.793 | -206.669 | 427.502 | 0.135 | 0.853 |
| | Parsnip | Topo - DTR Model | 7 | 521 | 0.792 | -207.108 | 428.379 | 0.087 | 0.884 |
| | Parsnip | Vegetation - DTR Model | 6 | 521 | 0.784 | -208.366 | 428.849 | 0.069 | 0.858 |
| Summer/ Fall | Kennedy | Vegetation - Topo Model 1 | 14 | 1388 | 0.788 | -526.269 | 1080.804 | 0.937 | 0.936 |
| | Kennedy | Vegetation - Topo Model 2 | 10 | 1388 | 0.775 | -533.432 | 1086.996 | 0.042 | 0.938 |
| | Moberly | Topo Model 1 | 7 | 1999 | 0.761 | -799.042 | 1612.126 | 1.000 | 0.946 |
| | Quintette | Topo Model 1 | 7 | 1178 | 0.721 | -495.911 | 1005.895 | 1.000 | 0.837 |
| | Parsnip | Vegetation - DTR Model | 9 | 2038 | 0.775 | -784.089 | 1586.250 | 0.898 | 0.930 |
| | Parsnip | Topo Model 1 | 7 | 2038 | 0.776 | -788.406 | 1590.853 | 0.090 | 0.906 |
| Early Winter | Kennedy | Topo Model 1 | 8 | 843 | 0.702 | -453.108 | 922.349 | 1.000 | 0.848 |
| | Moberly | Topo Model 1 | 7 | 2609 | 0.864 | -851.782 | 1717.596 | 1.000 | 0.787 |
| | Quintette | Topo Model 1 | 7 | 793 | 0.785 | -395.553 | 805.213 | 1.000 | 0.882 |
| | Parsnip | Topo Model 1 | 7 | 1260 | 0.796 | -509.466 | 1032.999 | 0.999 | 0.894 |
| Late Winter | Kennedy | Vegetation - Topo Model 1 | 15 | 2013 | 0.745 | -798.803 | 1627.816 | 0.792 | 0.897 |
| | Kennedy | Vegetation - Topo Model 2 | 11 | 2013 | 0.739 | -804.506 | 1631.123 | 0.152 | 0.901 |
| | Kennedy | Vegetation - DTR Model | 12 | 2013 | 0.739 | -804.505 | 1633.142 | 0.055 | 0.920 |
| | Moberly | Topo Model 1 | 7 | 3588 | 0.809 | -1319.033 | 2652.089 | 1.000 | 0.970 |
| | Quintette | Topo Model 1 | 7 | 2539 | 0.804 | -1021.047 | 2056.126 | 1.000 | 0.911 |
| | Parsnip | Topo Model 1 | 7 | 2260 | 0.790 | -851.076 | 1716.190 | 1.000 | [a] |

[a] K-fold cross validation procedures were unsuccessful (see results).

winter. In contrast to the Quintette and Moberly herds, the Kennedy caribou selected for northern aspects in summer/fall and areas with no aspect (slope = 0) in late winter. Aspect was significant for the Parsnip herd only during calving and late winter. The Parsnip caribou selected for southern aspects during calving and similar to the Quintette and Moberly herds, selected western aspects and avoided eastern aspects in late winter. No aspect (slope = 0) was dropped from the models for the Parsnip, Moberly and Quintette herds due to zero or rare ($n < 4$) occurrences of use.

*Vegetation-cover type*

Vegetation-cover type only entered into the competing model set for all herds during calving, for the Parsnip herd during summer/fall and for the Kennedy herd during summer/fall and late winter (Table 3). Selection coefficients for relatively few vegetation-cover types were significant for herds during these seasons, and selected vegetation-cover types were typically lower-elevation forested stands not explained by elevation. The Moberly herd selected parkland and the Kennedy herd selected spruce-leading stands during calving. Although a higher percentage of use locations were in alpine during calving (Table 2), some individuals in these herds moved from alpine to forested stands (Kennedy) during parturition and returned to alpine after calving.

*Vegetation-cover type model*

Selection for mid- and high-elevation areas was evident among herds and ecotypes, and elevation typically overshadowed vegetation-cover type in explaining differences among used and available locations. Because use data (Table 2) showed a clear disparity in use of different vegetation-cover types among herds, and understanding selection for vegetation cover is an important component for recovery planning, we examined the coefficients for vegetation-cover types in the absence of other variables (Vegetation Model, Table 1).

*Alpine*

The northern-ecotype herds selected alpine in all seasons with the exception of the Moberly herd during spring and the Kennedy herd during summer/fall. The Moberly herd in spring was almost exclusively located in alpine (98% of locations, Table 2), but selection for alpine was not statistically significant as only two vegetation-cover types could be included in the model (all other available vegetation-cover types were removed to avoid issues of perfect or near-perfect separation), and both were used in similar proportion to availability (following removal of unused vegetation-cover types). Selection for alpine by Moberly caribou in spring is easily inferred from use. In contrast, the Parsnip herd selected alpine only during spring and avoided alpine in summer/fall.

*Parkland, fir and fir-leading stands*

Selection for forested stands that typically occur at high elevations (parkland, fir and fir-leading) was variable among the northern-ecotype herds in all seasons. The Moberly caribou selected for parkland during calving and summer/fall, and fir stands in late winter, while the Quintette herd selected fir stands during spring. Fir stands were avoided by the Moberly herd in summer/fall and the Quintette herd in early winter. The Kennedy herd selected fir during calving, summer/fall and late winter and never showed avoidance of fir stands. Avoidance of fir-leading stands, which commonly occurred at lower-elevations than parkland or pure fir stands, was typical for the northern-ecotype herds across all seasons. The Parsnip herd selected fir stands in all seasons and in contrast to the northern-ecotype herds, selected fir-leading stands in all seasons except spring.

*Spruce-leading*

Spruce-leading stands typically occur in low-elevation subalpine or valley-bottom forests. All herds avoided spruce-leading stands during calving and summer/fall and none of the herds selected spruce-leading stands in any season. None of the northern-ecotype herds were located in spruce-leading stands during spring (Table 2), and the Parsnip herd avoided spruce-leading stands during this season. In early and late winter all of the herds either avoided, or were never located, in spruce-leading stands.

*Pine-leading*

The northern-ecotype herds on the eastern side of the Rockies were never located in pine-leading stands with the exception of the Quintette herd during summer/fall (Table 2). In contrast, the Kennedy herd selected for pine-leading stands in summer/fall and late winter. Similar to the northern-ecotype herds on the eastern side of the Rockies, the Parsnip caribou were never located in pine-leading stands.

*Deciduous/shrub, young-coniferous, open-nonvegetated, open-vegetated*

These vegetation-cover types were typically dropped from the models for all herds in all seasons due to rare occurrences of use (Table 2). The GPS models showed avoidance of deciduous/shrub in summer/fall and late winter and selection of open-vegetated areas in spring for the Kennedy herd. The Moberly herd selected open-nonvegetated areas in summer/fall and open-vegetated areas in late winter. Although selection of young-coniferous stands was not significant for the Kennedy herd during winter, Kennedy caribou were commonly located in an approximately 10-year old, winter-logged clearcut within their winter range.

## Discussion

Differences in habitat use (specifically use of different vegetation-cover types) and selection were apparent between ecotypes and among herds of woodland caribou, as well as within herds in different seasons. Concurrent examination of habitat use and selection among herds and ecotypes during this study indicated that differences among ecotypes of woodland caribou were not necessarily inherent in temporal variation among studies examining one herd or ecotype of woodland caribou. As well, differences in use and selection among herds and ecotypes were evident in all seasons, and not isolated only to winter.

### *Spatial separation and use of vegetation-cover types*

Although some spatial overlap occurred among most herds (except in early winter), overlapping areas generally accounted for only a small portion of the seasonal range of each herd. Spatial overlap and separation was, in part, an artifact of the number and distribution of the collared-caribou in this study, our method of assigning individuals to herds, and our method of inferring spatial overlap. For example, spatial separation between the Moberly and Quintette herds may have been a result of the sample size and home ranges of caribou collared in these herds. During caribou captures, however, we did not find caribou in the area between the Moberly and Quintette herds, and other surveys (Seip, 2002) suggest that caribou may be absent from this region. Similarly, other methods of defining seasonal ranges may have yielded different results (Boulanger & White, 1990; Girard *et al.*, 2002) and range overlap may vary depending on herd densities (e.g., spatial overlap may increase at higher densities). Despite limitations in quantifying spatial overlap, our data suggest that spatial overlap or adjacency of herds is not synonymous with ecological overlap. Ecological differences (habitat use and selection) were most evident between herds that spatially overlapped (e.g., Quintette and Parsnip), whereas ecological similarities were most apparent among herds that were spatially separated (Moberly and Quintette).

The VHF locations indicated that patterns in use of vegetation-cover types by herd and season were generally consistent with GPS data. VHF data did differ somewhat from GPS data in use of forested vegetation-cover types for each herd, and VHF data indicated greater use of forested stands by the northern-ecotype herds. The VHF data contained fewer locations on a larger number of individuals over a greater time period. As such, variation in use of vegetation-cover types across multiple years and among individuals in a herd may have been greater than variation in the GPS data. Also, different biases are inherent to different methods of obtaining locations. Locations obtained using aerial telemetry may not be as accurate as GPS locations, and as such, VHF locations are more likely to be assigned to the wrong vegetation-cover type. GPS locations over represent use of open areas by collared animals (Rempel & Rodgers, 1997). Consequently, use of alpine by caribou may have been overestimated and use of forested vegetation-cover types by caribou may have been underestimated using GPS data. Differences in fix rates among GPS collars and collar malfunctions resulted in a different number of locations for some individuals compared to others and GPS-collar data may be biased towards individuals that contributed more locations. Because we built our models using GPS-collar data, and from only a few individuals in each herd ($n \leq 5$), inferences about selection by herds are subject to these same biases. Despite biases and inconsistencies, the GPS data was similar to the VHF data in showing general patterns of use of vegetation-cover types by caribou in each herd, suggesting that GPS-collared caribou were representative of other individuals within their herd.

### *Seasonal habitat selection*

Habitat selection by caribou likely involves a trade-off between forage quality and abundance, and risk of predation (Bergerud *et al.*, 1984; Rettie & Messier, 2000; Barten *et al.*, 2001; Gustine *et al.*, 2006a). The influence of these factors on selection by caribou may vary at different scales. At course scales (e.g., seasonal range), caribou likely select or are able to exist in areas with a low risk of predation and then select for forage at finer scales within those areas (Bergerud *et al.*, 1990; Rettie & Messier, 2000; Gustine *et al.*, 2006a).

Similarly the trade-off between forage and risk of predation by caribou may vary in different seasons. Adults and calves are particularly vulnerable to predation during spring, calving, and summer/fall (Bergerud *et al.*, 1984; Edmonds, 1988; Seip, 1990; Seip, 1992a). Caribou herds for which calving or summer ranges overlap with moose and wolves have higher mortality rates than herds that spatially separate from areas used by wolves and moose (Bergerud & Page, 1987; Seip, 1992a). Females may compromise nutritional gains by using alpine areas where predation risk may be lower (Bergerud *et al.*, 1984; Bergerud & Page, 1987; Bergerud *et al.*, 1990; Gustine *et al.*, 2006a), but survival is higher (Seip & Cichowski, 1996) than in lower-elevation forests. During seasons when nutritional demands for caribou are high (e.g., pregnant or lactating females in spring), caribou may move to areas containing more abundant or high-quality forage and increase risk of predation (Gustine *et al*., 2006a).

As climate and disturbance regimes differ between the eastern and western side of the Rockies (Meidinger & Pojar, 1991; Delong, 1994), caribou herds in our study may be employing different strategies in response to differences in forage quality, availability or predation risk resulting from different precipitation levels between the eastern and western portions of the study area. During calving and summer/fall, the northern ecotypes on the eastern side of the Rockies selected alpine. Other studies have found that caribou herds residing on the eastern side of the Rockies also select alpine or parkland areas, particularly during calving and summer/fall (Edmonds & Bloomfield, 1984; Culling *et al*., 2005). In contrast to caribou herds on the eastern side of the Rockies, we found the northern ecotype herd on the western side of the Rockies commonly used and selected lower-elevation forested stands during calving and summer/fall. Ungulate density at low-elevations may be higher in the dry eastern region, and the forb layer in subalpine forests on the western side of the Rockies is more productive and less sparse than on the eastern side (Meidinger & Pojar, 1991). Caribou on the western side of the Rockies may be obtaining a combination of better forage and lower risk of predation, compared to the eastern herds, when using lower-elevation forests.

Selection by northern caribou in winter is similarly influenced by forage abundance, availability and predation risk by wolves (Johnson *et al*., 2001). In our study, the northern-ecotype herds on the eastern side of the Rockies primarily selected alpine in winter. In contrast, the northern ecotype herd on the western side of the Rockies migrated to a low-elevation pine forest. Other northern ecotype herds on the western side of the Rockies also use low-elevation pine forests in winter (Wood, 1996; Johnson *et al*., 2002). Other northern ecotype herds on the eastern side of the Rockies were much more variable in use or selection of different vegetation-cover types in winter (Edmonds & Bloomfield, 1984; Culling *et al*., 2005; Saher, 2005) than eastern herds in this study.

Differences in selection by herds residing on the eastern and western side of the Rockies in our study may have been influenced by differences in snow conditions between the eastern and western regions. Snow depths are notably lower on the eastern as opposed to western side of the Rockies (Jones, unpubl. data). Movement by caribou in the subalpine forest may be more energetically costly for eastern compared to western herds because the snowpack may not harden on the drier eastern side of the Rockies (Culling *et al*., 2005). Alpine areas in the eastern portion of our study area are typically windswept, often containing more snow-free areas than the western region. The energetic demands for cratering in alpine for caribou on the western side of the Rockies may outweigh the lower risk of predation in this vegetation-cover type (Johnson *et al*., 2004), whereas caribou on the eastern side of the Rockies can forage in snow-free alpine areas.

Although Kennedy caribou typically have to crater through snow to access lichens in pine stands, ground lichens were more abundant in pine stands compared to alpine areas used by Kennedy caribou (Jones, unpubl. data). Caribou wintering in pine stands also have access to arboreal lichens that are not available in alpine. The energetic benefits of foraging in pine stands over alpine may outweigh the lower predation risk in alpine (Johnson *et al*., 2004). At our scale of analysis, pine stands were not available to the mountain-ecotype herd on the western side of the Rockies in winter, signifying that availability of vegetation-cover types may also influence differences between ecotypes.

In early winter, mountain caribou in southern British Columbia typically select low-elevation forests (Servheen & Lyon, 1989; Apps *et al*., 2001), whereas mountain caribou in the more northern regions tend to stay at higher elevations (Seip, 1992a; Terry *et al*., 1996). Differences among regions may be related to predation risk by wolves (Terry *et al*., 1996), variation in energetic costs of movement or lichen availability due to snow differences (Apps *et al*., 2001), or the lack of a major early-winter food, falsebox (*Pachistima myrsinites*), in low-elevation forests in northern compared to southern areas (Terry *et al*., 1996). In late winter, mountain caribou move to higher elevations than early winter using subalpine forest and parkland areas (Servheen & Lyon, 1989; Seip, 1990; Seip, 1992a; Apps *et al*., 2001).

Consistent with seasonal habitat selection of mountain caribou in the more northern regions of their distribution, we found that Parsnip caribou typically selected fir and fir-leading stands between approximately 1200 to 1600 m with no evidence of selection for lower elevations in spring or early winter. These results support theories that selection by mountain caribou may be related to differences in forage or risk of predation between northern and southern regions (Terry *et al*., 1996; Apps *et al*., 2001).

The general pattern for both northern and mountain ecotypes appears to be use of productive forests at low-elevations in spring (Servheen & Lyon, 1989;

Cichowski, 1993; Apps *et al*., 2001; Culling *et al*., 2005, Saher, 2005). Caribou using low-elevation areas are likely obtaining more green forage than those occupying other areas (Servheen & Lyon, 1989; Seip, 1990; Seip, 1992b; Apps *et al*., 2001). Our models indicated that none of the herds in this study use low-elevation forests in spring. Risk to caribou from predation by wolves may be higher in lower-elevation forested areas compared to alpine (Johnson *et al*., 2004), and caribou may be trading off nutritional gain obtained from green forage against predation risk (Bergerud *et al*., 1984; Bergerud & Page, 1987; Gustine *et al*., 2006a). Conversely, we did observe variation among Parsnip caribou individuals in model predictions of selection. For example, we occasionally located two of the 10 collared mountain caribou in snow-free areas at low elevations in spring. During telemetry flights we noted that more southern areas in the Parsnip range became snow-free earlier in spring compared to northern areas and thus snow-free areas may not be available to all Parsnip caribou in spring and similarly to individuals in other herds.

Despite differences in selection and use among herds and ecotypes, our results suggest that some commonalities were apparent among herds and in each season. With the exception of the Kennedy herd in summer/fall, early and late winter, caribou selected elevations >1300 m and avoided or did not use pine-leading, spruce-leading, deciduous/shrub and young-coniferous stands. Studies conducted in other areas suggest that moose and subsequently wolf density may be higher in early-seral forests (Schwartz & Franzmann, 1989), and predation risk for caribou from wolves may be higher in pine-leading and spruce-leading stands (Johnson *et al*., 2002). Caribou may be avoiding these vegetation-cover types across their range in order to increase spatial separation from wolves (Seip, 1992a). All herds avoided steeper slopes, and selection for western and southern aspects were common, whereas eastern and northern aspects were typically avoided. Western and southern aspects may contain more abundant vegetation in spring, calving and summer/fall, and wind patterns may result in lower snow depths on western compared to eastern aspects in early and late winter.

### *Scale and model limitations*

Selection by woodland caribou may differ at different scales of analysis (Rettie & Messier, 2000; Apps *et al*., 2001; Johnson *et al*., 2001) and quantifying scale-dependent differences in selection may provide further insight into determining appropriate management strategies for woodland caribou (Johnson *et al*., 2001). Although we recognize that examining selection at different scales may have resulted in broader conclusions, our analyses of smaller-scale levels of selection were constrained by 20-h fix intervals, vegetation-cover resolution and sample size. Using 20-h fix intervals precluded using movement rates (Johnson *et al*., 2001) to identify scales of selection related to small-scale behavioral decisions (e.g., selection of feeding sites), and variables related to selection at these scales typically must be collected on the ground. The VRI data did not contain vegetation-cover classifications relative to a smaller scale of selection (e.g., alpine-lichen, alpine-barren) and had this data been available, our analytical tests would have likely been constrained by rare or zero cell counts in these categories as a result of small sample sizes.

Using a larger-scale definition of availability (e.g., annual home range, study area), in addition to examining availability at the scale of daily movement capability, may have further contributed to understanding selection by woodland caribou in our study area. For example, in early winter, Kennedy caribou migrate from mountainous terrain to an expansive low-elevation pine forest. At our scale of analysis, selection for pine was not significant, although 75% of locations occurred in pine-leading stands within this range. The 95th percentile movement distance for Kennedy caribou in early winter was 4960 m, and as such, the majority of available locations also occurred within this extensive pine range. Examining selection at the scale of annual home range would likely have resulted in a high availability of sites in the adjacent mountains, and selection for pine may have become apparent at this scale. Quantifying selection at larger scales, however, would have involved defining areas as available that may not have been available to caribou.

We recognize that our definition of availability was still somewhat arbitrary (e.g., we chose the 95th percentile movement distance), but available locations were constrained within biologically defined areas that caribou could almost certainly use. Our scale of analysis was analogous to a large scale definition of availability for caribou occupying mountainous terrain (because valley bottom to alpine was often available). For caribou occupying an expansive and homogenous area (e.g., low-elevation pine), however, a larger scale of analysis or classifying vegetation-cover types at a finer scale may have yielded different results. In the future, a larger scale of analysis, using a larger sample of collared caribou, would be valuable to obtain a broader understanding of the seasonal ecology of these or other caribou herds.

We may have made different inferences about selection of these herds had we modeled selection of individual caribou or selection in each year. Similarly, our classification of individuals into herds and seasonal definitions may have influenced our results. These types of analyses were constrained by having a limited number of locations (particularly in shorter seasons) for only a few individuals in each herd. For example, examination of locations for individual caribou during calving, regardless of herd or ecotype, indicated that parturition commonly occurred in the subalpine forest and caribou moved to higher elevations after their calf was born. Selection models, however, indicated that northern ecotype herds selected alpine during calving. Differences in selection during parturition and post-calving may have been apparent had these periods been modeled separately.

Topographic variables and the topographic model were useful for predicting caribou locations at the scale of analysis of this study, but likely do not encompass all variables influencing selection of habitat by woodland caribou. A different scale or type of analysis may have emphasized the importance of other variables. Location data (both GPS and VHF) clearly indicated that caribou disproportionately used specific vegetation-cover types, but vegetation-cover type performed poorly in the selection models. Topographic variables (particularly elevation) may be more related to variables that influence selection by caribou (e.g., forage quality, snow characteristics and risk of predation) than vegetation-cover type. This may be a result of inaccuracies associated with the mapping of vegetation-cover types or by defining vegetation-cover classes that are not related to factors influencing selection by caribou.

We found that selection of vegetation-cover types at our scale of analysis was not always consistent with use of vegetation-cover types by caribou. Because our method of analysis required the removal of vegetation-cover types that were rarely or never used by caribou, selection for vegetation-cover types that were occasionally used (e.g., forested calving sites) or used in similar proportion to availability (e.g., use of pine by Kennedy caribou) may have been underestimated (as available locations in unused vegetation-cover types were also excluded from the models). Similarly, vegetation-cover types that were removed from our models may have been slightly correlated with topographical (e.g., elevation) or distance to nearest road variables, resulting in a biased estimate of availability for these variables. An examination of the relationship between elevation and vegetation-cover type, however, showed considerable overlap in ranges of elevation and non-significant differences among the majority of vegetation-cover classes.

Because selection models were constrained by our scale of analysis, small samples of individual caribou, and seasonal delineation, we recommend that use and selection of vegetation-cover types by caribou be considered when identifying critical habitat for caribou herds in this study. Conversely, planning strategies that focus solely on vegetation cover (in the absence of topographic variables) may not identify suitable habitat for caribou.

This research demonstrates that seasonal use and selection by herds and ecotypes is much more variable then general ecotype descriptions suggest. Discrepancies between ecotype classifications and habitat use and selection by caribou herds in this study illustrate the importance of determining seasonal use and selection for woodland caribou herds across their range. Consequently, we recommend that recovery planning and mapping of critical habitat for woodland caribou be undertaken on a seasonal and herd-specific basis.

Although we found evidence of spatial overlap among previously identified herds, our results suggest that these herds may be ecologically different (e.g., seasonal use and selection). Despite ecological differences among herds, we do not know if herds can be considered distinct populations (in which no genetic exchange occurs). Caribou in this study may belong to one population, but respond to climatic and terrain variability at a more regional scale. Maintaining habitat predominantly used and selected by caribou, combined with reducing habitat avoided by caribou across their range, may ensure population stability by preserving or initiating genetic flow among herds of caribou.

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