

**Use, Selection And Winter Foraging Patterns Among Woodland Caribou Herds In
Central British Columbia**

Elena S. Jones

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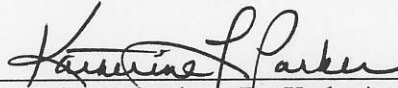
Name: Elena Jones
Degree: Master of Science
Thesis Title: Use, Selection And Winter Foraging Patterns Among Woodland Caribou Herds In Central British Columbia
Examining Committee:



Chair: Dr. Robert Tait
Dean of Graduate Studies
University of Northern British Columbia



Supervisor: Dr. Michael Gillingham, Associate Professor
Natural Resources and Environmental Studies Program
University of Northern British Columbia



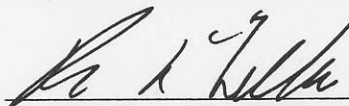
Committee Member: Dr. Katherine Parker, Associate Professor
Natural Resources and Environmental Studies Program
Ian McTaggart Cowan Muskwa-Kechika Research Professor
University of Northern British Columbia



Committee Member: Doug Heard, Adjunct Professor
Natural Resources and Environmental Studies Program
University of Northern British Columbia



Committee Member: Dr. Dale Seip
Wildlife Habitat Ecologist
BC Ministry of Forests and Range



External Examiner: Dr. Bruce McLellan, Adjunct Professor
Department of Forest Sciences
University of British Columbia

Date Approved:

February 5, 2007

Abstract

Woodland caribou (*Rangifer tarandus caribou*) in British Columbia have been classified into three ecotypes: mountain, northern, and boreal based on differences in their use of habitat and forage (ground versus arboreal lichens) in winter. Woodland caribou in the southern two-thirds of British Columbia are nationally threatened and recovery planning is mandatory. Recovery planning focuses on ecotypes but habitat use, selection and foraging ecology may also differ among woodland caribou herds. I used locations from radio-collared caribou to examine whether spatial or ecological (habitat use and selection) separation was apparent among four caribou herds (three northern, one mountain) at the transition zone from northern to mountain caribou in central British Columbia. In winter, I followed caribou tracks in snow to determine whether caribou in each herd used the same foraging method (ground versus arboreal) in the same vegetation type (alpine, parkland and subalpine forest). Spatial overlap among herds was apparent throughout the year except in early winter, but herds differed in their use and selection of habitat. Caribou using the same vegetation type in winter typically used the same foraging method. I also examined differences in forage abundance, forage accessibility (snow depths and hardness) and sinking depths of caribou within a low-elevation pine forest used by one northern ecotype herd (Kennedy Siding) in winter. There were no differences in snow conditions among stand types (clearcut to old pine), but forage abundance differed among stands. Kennedy Siding caribou responded to differences in snow conditions throughout the winter by altering foraging method, abandoning specific stand types, or leaving the pine stands to return to mountainous terrain. This research provides a rationale for developing herd-specific management strategies, and for implementing specific silvicultural regimes within pine forests used by caribou in winter.

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Chapter 1: Introduction

Context

In Canada, caribou (*Rangifer tarandus*) have been classified into five subspecies based on differences in skull and antler characteristics (Banfield, 1961). This categorization is the most widely accepted taxonomical division of the caribou species (Bergerud, 1978). All subspecies of caribou can also be grouped as barren-ground or woodland caribou (Banfield, 1961). Barren-ground caribou forage primarily on ground lichens in winter and inhabit the circumpolar regions of the arctic, migrating between barren tundra and boreal forests (Banfield, 1961). Woodland caribou typically forage on ground and arboreal lichens in winter and are commonly associated with mature forests, bogs and alpine (Kelsall, 1983). Barren-ground caribou are absent from British Columbia and only woodland caribou (*Rangifer tarandus caribou*) currently inhabit the province (Banfield, 1961; Bergerud, 1978).

Woodland caribou in British Columbia have been classified into three ecotypes: mountain, northern, and boreal (Bergerud, 1978; Stevenson & Hatler, 1985; Heard & Vagt, 1998). These ecotypes are distinguished by their use of different habitats and foraging ecology in winter (Stevenson & Hatler, 1985). Mountain caribou inhabit mountainous terrain in southeastern British Columbia (Stevenson & Hatler, 1985; Heard & Vagt, 1998). This area is characterized by heavy snowfall during winter (Stevenson & Hatler, 1985), which limits access to ground vegetation by caribou. As such, mountain caribou forage almost exclusively on arboreal lichens (Antifeau, 1987; Stevenson & Hatler, 1985; Seip, 1992b). Mountain caribou typically winter in old-growth forests, where arboreal lichens are abundant (Antifeau, 1987; Rominger & Oldemeyer, 1989; Apps *et al.*, 2001).

In contrast, northern caribou inhabit the mountainous northern and western areas of

British Columbia. Snowfall is lower in these areas (Bergerud, 1978; Stevenson & Hatler, 1985) and these caribou crater through snow to access ground vegetation (Cichowski, 1993; Wood, 1996; Johnson *et al.*, 2000). Northern caribou typically forage on ground lichens during winter in alpine or in lower-elevation pine (*Pinus contorta*) or black-spruce (*Picea mariana*) forests (Cichowski, 1993; Wood, 1996; Johnson *et al.*, 2000), although use of subalpine forests has been documented (Cichowski, 1993; Wood, 1996; Johnson *et al.*, 2000) and is sometimes prevalent (Poole *et al.*, 2000).

Boreal caribou inhabit boreal forests in northeastern British Columbia (Heard & Vagt, 1998), where they typically crater for ground lichens in peatland areas (Bergerud, 1978; Fuller & Keith, 1981; Bradshaw *et al.*, 1995; Rettie & Messier, 2000). These caribou remain within the boreal forest in all seasons (Fuller & Keith, 1981; Bradshaw *et al.*, 1995) and they have often been grouped with northern caribou (Heard & Vagt, 1998; Spalding, 2000).

Differences in use of habitats and forage (ground versus arboreal lichens) by woodland caribou ecotypes are believed to be related to snow conditions and lichen distribution across their range (Bergerud, 1978; Stevenson & Hatler, 1985). Numerous studies have illustrated differences in use of habitats or foraging ecology between woodland caribou ecotypes occupying distinctly different geographical areas (Antifeau, 1987; Seip, 1992a; Cichowski, 1993; Johnson *et al.*, 2001). These studies, however, have focused on one herd or ecotype of woodland caribou and were conducted in different years. Concurrent examination of habitat use and foraging ecology between woodland caribou ecotypes has not occurred in British Columbia, and differences between ecotypes in seasons other than winter have received little attention. The transition zone between northern and mountain caribou in British Columbia allows for ecological comparisons between herds and ecotypes of woodland caribou occupying a similar geographical area.

Four woodland caribou herds were previously identified in the geographical area surrounding the current transition zone between northern and mountain ecotypes: Quintette, Kennedy Siding (hereafter termed Kennedy), Moberly and Parsnip. The Quintette, Kennedy and Moberly herds were considered to be northern caribou, whereas the Parsnip herd was categorized as a mountain-caribou ecotype. A preliminary study (Seip, 2002) indicated that variation in use of habitat by woodland caribou herds and ecotypes occurred in this area, but the geographic distribution, seasonal selection and use patterns, and foraging habits of these herds were relatively unknown. Determining the geographical areas used by each herd, and examining the range of variation in seasonal use, selection and winter foraging habits among herds is important to assess whether land-management strategies should be herd or ecotype-specific.

Mountain caribou were provincially “red-listed” (extirpated, endangered or threatened) in 2000 and northern caribou are currently “blue-listed” (of special concern). Both ecotypes within the Southern Mountains National Ecological Area (COSEWIC, 2002) have been nationally designated as “threatened” by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2002). British Columbia has a legal responsibility to ensure that habitat for woodland caribou is of suitable quality to maintain populations throughout the province (Hatter, 2002). In order to provide or maintain suitable habitat for woodland caribou, it is important to determine whether geographical overlap exists between ecotypes or herds, and if so, whether herds using the same areas are ecologically different. Also, in areas that have been specifically designated as protected habitat for caribou, it is important to ensure that management objectives are consistent with the habitat requirements of woodland caribou.

In autumn, the Kennedy herd migrates from the mountains to a pine-dominated winter

range in the subboreal forest. This area was designated as Ungulate Winter Range (UWR) in 2003, under the provincial Forest and Range Practices Act (FRPA). Under FRPA, an UWR is defined as “an area that contains habitat that is necessary to meet the winter habitat requirements of an ungulate species” and forestry activities within an UWR are required to correspond to the identified objectives. Presently, the main stand-management objective for the Kennedy Siding UWR is to maintain the area on a 100-year rotation in order that half of the UWR contains stands 0 to 50 years, and half contains stands 50 to 100 years of age (Arthur, 2002).

The Kennedy Siding UWR includes a large clearcut area, and past fires have resulted in a variety of pine stands of different ages. In addition, some of the pine stands were spaced, resulting in more open stands than are typical for mature-pine forests. Energetic costs may increase for woodland caribou in winter due to higher energetic requirements for cratering (Fancy & White, 1985) and walking (Parker *et al.*, 1984; Fancy & White, 1987) through snow. Forested stands of different species composition, canopy closure or age may influence snow characteristics (Bunnell *et al.*, 1990a; Schaefer, 1996) and forage species or abundance (Schaefer, 1996; Pharo & Vitt, 2000; Coxson & Marsh, 2001). Management strategies may improve habitat for woodland caribou at Kennedy Siding and elsewhere if we can identify differences in forage abundance and accessibility among pine stands of different ages, and determine whether caribou respond to these potential differences. In addition to management direction, ecological insight may be gained as to whether caribou use stand types or foraging methods to obtain more abundant forage and/or minimize the energetic costs of accessing forage.

Objectives

In order to examine spatial and ecological overlap (i.e., habitat use, selection and method of foraging) among herds and between ecotypes of woodland caribou during the same time period, my objectives were to determine: 1) whether the Kennedy, Quintette, Moberly and Parsnip woodland caribou herds were spatially separated or if distribution was continuous across the landscape; 2) if seasonal differences in habitat use and selection were apparent between ecotypes and herds of woodland caribou; and 3) whether there was a difference in use of foraging method (ground versus arboreal) by caribou in winter among herds using the same habitat. I 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 habitat use and selection and differ from the mountain-ecotype herd (Parsonip), particularly during winter.

To assess whether management strategies could promote forage abundance and accessibility for caribou occupying a pine-dominated winter range, my objectives were to determine: 1) whether there were differences in snow conditions (snow depths, snow hardness) and sinking depths of caribou among stand types; 2) whether there were differences in forage species composition and abundance among stand types; and 3) whether caribou responded to changes in forage abundance or accessibility by using different stand types or foraging methods. I hypothesized that snow conditions and forage abundance would differ among stand types, and that caribou behavior (use of stand types and method of foraging) would be influenced by differences in forage abundance and accessibility.

Thesis organization

I organized this thesis into four separate chapters. Chapter One introduces this research

and provides the background, rationale and objectives of this study. Chapter Two compares the spatial distribution, habitat use and selection among herds and between ecotypes of woodland caribou by season. Chapter Three focuses on a pine-dominated range used by the Kennedy herd in winter, and specifically, whether there were differences in forage abundance and accessibility among stand types and how caribou activities were influenced by potential differences. Chapters Two and Three are stand-alone chapters that are to be submitted to peer-reviewed journals for publication. Chapter Four summarizes the main findings of my research and provides management recommendations. Additional data focusing on foraging methods (ground versus arboreal) for herds using the same habitat in winter are provided in this final chapter.

Chapter 2: Comparison of seasonal habitat selection between two woodland caribou ecotypes in central British Columbia¹

Abstract: Woodland caribou (*Rangifer tarandus caribou*) in British Columbia have been classified into ecotypes based on differences in use of habitat and forage types (ground versus arboreal lichens) 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 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 (Moberly and

¹ This chapter has been submitted to *Rangifer* for publication under the authorship of E. S. Jones, M. P. Gillingham, D. R. Seip and D. C. Heard. In recognition that many aspects of this research did not take place without the valuable assistance of the contributing authors, I use “we” throughout this chapter to denote activities undertaken by myself, others or both myself and others.

Quintette). Differences in habitat use and selection within the northern-ecotype herds were likely related to different climatic regimes (influencing forage distribution, abundance, snow conditions and risk of predation) on the eastern and western side of the Rockies. 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.

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 or at different times of the year. Research that quantifies variables that influence seasonal habitat selection of large ungulates is essential to resource management and species-conservation strategies.

Woodland caribou (*Rangifer tarandus caribou*) display considerable variation in seasonal habitat use within British Columbia (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. 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 (Hatter, 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 plans for woodland caribou in British Columbia focus 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 km² and is located in the Rocky Mountains of central British Columbia (Figure 2.1). 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. The BWBS zone occurs on the eastern side of the Rocky Mountains, ranges

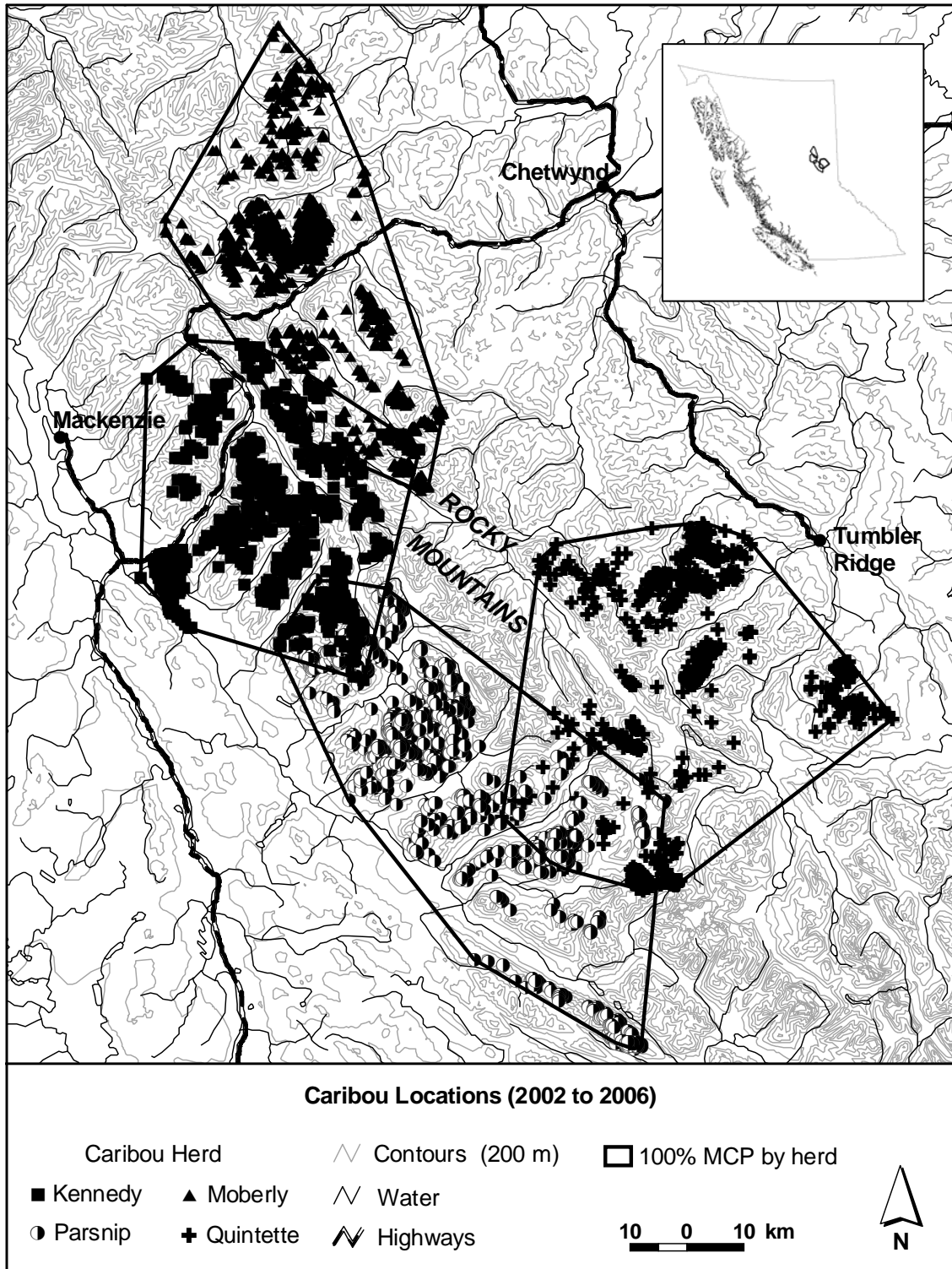


Figure 2.1 Study area and caribou locations from May 2002 to January 2006 for woodland caribou in central British Columbia. The study area is depicted by a 100% minimum convex polygon (MCP) around all caribou locations for each herd.

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. 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, sedges 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 region of the study area is drier than in the western region. The ESSF 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 region of the study area whereas the Moberly and Quintette (northern ecotype) herds typically occupy the eastern side of the Rocky Mountains (Figure 2.1). 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 (Appendix A). 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 locations with 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 types (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 depths on the west side of the mountains typically exceeded 1 m and the

snowpack had settled and hardened.

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 20 h) for locations occurring after a missed fix (i.e., 40-h 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 2.1) to

Table 2.1 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).

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: alpine, parkland, fir, fir-leading, spruce-leading, pine-leading, coniferous-unknown, young-coniferous, deciduous/shrub, open-nonvegetated and open-vegetated (Appendix B). 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 ≤ 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 + elevation²), 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 score (typically the quadratic model) was

used in the model set (Table 2.1).

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 (β_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 ($P < 0.05$). We averaged validated competing models (Burnham & Anderson, 2002) to obtain a final model for each herd in each season. Significance of selection coefficients (β_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 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 (Figure 2.2), calving (Figure 2.3), summer/fall (Figure 2.4) and late winter (Figure 2.6), but not in early winter (Figure 2.5). 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.

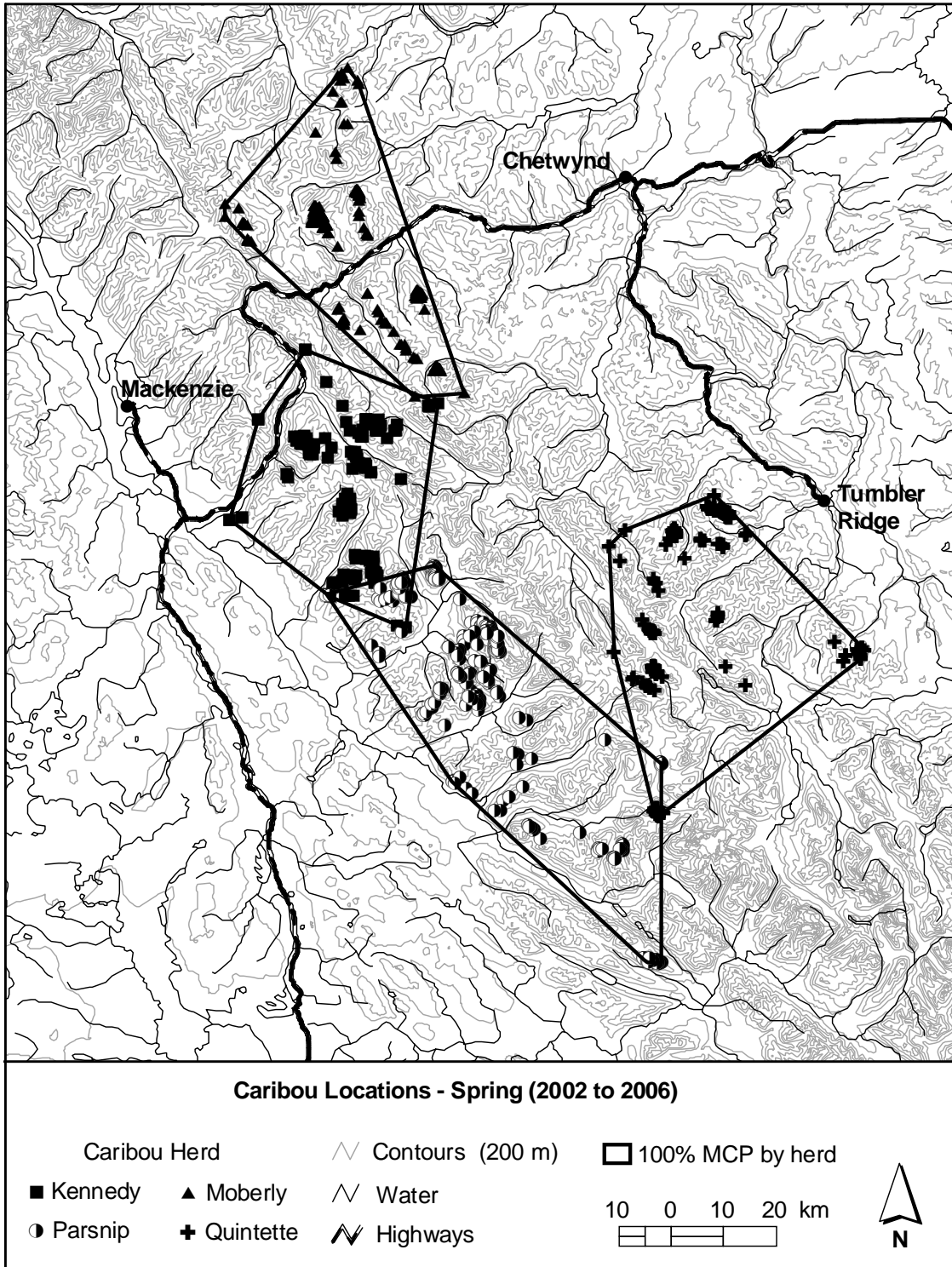


Figure 2.2. Spring locations of caribou (2002 to 2006), by herd, showing some spatial overlap during this season for woodland caribou in central British Columbia.

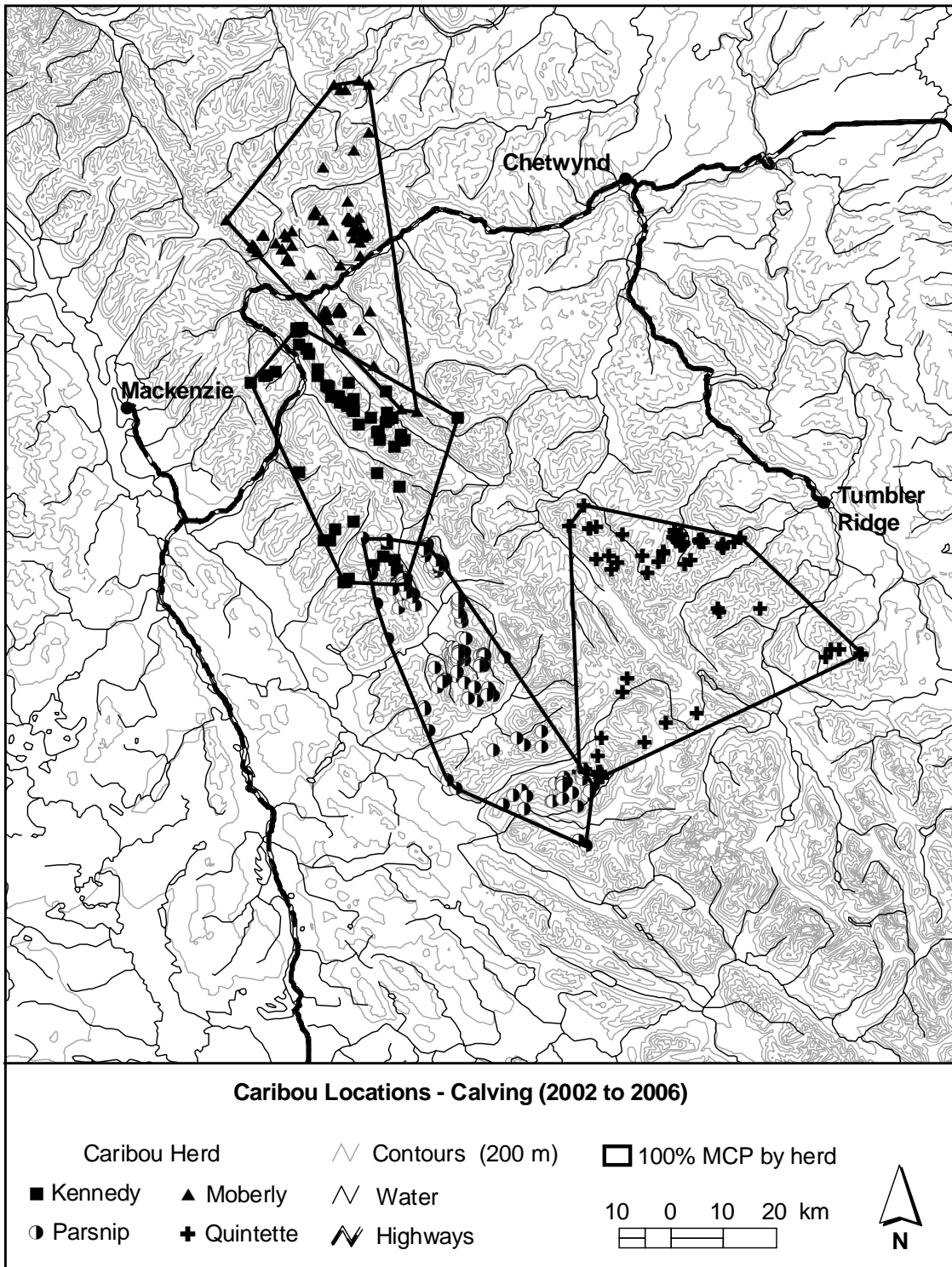


Figure 2.3. Calving locations of caribou (2002 to 2006), by herd, showing some spatial overlap during this season for woodland caribou in central British Columbia.

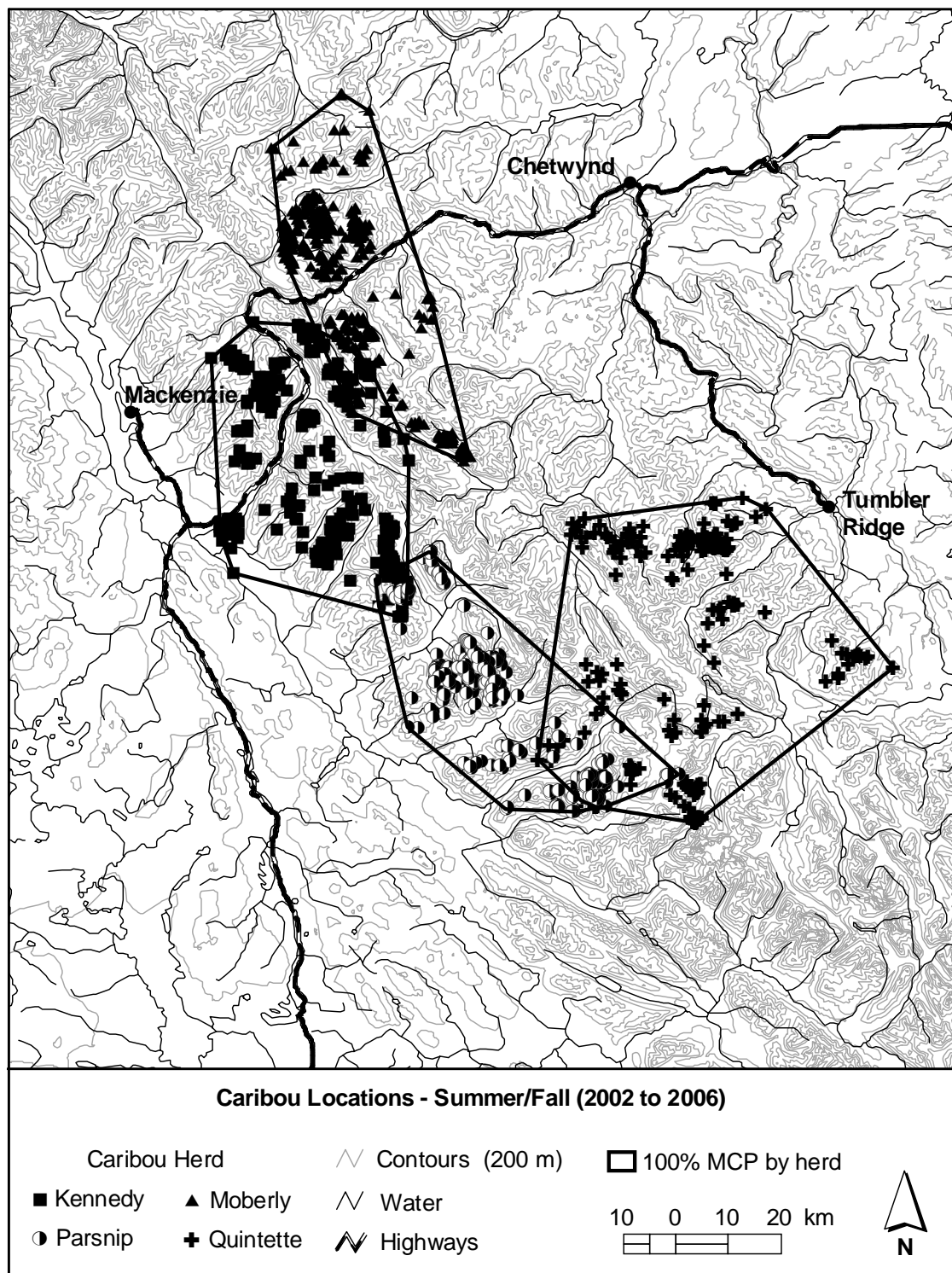


Figure 2.4. Summer/fall locations of caribou (2002 to 2006), by herd, showing some spatial overlap during this season for woodland caribou in central British Columbia.

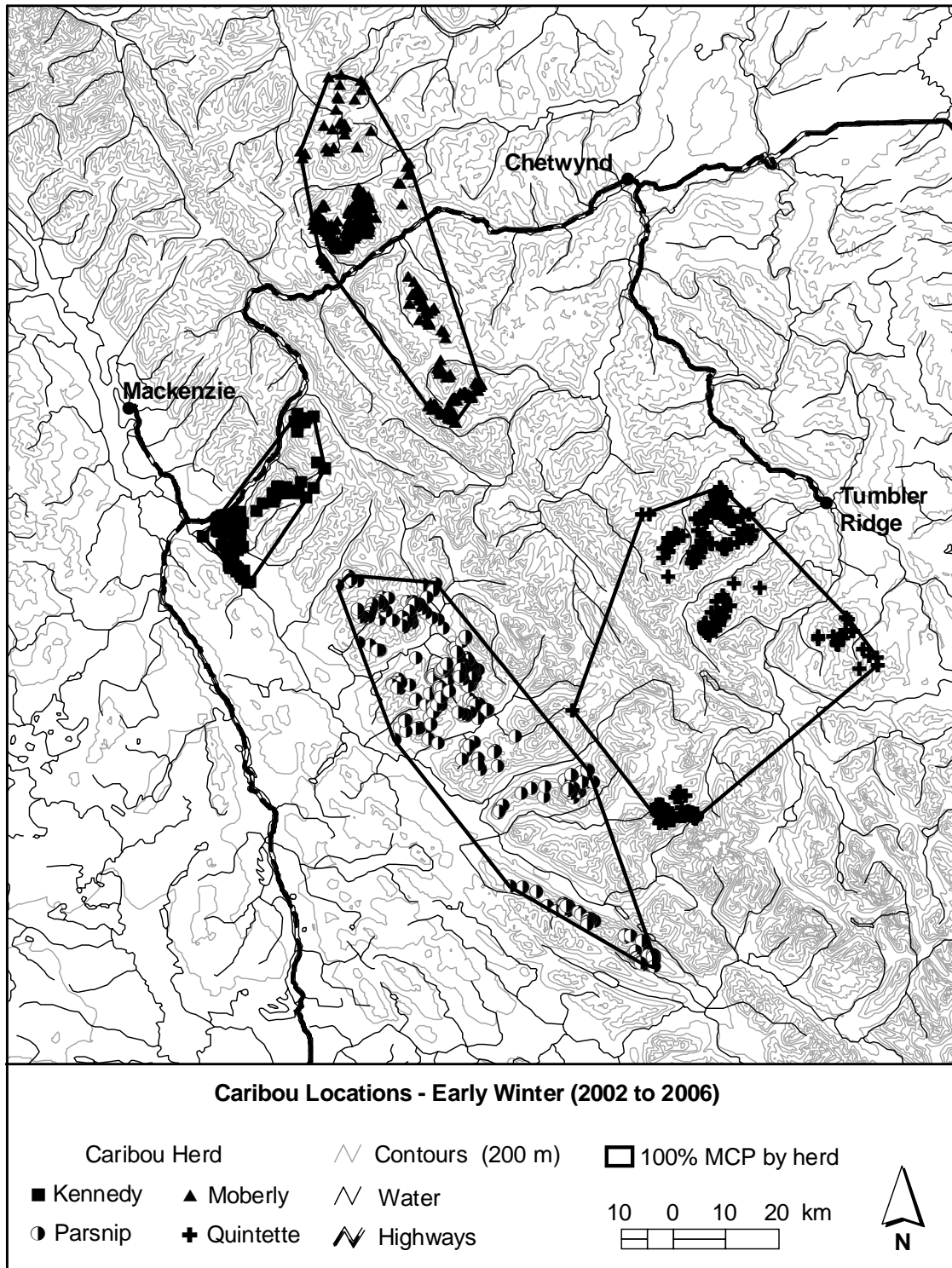


Figure 2.5. Early winter locations of caribou (2002 to 2006), by herd, showing lack of spatial overlap during this season for woodland caribou in central British Columbia.

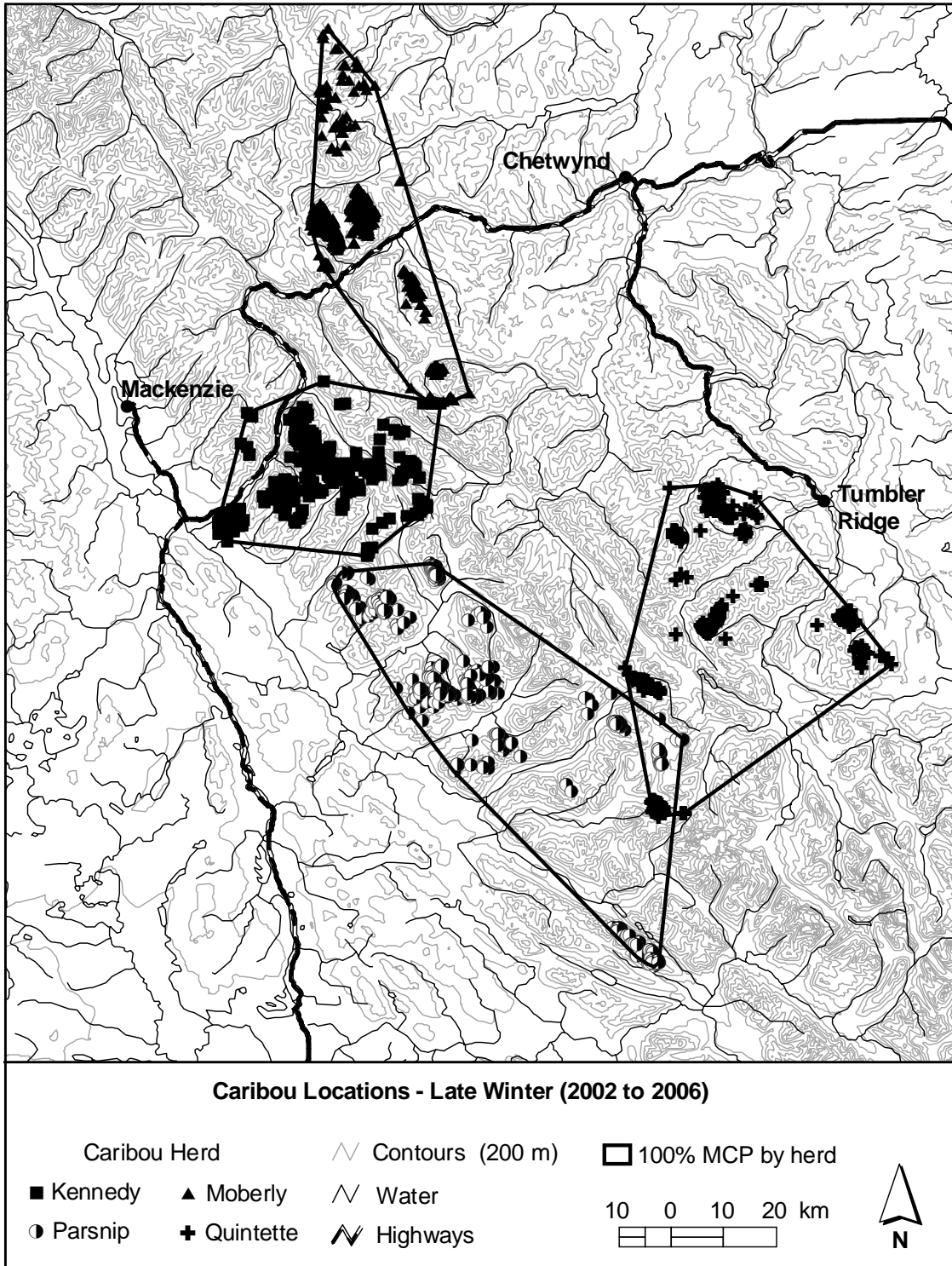


Figure 2.6. Late winter locations of caribou (2002 to 2006), by herd, showing some spatial overlap during this season for woodland caribou in central British Columbia.

Use of vegetation-cover types by GPS-collared caribou varied among herds and seasons (Table 2.2), but some patterns were evident. The northern-ecotype herds that inhabited the eastern side of the Rockies (Moberly and Quintette) were predominately located 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 2.2). 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 mostly 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 2.2). 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.

Table 2.2. 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 |
| <i>n</i> | 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) |

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

Table 2.2. Continued

| | Kennedy | | Moberly | | Quintette | | Parsnip | |
|----------------|-------------------|-----------|------------------|-----------|-------------------|-----------|--------------|-----------|
| Calving | Used | Available | Used | Available | Used | Available | Used | Available |
| <i>n</i> | 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 |

^a Vegetation-cover type removed from models when number of use locations <4.

Table 2.2. Continued.

| Summer/Fall <i>n</i> | Kennedy | | Moberly | | Quintette | | Parsnip | |
|--------------------------------|------------------|------------|------------------|------------|------------------|------------|--------------|------------|
| | Used | Available | Used | Available | Used | Available | Used | Available |
| | 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 number of use locations <4.

Table 2.2. Continued.

| | Kennedy | | Moberly | | Quintette | | Parsnip | |
|---------------------|------------------|------------|------------------|------------|-------------------|------------|--------------|------------|
| Early Winter | Used | Available | Used | Available | Used | Available | Used | Available |
| <i>n</i> | 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) |

^a Vegetation-cover type removed from models when number of use locations <4.

Table 2.2. Continued.

| | Kennedy | | Moberly | | Quintette | | Parsnip | |
|--------------------|------------------|------------|------------------|------------|------------------|------------|-------------------|------------|
| Late Winter | Used | Available | Used | Available | Used | Available | Used | Available |
| <i>n</i> | 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 ^a | 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 number of use locations <4.

Selection models

The model containing all topographic variables (Topo Model 1, Table 2.3) 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 variation in selection 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 2.3) 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 + elevation² 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 (Appendix C, Table C.3). 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 2.3).

Elevation

Differences in selection patterns for elevation by caribou herds were most apparent in early winter (Figure 2.7), but selection for elevation varied among herds in all other seasons.

Table 2.3. Top or competing models, by season and herd, for woodland caribou in central British Columbia. Model variables are presented in Table 2.1. Competing models are sorted by Akaike model weights (w_i), and competing models for each herd in each season are indicated by no spacing between lines. 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 |
| | Kennedy | Topo Model 2 | 6 | 438 | 0.792 | -166.274 | 344.687 | 0.099 | 0.797 |
| | Kennedy | 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 |

^a K-fold cross validation procedures were unsuccessful (see text).

Table 2.3. Continued.

| Season | Herd | Model | K | <i>n</i> | ROC | LL | AIC _c | <i>w_i</i> | \bar{r}_s |
|-----------------|-----------|---------------------------|----|----------|-------|-----------|------------------|----------------------|--------------|
| 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 | Kennedy | Topo Model 1 | 8 | 843 | 0.702 | -453.108 | 922.349 | 1.000 | 0.848 |
| Winter | 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 | Kennedy | Vegetation - Topo Model 1 | 15 | 2013 | 0.745 | -798.803 | 1627.816 | 0.792 | 0.897 |
| Winter | Kennedy | Vegetation - Topo Model 1 | 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 text).

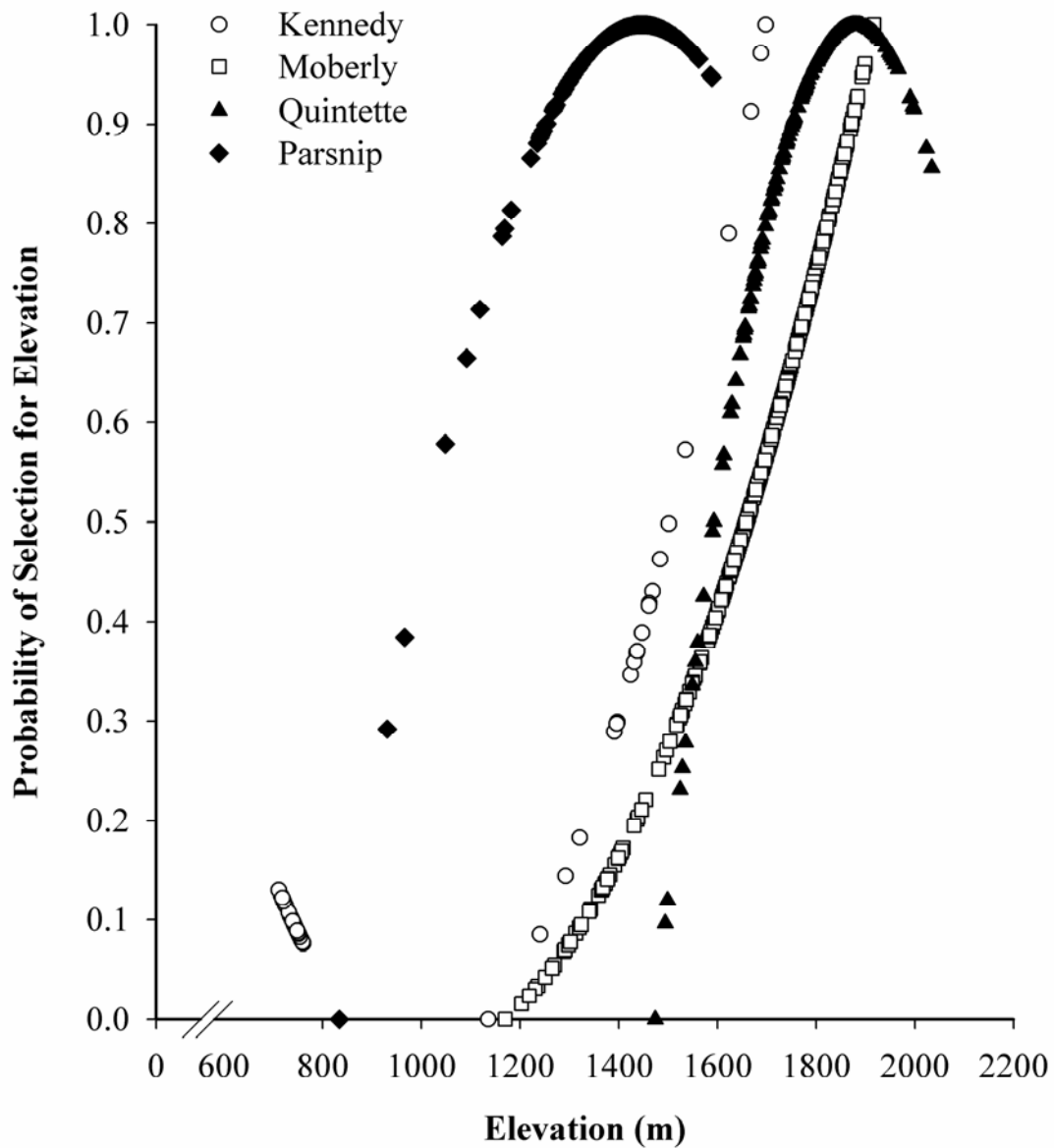


Figure 2.7. Probability of selection for elevation in early winter from the top or averaged selection model, by herd, for woodland caribou in central British Columbia. The elevation function was determined by holding other variables in the model constant and calculating the sum of $\beta_{i(elevation)} \times \text{elevation}$ and $\beta_{i(elevation^2)} \times \text{elevation}^2$ (scaled between 0-1) at use locations of woodland caribou for that season. Elevation and elevation² were significant ($P < 0.05$) for each herd.

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, Figure 2.7). In contrast, selection for elevation by the mountain-ecotype herd was distinctly quadratic in all seasons (e.g., Parsnip herd, Figure 2.7), 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, Figure 2.7).

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 and selected elevations above 1600 m in all seasons (range of use: Moberly, 1175 to 2005 m; Quintette, 1250 to 2035 m). 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 (Appendix C, Table C.1), early winter (Appendix C, Table C.4) and late winter (Appendix C, Table C.5) with the exception of the Kennedy herd where slope was not significant in late winter (Appendix C, Table C.5). Slope was not significant for any of the herds during calving (Appendix C, Table C.2) or for the Kennedy and Parsnip herds during summer/fall (Appendix C, Table C.3). 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 (Appendix C, Tables C.1 to C.5) with the exception of the Moberly herd in spring, where western aspects were not significant (Appendix C, Table C.1). Both herds selected for southern aspects in spring (Appendix C, Table C.1) and the Quintette herd avoided northern aspects in spring (Appendix C, Table C.1) and early winter (Appendix C, Table C.4). Both herds avoided northern aspects in late winter (Appendix C, Table C.5).

Aspect was significant for Kennedy caribou during spring (Appendix C, Table C.1), summer/fall (Appendix C, Table C.3) and late winter (Appendix C, Table C.5). 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 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 (Appendix C, Table C.2) and late winter (Appendix C, Table C.5). 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 2.3). 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 (Appendix C, Table C.2). Although a higher percentage of use locations were in alpine during calving, some individuals in these herds moved from alpine to forested stands 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 2.2) 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 (Appendix D) in the absence of other variables (Vegetation Model, Table 2.1).

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 2.2), 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 (Appendix D).

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 (Appendix D).

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 (Appendix D). None of the northern-ecotype herds were located in spruce-leading stands during spring (Table 2.2), 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 2.2). In contrast, the Kennedy herd selected for pine-leading stands in summer/fall and late winter (Appendix D). 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 2.2). 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 (Appendix D). Although selection of young-coniferous stands was not significant for the Kennedy herd during winter (Appendix D), 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 also vary depending on herd densities (e.g., spatial overlap may increase at higher densities). Despite limitations in quantifying spatial overlap, our data demonstrate 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 coarse 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 regions 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 selected 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 these 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 area. 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 calves were 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 the vegetation-cover type model was never in the competing model set. 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 habitats 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 habitat use and selection may be inherently different among and within woodland caribou ecotypes despite adjacency or evidence of spatial overlap. Consequently, we recommend that recovery planning and mapping of critical habitat for woodland caribou be undertaken on a seasonal and herd-specific basis.

Chapter 3: Comparison of lichen availability and foraging activity by woodland caribou among different stand types in a pine-dominated winter range¹

Abstract: Increased energetic demands in winter usually result in loss of body mass by caribou (*Rangifer tarandus*). Reduced body mass in female caribou has been associated with decreased calving success or recruitment. We used measurements from permanent transects and along woodland caribou (*Rangifer tarandus caribou*) tracks in winter, as well as line-transect vegetation surveys in summer, to determine if forage abundance or variables related to the energetic cost of movement (caribou sinking depths) or foraging (snow depths and snow hardness) by caribou varied within a pine- (*Pinus contorta*) dominated winter range. We compared forage abundance and snow conditions among five stand types (clearcut, young, mature, spaced and old pine) to determine if management regimes in pine stands used by caribou in winter could influence forage abundance and accessibility. We found no differences in snow depths, hardness or sinking depths by caribou among stands, but forage abundance varied. There were differences in snow conditions at different time periods throughout the winter, consistent across all stand types. Although mature pine stands contained the highest abundance of typical lichen forage species (*Cladina* spp. and *Bryoria* spp.), caribou used all stand types. Caribou appeared to respond to differences in snow conditions (primarily hardness) throughout the winter by abandoning stand types (clearcut), using different methods of foraging (ground versus arboreal), and migrating from the pine-

¹ This chapter will be submitted to Forest Ecology and Management for publication (authorship not yet determined). In recognition that many aspects of this research did not take place without the valuable assistance of the contributing authors, I use “we” throughout this chapter to denote activities undertaken by myself, others or both myself and others.

dominated winter range. Differences among stand types indicate that management strategies may be able to positively influence forage abundance for caribou in pine forests.

Introduction

In winter, the primary foods consumed by woodland caribou (*Rangifer tarandus caribou*) consist of arboreal and/or ground lichens (Edmonds & Bloomfield, 1984; Stevenson & Hatler, 1985; Cichowski, 1993; Terry *et al.*, 2000; Johnson *et al.*, 2001). Lichens are high in digestible energy, but low in protein (Kelsall, 1968; Thomas *et al.*, 1984; Klein, 1990; Danell *et al.* 1994). Caribou and reindeer (*Rangifer tarandus tarandus*) with unlimited access to lichens (e.g., *Cladina* spp.) or low-protein feed in feeding trials lose body mass and fat reserves in winter (Holleman *et al.*, 1979; Soppela *et al.*, 2000; Parker *et al.*, 2005), and limiting access to lichens results in even greater mass losses by reindeer (Soppela *et al.*, 2000). Less-than-average maternal body mass has been related to parturition failure (Cameron *et al.*, 1993; Adams & Dale, 1998a; Tveraa *et al.*, 2003), delayed parturition (Cameron *et al.*, 1993; Adams & Dale, 1998b), and neonate (Skogland, 1984; Cameron *et al.*, 1993; Tveraa *et al.*, 2003) and calf mortality (Kojola & Eloranta, 1990; Cameron *et al.*, 1993; Tveraa *et al.*, 2003).

Ungulates may lose body mass because forage abundance and quality decreases or the energetic costs of obtaining forage increases in winter (Parker *et al.*, 1999). Foraging strategies that increase the quality or intake of forage may augment mass gain by caribou (White, 1983). Although predation is the primary factor limiting most woodland caribou herds (Seip, 1991; Bergerud, 1996; Wittmer *et al.*, 2005), poor condition of female caribou in winter may contribute to further decreases in calf recruitment. Suitable winter range for woodland caribou, therefore, should contain an abundance of foods (e.g., lichens), as well as

low energetic costs to caribou of obtaining that food.

The northern ecotype of woodland caribou typically inhabits wind-swept alpine or low-elevation pine (*Pinus contorta*) stands during winter (Cichowski, 1993; Wood, 1996; Johnson *et al.*, 2000). In winter, northern caribou feed primarily on ground lichens and, to a lesser extent, arboreal lichens (Cichowski, 1993; Wood, 1996; Johnson *et al.*, 2001). Lichen accessibility in winter is mainly influenced by snow depth and snow hardness (Johnson *et al.*, 2001), as caribou typically must crater through snow to obtain ground lichens, or walk on or through snow to obtain arboreal lichens. The energetic costs for caribou to obtain ground lichens increase with increasing snow depths and hardness, as more energy is required to crater in harder snow and more hoof strokes are required to access vegetation in deeper snow (Fancy & White, 1985). The energetic cost of movement for caribou also varies under different snow conditions, as snow depths and hardness influence ungulate sinking depths, and the energetic cost of movement increases with increasing ungulate sinking depths (Parker *et al.*, 1984; Fancy & White, 1987).

Forage abundance or accessibility may differ among forest stand types or time periods throughout the winter. Snow conditions (e.g., depths and hardness) and sinking depths of ungulates differ in forest stands with different canopy closure and age (Bunnell *et al.*, 1990a; Schaefer, 1996). Similarly, ground-lichen species and abundance (Schaefer, 1996; Pharo & Vitt, 2000; Coxson & Marsh, 2001), or abundance of arboreal lichens may differ among stands.

Caribou typically respond to differences in lichen abundance and accessibility in one of two ways. They may select feeding areas where forage is more abundant or accessible than in other areas (Bergerud, 1978). Snow conditions influence selection by caribou of winter ranges, feeding areas within winter ranges, as well as feeding sites within feeding areas

(LaPerriere & Lent, 1977). At the scale of the feeding area, studies indicate that northern caribou avoid stands where snow depths and hardness levels impede cratering for ground lichens (Edmonds & Bloomfield, 1984; Cichowski, 1993). Alternatively, caribou may remain in the same area, but alter their method of foraging (ground versus arboreal) once snow depths or snow hardness exceeds a specific threshold (Brown & Theberge, 1990; Johnson *et al.*, 2001; Kinley *et al.*, 2003).

Kennedy caribou are a herd of woodland caribou that migrate from mountainous terrain to a low-elevation pine forest in early winter (see Chapter 2). This herd is one of several nationally threatened northern-ecotype herds inhabiting the Southern Mountains National Ecological Area in central British Columbia (Hart and Cariboo Mountains Recovery Implementation Group, 2005). Maintaining or enhancing winter range conditions may contribute to improving conservation status for threatened caribou herds and ensuring that herds are naturally self-sustaining.

The low-elevation pine forest used by Kennedy caribou in winter was designated as Ungulate Winter Range (UWR) in 2003, under the provincial Forest and Range Practices Act (FRPA). Under FRPA, an UWR is defined as “an area that contains habitat that is necessary to meet the winter-habitat requirements of an ungulate species”. Natural and anthropogenic disturbances in this area have resulted in a mixture of pine stands containing different structural attributes (e.g., canopy closure, age). In light of the mountain-pine beetle (*Dendroctonus ponderosae*) epidemic (numerous attacked and killed pine trees) in British Columbia (Natural Resources Canada, 2005) and more recently Alberta, many pine-dominated caribou winter ranges have been impacted (Cichowski & Williston, 2005), and will be subject to rapid changes in stand structure and age. Examining forage abundance and accessibility prior to mountain-pine beetle impacts and in different types of pine stands will

aid management directives of pine-dominated areas used by caribou in winter.

To examine whether there were differences in forage abundance and accessibility among stand types in a pine-dominated winter range and whether caribou responded to potential differences within and among stands, our objectives were to determine: 1) whether there were differences in snow depths, snow hardness and sinking depths of caribou among stand types; 2) whether there were differences in the abundance of ground vegetation and arboreal lichens among stand types; and 3) whether forage accessibility and abundance influenced use of stand types, method of foraging (ground versus arboreal), selection of trees when foraging on arboreal lichens, and use of a forage species (within a crater) by caribou. We hypothesized that snow conditions and forage abundance would differ among stand types, and that caribou behavior (use of stand types, feeding sites and foraging method) would be influenced by differences in forage abundance and accessibility.

Study area

The study area is contained within the Kennedy Siding UWR between 122°47'W and 122°57'W and from 55°05'N to 55°09'N, and is located approximately 10 km east of the Mackenzie Junction (Highway 97 and Highway 39) in central British Columbia (Figure 3.1). The UWR (approximately 2900 ha) occurs on relatively flat terrain at an elevation of approximately 800 m, and is a dry pine-dominated forest of low to moderate productivity (Arthur, 2002). Soil parent material is alluvial, and the depth of the soil organic layer is typically less than 2 cm. The majority of the UWR contains stands approximately 70 to 80 years of age, and to a lesser extent young (typically 10 to 40 years) and old (approximately 80 to 120 years) pine stands (British Columbia Ministry of Sustainable Resource Management, Land and Resource Data Warehouse, 2005b). A 1.6- x 1.6-

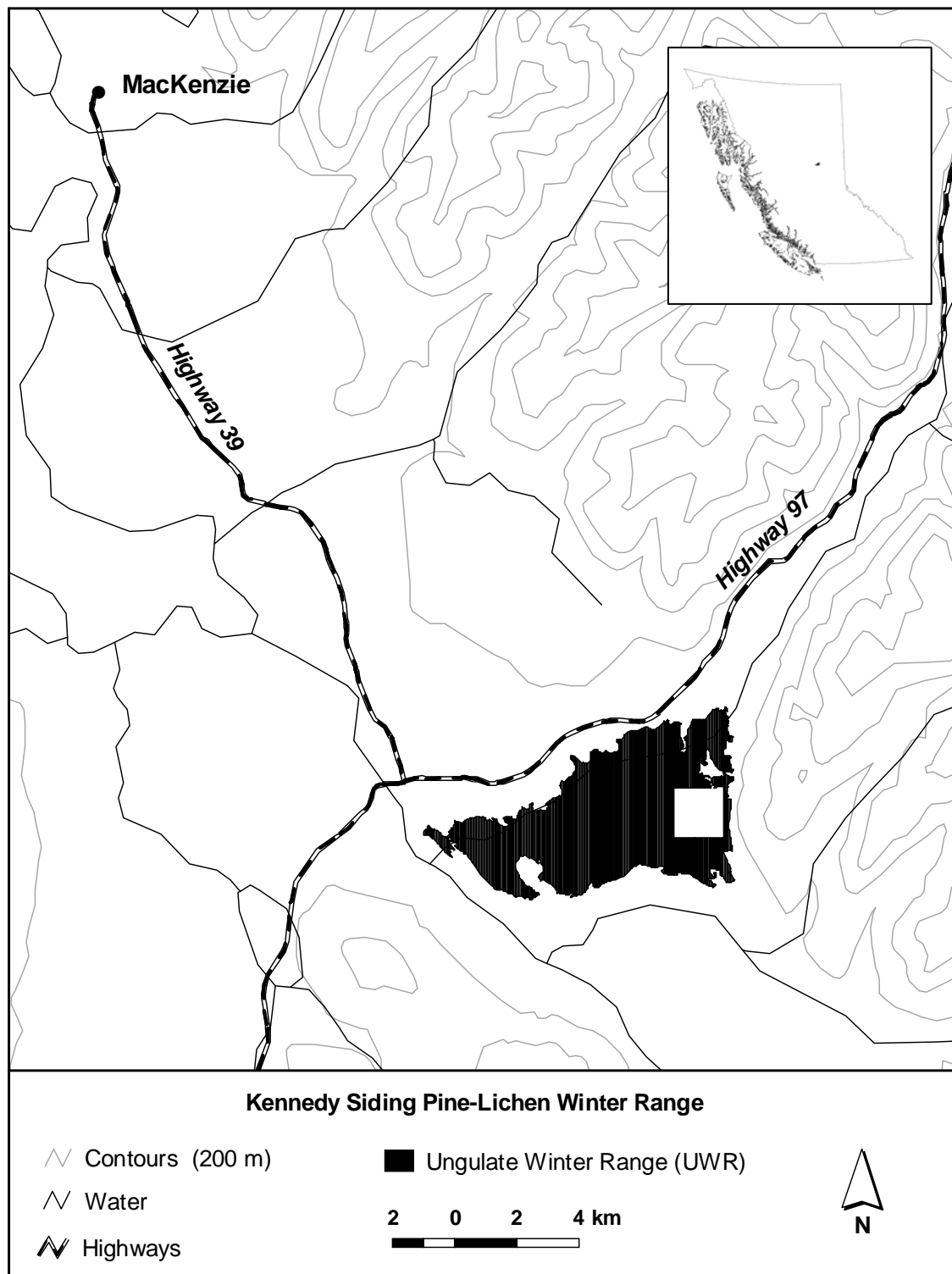


Figure 3.1 Kennedy Siding Ungulate Winter Range (UWR) showing extent of the study area in central British Columbia. The white square in the middle of the UWR is private land that was clearcut in the 1990s.

km portion of the UWR was clearcut in the 1990s and comprises the majority of clearcut stands within the study area. Pine is the dominant tree species throughout the area, and white spruce (*Picea glauca*) and subalpine fir (*Abies lasiocarpa*) are sparse in the understory of older stands. Moss and lichens (primarily *Cladina* spp.) constitute the main portion of the ground layer. The predominant dwarf shrubs include blueberry (*Vaccinium vitis-idaea*) and knickknick (*Arctostaphylos uva-ursi*) with a sparse forb layer containing bunchberry (*Cornus canadensis*), bastard toad-flax (*Geocaulon lividum*), cow-wheat (*Melampyrum lineare*), and various clubmosses (*Lycopodium* spp.) (Jones, unpubl. data).

A winter-plowed gravel road runs through the UWR providing access to a railway site and a hydro-electric station. There is a powerline at the southeast end of the UWR and one occupied trapper's homestead in the area. Hunting and discharge of firearms are prohibited within the UWR, with the exception of hunting rights of First Nations. Although a few mature bulls were harvested in the UWR during the study, a policy of no hunting within the UWR was supported by the local First Nation group. Caribou typically migrate to the Kennedy Siding pine stands in October and migration of caribou from this area varies annually but has never been observed beyond April.

Materials and methods

Data collection along permanent, caribou-track and ground-vegetation transects

We used permanent and caribou-track transects in winter and ground-vegetation transects in summer to measure stand attributes, snow characteristics, and forage abundance in different stand types within the Kennedy Siding UWR. Data were collected along permanent transects and caribou-track transects approximately twice per week from November 2003 to March 2004, and November 2004 to April 2005. Each transect was

revisited in the following summer (when snow did not impede measurements) to quantify ground vegetation.

We classified stands into five categories *a priori* based on tree-species composition, canopy closure, and age: clearcut, young (natural-pine regeneration), spaced (spaced-pine forest), mature (mature-pine forest), and old (old-pine forest). We defined clearcut as a logged stand <10 years of age, young as a pure-pine stand where the majority of trees were <10 m in height, mature as a pure-pine stand where the majority of trees were >10 m in height, spaced as a mature-pine forest in which single trees had been removed by logging throughout the stand, and old as a pine-dominated forest with an understory dominated by fir and spruce.

We established three permanent, 100-m snow transects in each stand type for a total of 15 permanent transects. We selected the general location for each permanent transect based on accessibility by vehicle. We selected a starting point once we had walked 10 to 20 m within the stand type, and determined the transect direction using a random compass bearing. We measured snow depth and qualified snow hardness at 10-m intervals along each transect (for a total of 11 measurements per transect). We recorded the depth that we sank into the snowpack (biologist sinking depth) at five random locations along each permanent transect. All depths were measured to the nearest cm using an avalanche pole (Life-Link International Inc., Jackson Hole, Wyoming, USA. Model: Carbon Speed Probe 280) marked in 5-cm increments. We classified snow hardness into one of five categories based on the ability of a person to kick through snow and ease of snow probe penetration: soft (no effort to kick through), soft/medium (some effort to kick through), medium (difficult to kick through), medium/heavy (very difficult to kick through - snow probe easy to push through), and heavy (very difficult to kick through - snow probe difficult to push through).

In addition to permanent transects, we collected data along woodland caribou tracks (caribou track-transects) in each of the five previously defined stand types. Fresh tracks were noted along a 10-km drive through the Kennedy Siding UWR, and we selected caribou tracks to follow that represented the range of different stand types used by caribou on each day of sampling. We began each caribou-track transect at the first observed sign of feeding by caribou and ended after following tracks for 100 m. We classified the method of foraging by caribou as “ground” when caribou had cratered to the ground through snow, and as “arboreal” when both caribou tracks and broken twigs or fallen arboreal lichens were present at the base of lichen-bearing trees (Johnson *et al.*, 2000).

We recorded foraging method (ground or arboreal) at each forage site observed within 1 m of either side of a caribou-track transect. We recorded presence (ground) or abundance (arboreal) of potential caribou forage at a random subsample (up to 10 for each forage method) of forage sites along each caribou-track transect. For ground feeding, we recorded the presence of ground lichens (by genus) and vegetation types (dwarf shrub, forb, grass/sedge, moss or clubmoss) exposed in a crater. Exposed ground within a crater was typically about 10 cm x 10 cm. For arboreal feeding, we recorded the percent *Bryoria* spp. and *Alectoria sarmentosa* available to caribou (<2.5 m above snowpack, Stevenson *et al.*, 1998), and categorized abundance of each genus into one of six abundance classes (Stevenson *et al.*, 1998): 0 (0 g), 1 (0 to 5 g), 2 (>5 to 50 g), 3 (>50 to 250 g), 4 (>250 to 650 g), and 5 (>625 g).

At 10-m intervals along each caribou-track transect, we also measured snow depth and snow hardness following the same procedures used along permanent transects. Biologist sinking depth and caribou sinking depth were measured at five random locations. At each 20-m interval, we recorded arboreal lichen species and abundance (as described above) for

the six trees nearest the transect ($n = 30$ per transect), and identified which trees within that sample had been fed on by caribou.

At the 60-m point of each caribou-track transect, we measured stand attributes (canopy closure, basal area, and depth of soil organic layer). We used a spherical densiometer (Robert E. Lemmon, Forest Densiometers, 5733 SE Cornell Drive, Bartlesville, Oklahoma, USA. Model-C) to measure canopy closure (%), and a wedge prism (Cruise-Master Prisms Inc., 5790 Drift Creek Road SE, Sublimity, Oregon, USA. Model: 4M) to measure stand basal area (m^2/ha). Depth of soil organic layer (cm) was measured using a ruler to the nearest 0.5 cm.

In summer, we used a line-transect method oriented in the direction of the original caribou-track transect to quantify the percent cover of ground lichens and vegetation types (same categories as those identified in craters). Non-linear foraging paths of caribou prohibited measuring ground species and abundance following the exact winter-track transect. Presence of a ground lichen or vegetation type was recorded every 1 m (as indicated by what touched the tip of a randomly placed pole) along the length of each 100-m transect. Arboreal lichen abundance, stand attributes and percent cover of ground vegetation (as described above) were also collected in summer along permanent transects.

Forage accessibility (snow depths, hardness) and caribou sinking depths among stands

We used a repeated measures ANOVA (Zar, 1999) to determine whether snow depths, snow hardness and sinking depths of caribou (measured along permanent transects) differed among stand types (Objective 1). Because sampling intervals were irregular, we calculated mean snow depth, hardness and caribou sinking depth by week (the longest time interval between transect measurements) for each permanent transect, for each winter.

We used biologist sinking depths to estimate sinking depths of caribou using the regression between the depth of caribou tracks and our own sinking depth (as in Bunnell *et al.*, 1990b), collected along caribou-track transects. Although the slopes and intercepts of the three observer-specific regression lines did not differ ($P > 0.05$), we used observer-specific equations (Observer 1: $y = 0.9398x + 0.8515$, $n = 935$; Observer 2: $y = 0.7751x + 5.0129$, $n = 43$; and Observer 3: $0.9825x + 1.0935$, $n = 130$) to minimize estimation error in caribou sinking depths. The percent of the variation in caribou sinking depths explained by observer sinking depths (r^2) was high: 97.5, 87.2 and 92.6 for Observer 1, 2 and 3, respectively.

Repeated measures ANOVA requires that each transect be measured during each time period. In winter 2004/2005, we dropped one time period (30 March to 5 April) from the data set as no transects were measured during this time period. Data were analyzed using SAS (version 9.1, SAS Institute Inc., 2003), and all P -values were adjusted using the Greenhouse-Geisser correction as is appropriate when the assumption of homogeneity of variance for differences between time periods is violated (Girden, 1992).

In winter 2003/2004, seven of the eight caribou monitored by aerial telemetry left Kennedy Siding on the same day and migrated east to their late-winter subalpine forest/alpine range (collared caribou were located in the mountains in five separate groups so migration behavior was likely somewhat independent). Although not part of our original objectives, this behavior prompted us to examine whether there was a difference in forage accessibility (snow depths and hardness) and sinking depths of caribou between the time periods that caribou were at Kennedy Siding and the day caribou left. Analyses were done in SAS (version 9.1, SAS Institute Inc., 2003), following the repeated measures ANOVA analysis by using the CONTRAST command.

Forage abundance (ground and arboreal) among stands

We used a Kruskal-Wallis (Zar, 1999) test (as data could not be normalized for ground vegetation, and abundance of arboreal lichens was measured on an ordinal scale) to determine whether there were differences in the abundance of ground vegetation or arboreal lichens among stand types (Objective 2) using the transect as our sampling unit. Following the Kruskal-Wallis test, we used a multiple comparison test to determine which stand types differed. Kruskal-Wallis and multiple comparisons were conducted using the KWALLIS2 (Casi, 1999) command in STATA (version 8.0, StataCorp, 2005).

Proportional cover of ground lichens (by genus) and vegetation types (dwarf shrub, forb, grass/sedge, moss or clubmoss) for each transect was calculated by dividing the number of times a cover type was touched (every 1 m for 100 m) by the total number of touches (100 ± 5). For ease of interpretation, we converted proportional cover into percent cover (by multiplying by 100) to present the $\bar{x} \pm SE$ percent cover for each ground lichen and vegetation type averaged across transects, by stand type.

Alectoria sarmentosa were typically sparse (<5%) or absent on trees in all stand types. Therefore, we limited our analysis of the abundance of arboreal lichens to comparisons of *Bryoria* spp. abundance only. *Bryoria* spp. biomass (g/tree) was derived by multiplying the percent *Bryoria* spp. on each tree by a conversion factor for the recorded abundance class (Stevenson *et al.*, 1998). *Bryoria* spp. biomass (\bar{x}) for each transect was then calculated using the abundance estimates from the random sample of 30 trees collected along permanent and caribou-track transects.

Response of caribou to potential differences in forage abundance and accessibility

Use of stand types by caribou

We located radio-collared caribou by aerial telemetry weekly (weather permitting) in winter 2003/2004 ($n = 8$ individuals) and 2004/2005 ($n = 7$), and recorded the stand type each caribou used from the air, but we could only differentiate with certainty between pine forests and the clearcut. Two caribou also had GPS collars, which provided locations every 20 h from December 2003 to April 2005. We used spatial data from the Kennedy Siding UWR (Arthur, 2002) to classify GPS-collar locations into forested or clearcut stands. Additionally, we recorded visual observations of caribou tracks and caribou, by stand type, while driving along the main road, and while conducting bi-weekly measurements of permanent transects.

Selection of feeding trees by caribou

To determine whether there was a difference in abundance of *Bryoria* spp. between trees fed on and trees not fed on by caribou, by stand type, we used case-control logistic regression (Hosmer & Lemeshow, 2000), where fed-on trees and not fed-on trees were matched for each transect. This analysis allowed us to control variation among transects for variables that may influence arboreal-lichen feeding (e.g., snow characteristics, abundance of ground lichens), but that were not measured at each fed-on or not fed-on tree. Transects where arboreal-lichen feeding did not occur were excluded from the analysis. Because of zero or rare cell counts for fed-on trees in each class of *Bryoria* spp. abundance, we pooled abundance classes (Menard, 2002) 0, 1 and 2 (0 to 50 g) and classes 4 and 5 (>250 g) (Stevenson *et al.*, 1998). Regression analyses were conducted in STATA (version 8.0, StataCorp, 2005) and classes of *Bryoria* spp. abundance were modeled with deviation coding

using DESMAT (Hendrickx, 2001).

Ground lichens and vegetation types in craters excavated by caribou

We used a contingency table (Zar, 1999) to determine whether there were differences among stand types in the frequency of occurrence for each ground lichen or vegetation type observed within craters. To obtain frequencies, the presence of each ground lichen or vegetation type was summed for all craters within a stand type. Following a χ^2 test, we converted frequencies to proportions (by dividing frequencies by the total number of craters in each stand type) and used a Tukey-type multiple comparison test (Zar, 1999) to determine which stand types differed. For ease of interpretation, proportions were converted to percentages (by multiplying by 100) to present the percent frequency of occurrence for each ground lichen and vegetation type in each stand type.

Method of foraging (ground versus arboreal) by caribou

To determine whether lichen abundance and accessibility influenced method of foraging by caribou, we classified transects into categories based on foraging method (ground, ground and arboreal, or arboreal) observed at all forage sites along each caribou-track transect, and used logistic regression to model the influence of snow depths, snow hardness and percent cover of *Cladina* spp. on foraging method used by caribou. Rare or zero cell counts precluded including *Bryoria* spp. abundance as a variable in the models (Menard, 2002), and we limited our ground vegetation variable to the percent cover of *Cladina* spp. (the ground lichen most frequently observed in craters) to reduce the number of variables included in the model.

We conducted two separate analyses to examine the influence of snow depths, snow hardness and percent cover of *Cladina* spp. on method of foraging by caribou. For the first

analysis, we classified feeding along transects into ground (only ground feeding observed along transect), ground and arboreal (hereafter termed ground/arboreal), and arboreal (only arboreal feeding observed along transect). We used multinomial logistic regression (Hosmer & Lemeshow, 2000) to model the influence of snow depths, snow hardness and percent cover of *Cladina* spp. on foraging method by caribou. Because caribou may select ground-feeding sites where snow depth and hardness are lower compared to non-used sites (Johnson *et al.*, 2001), we ran two models: one in which snow depth and hardness were averaged for each transect, and one in which snow depth and hardness were modeled as the minimum along each transect.

For the second analysis, we classified feeding along transects into just ground (ground or ground/arboreal feeding observed along transect) and arboreal (only arboreal feeding observed along transect). We used logistic regression to model the influence of snow depth, snow hardness and percent cover of *Cladina* spp. on cessation of ground feeding by caribou. Consistent with the first analysis, we ran two models differentiated by mean and minimum snow depths and hardness. For both analyses, collinearity of variables in each model set was examined and all tolerance scores exceeded the acceptable level of 0.2 (Menard, 2002). Small sample sizes precluded modeling foraging method by caribou in any other stand type except mature. Regression analyses were conducted in STATA (version 8.0, StataCorp, 2005) and we used a post-estimation command (PRTAB) to present the predicted probabilities of foraging method by caribou for significant variables in the models.

Results

Because we defined stand types subjectively before we collected data along permanent and caribou-track transects, we present measurements ($\bar{x} \pm SE$) that quantify stand attributes

(basal area, canopy closure and depth of soil organic layer) for each stand type (Table 3.1).

Forage accessibility (snow depths, hardness) and caribou sinking depths among stands

There were no differences among stand types for snow depths, snow hardness or caribou sinking depths in winter 2003/2004 or winter 2004/2005 (all $P > 0.05$, repeated measures ANOVA), indicating that age, canopy closure, and basal area of pine trees did not influence snow conditions and as such, accessibility of ground lichens did not differ among different stand type. The lack of overall differences in snow conditions among stand types was in part due to large variation among permanent transects in the same stand type. There were, however, differences in snow depths, snow hardness, and caribou sinking depths across time in winter 2003/2004, and winter 2004/2005 (all $P < 0.0001$, repeated measures ANOVA), suggesting that lichen accessibility differed at Kennedy Siding at different time periods throughout both winters.

On 25 January 2004, seven of the eight collared caribou left Kennedy Siding and returned to the mountains. During this departure event of caribou, snow was not as deep as it had been earlier in the winter (Figure 3.2), but snow was harder (all $P < 0.0001$, Figure 3.3), and sinking depths were lower (all $P < 0.0001$, Figure 3.4) than any other time period when caribou were at Kennedy Siding.

In winter 2004/2005, departures of caribou from Kennedy Siding were more erratic and final departure dates were: 7 February ($n = 3$), 11 February ($n = 2$), and 18 April ($n = 2$). Variability in departure dates precluded comparisons between when caribou were present or left Kennedy Siding during this winter. Snow depths were typically lower (<50 cm, Figure 3.5) than snow depths in winter 2003/2004, but in both years depths peaked in late January. Peak snow depths in winter 2004/2005 were lower than peak levels in the previous winter.

Table 3.1. Summary of stand characteristics ($\bar{x} \pm SE$), by stand type (2003 to 2005), within the Kennedy Siding UWR in central British Columbia. Stand attributes were recorded at the 60-m point of each permanent and caribou-track transect.

| Stand Type | Basal Area (m ² /ha) | Canopy Closure (%) | Depth of Soil Organic Layer (cm) |
|------------|---------------------------------|---------------------------|----------------------------------|
| Clearcut | 0 ± 0.0 (<i>n</i> = 83) | 0 ± 0.0 (<i>n</i> = 83) | 1.3 ± 0.10 (<i>n</i> = 80) |
| Young | 16 ± 3.8 (<i>n</i> = 13) | 41 ± 5.8 (<i>n</i> = 12) | 1.3 ± 0.20 (<i>n</i> = 43) |
| Mature | 30 ± 1.4 (<i>n</i> = 43) | 62 ± 1.2 (<i>n</i> = 52) | 1.9 ± 0.13 (<i>n</i> = 53) |
| Spaced | 19 ± 2.3 (<i>n</i> = 9) | 51 ± 2.8 (<i>n</i> = 13) | 0.8 ± 0.07 (<i>n</i> = 13) |
| Old | 34 ± 2.8 (<i>n</i> = 13) | 66 ± 2.1 (<i>n</i> = 15) | 4.1 ± 1.35 (<i>n</i> = 14) |

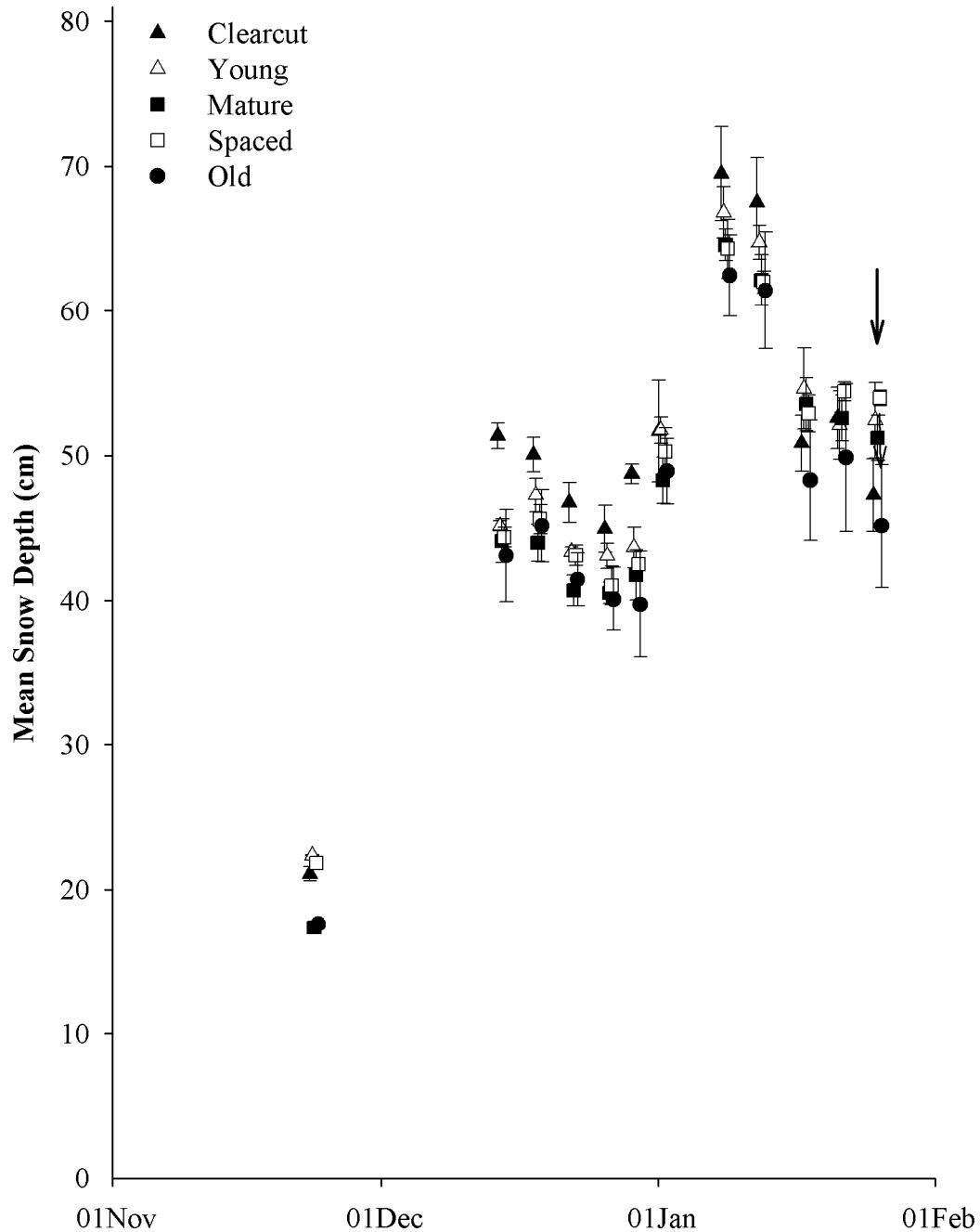


Figure 3.2. Snow depths ($\bar{x} \pm SE$) for permanent transects, by stand type during winter 2003/2004, within the Kennedy Siding UWR in central British Columbia. Snow depths were calculated for each stand type from measurements ($n = 11$) taken along each permanent transect ($n = 3$) within a stand. The arrow shows the date of the departure event of collared caribou ($n = 7$) from Kennedy Siding. Measurements among stands were taken on the same day, but slightly offset for improved readability.

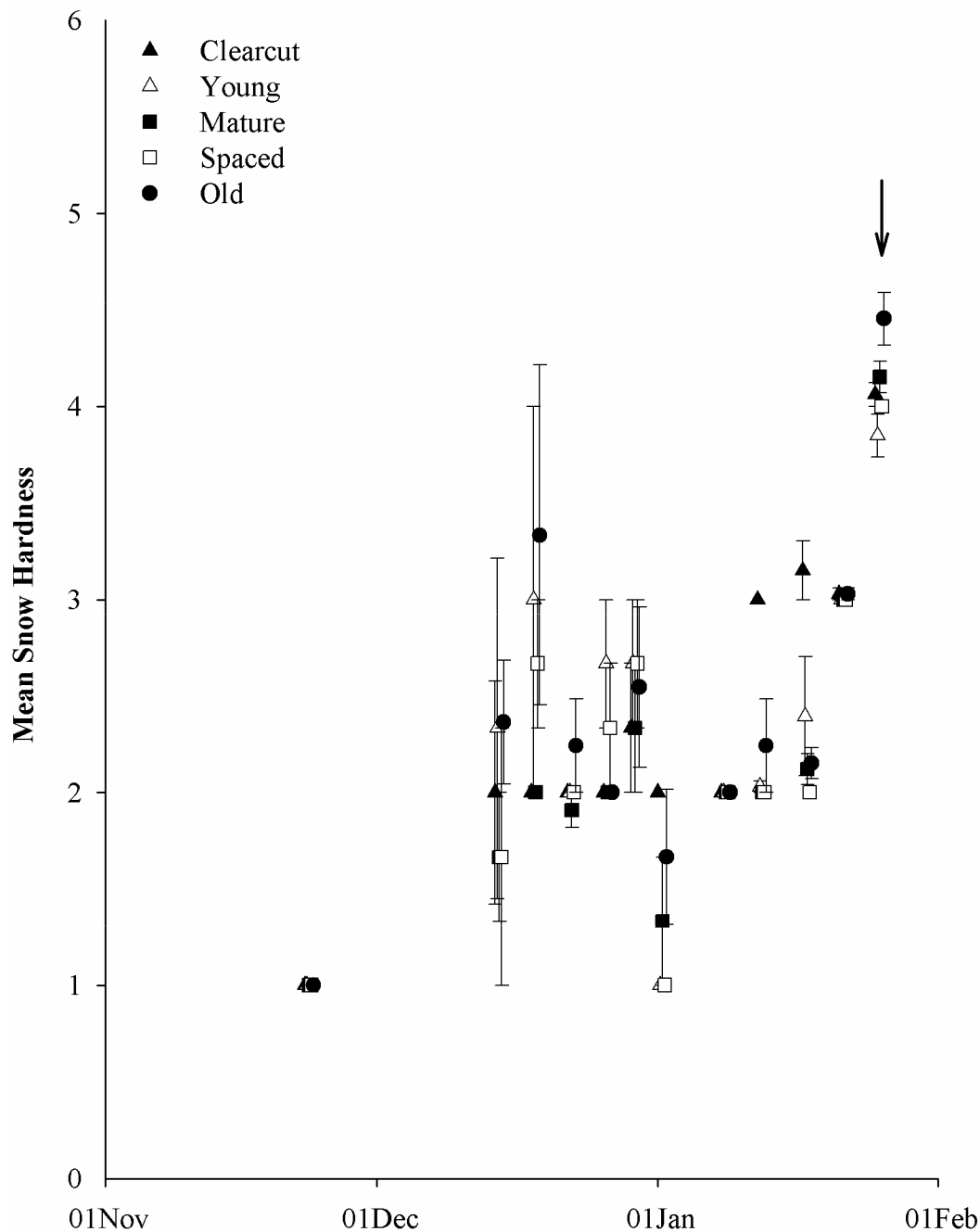


Figure 3.3. Snow hardness ($\bar{x} \pm SE$) for permanent transects, by stand type during winter 2003/2004, within the Kennedy Siding UWR in central British Columbia. See categorical definitions of hardness in text. Snow hardness was calculated for each stand type from measurements ($n = 11$) taken along each permanent transect ($n = 3$) within a stand. The arrow shows the date of the departure event of collared caribou ($n = 7$) from Kennedy Siding. Measurements among stands were taken on the same day, but slightly offset for improved readability.

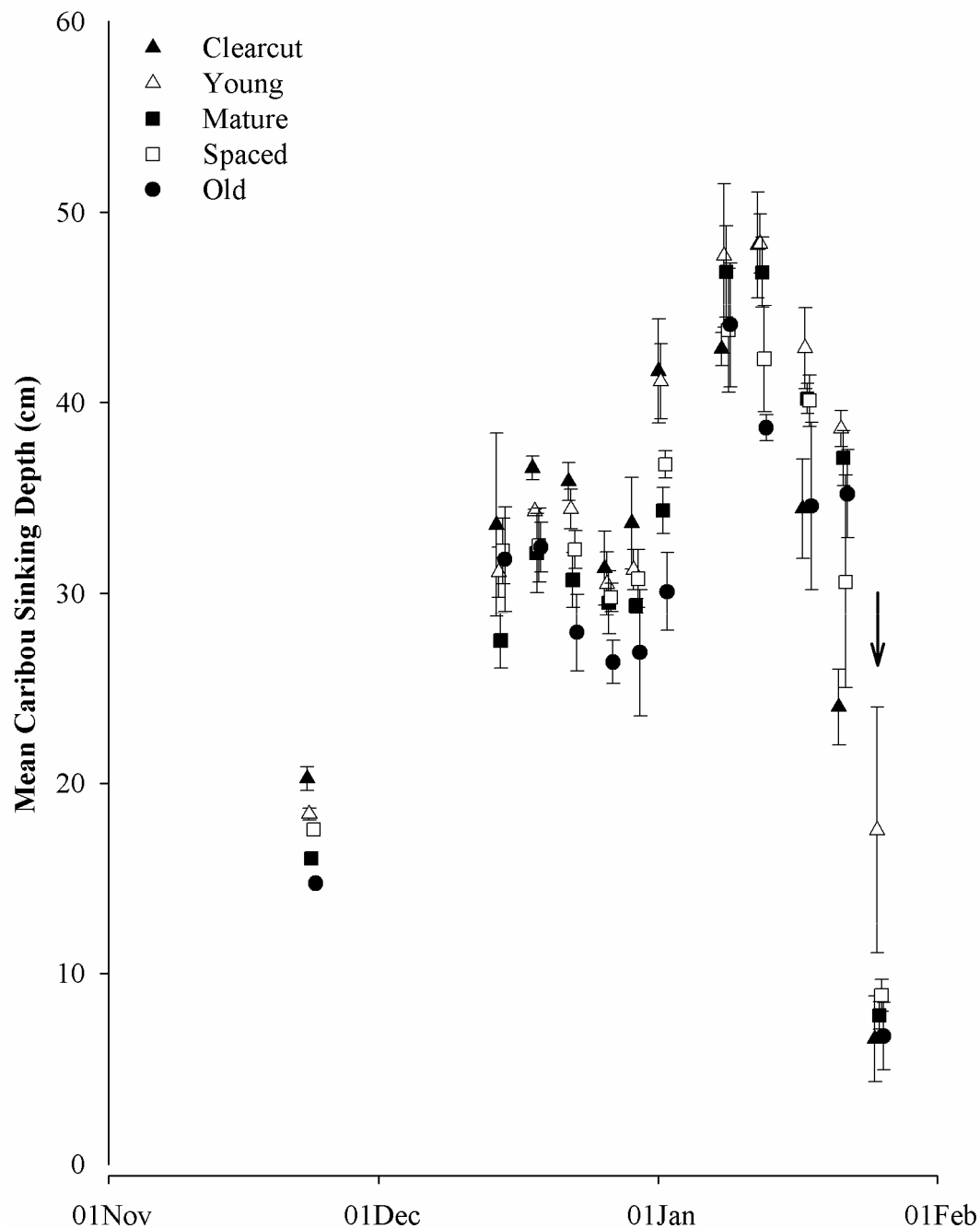


Figure 3.4. Caribou sinking depths ($\bar{x} \pm SE$) for permanent transects, by stand type during winter 2003/2004, within the Kennedy Siding UWR in central British Columbia. Caribou sinking depths were calculated for each stand type from measurements ($n = 5$) taken along each permanent transect ($n = 3$) within a stand. Caribou sinking depth was derived for each measurement using observer-specific regression equations (see text) between biologist and caribou sinking depth. The arrow shows the date of the departure event of collared caribou ($n = 7$) from Kennedy Siding. Measurements among stands were taken on the same day, but slightly offset for improved readability.

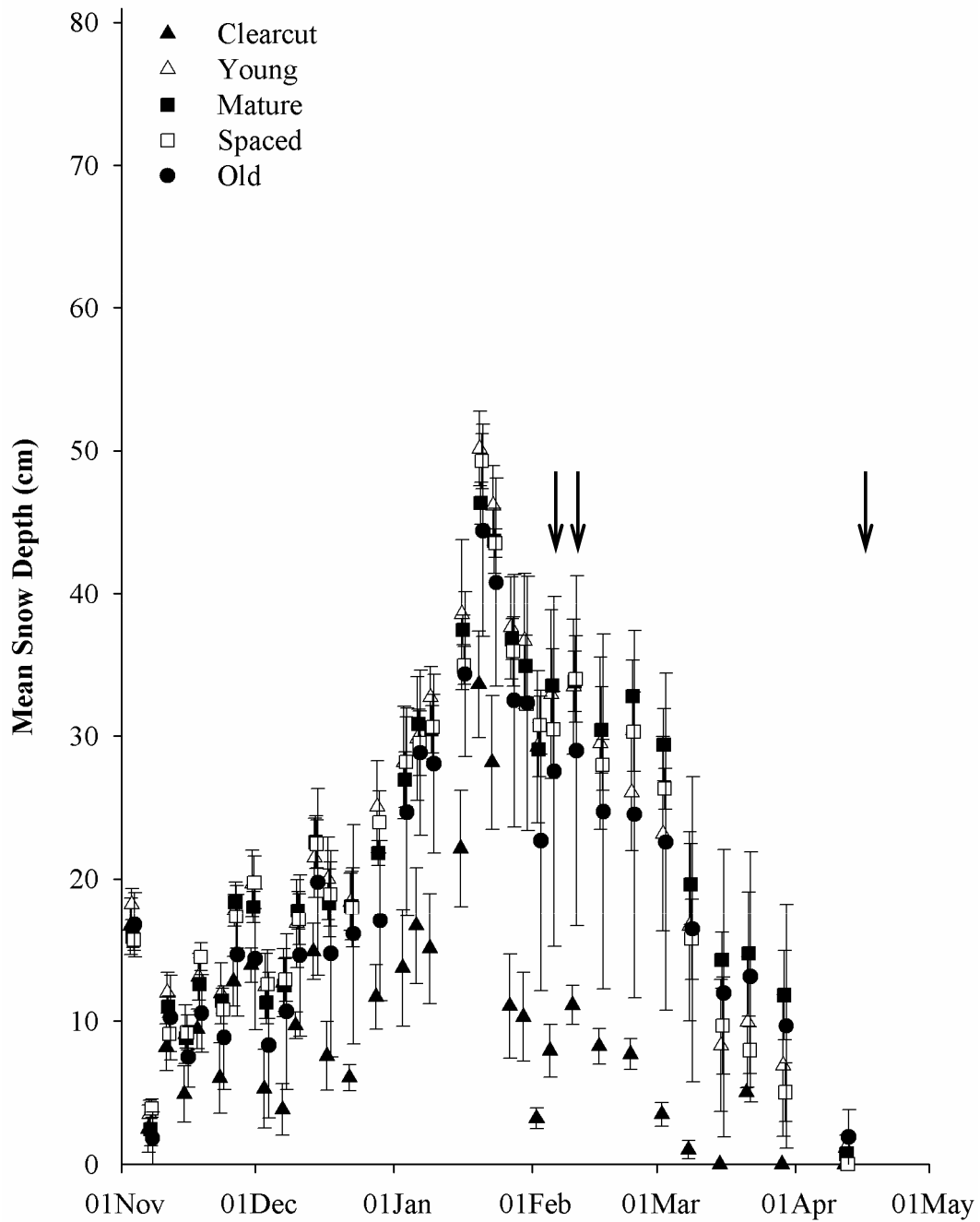


Figure 3.5. Snow depths ($\bar{x} \pm SE$) for permanent transects, by stand type during winter 2004/2005, within the Kennedy Siding UWR in central British Columbia. Snow depths were calculated for each stand type from measurements ($n = 11$) taken along each permanent transect ($n = 3$) within a stand. The arrows show the final dates of departure by collared caribou from Kennedy Siding: 7 February ($n = 3$), 11 February ($n = 2$), and 18 April ($n = 2$). Measurements among stands were taken on the same day, but slightly offset for improved readability.

Snow hardness in winter 2004/2005 (Figure 3.6) reached levels observed during the departure event of caribou in winter 2003/2004, but some caribou did not leave. Hardness was typically more variable in this second winter and presumably some areas still had softer snow. When the majority of caribou left Kennedy Siding in winter 2004/2005 (7 February to 11 February), however, snow hardness levels were typically >4 in all stand types (except old). Caribou sinking depths from early February to the end of winter 2004/2005 were similar to levels observed when caribou departed in winter 2003/2004, and variation in sinking depths was typically low during this period (Figure 3.7).

Forage abundance (ground and arboreal) among stands

The mean abundance of *Bryoria* spp. differed among stand types ($P < 0.0001$). There were no differences ($P > 0.0025$, adjusted for multiple comparisons), however, in mean abundances between mature (90 ± 6.2 g/tree, $n = 53$) and spaced (99 ± 10.5 g/tree, $n = 13$), or young (26 ± 12.3 g/tree, $n = 13$) and old (54 ± 11.1 g/tree, $n = 15$) stands. *Bryoria* spp. were significantly ($P < 0.0025$, adjusted for multiple comparisons) more abundant in the mature and spaced stands than in the young and old stands, suggesting that *Bryoria* spp are most abundant in middle-aged pine stands.

Abundance of ground lichens also varied among stand types, as there were significant differences in the percent cover of each genus of ground lichen among stand types (Kruskal-Wallis, Table 3.2). The percent cover of *Cladina* spp. was higher than the percent cover of any other genus of ground lichen in all stand types and did not differ among clearcut, young, mature and spaced stands (Table 3.2). Among young, mature and spaced stands there were no differences in the percent cover of any single genus of ground lichen (Table 3.2). The percent cover of *Cladina* spp. and *Stereocaulin* spp. was lower in old stands than other stands

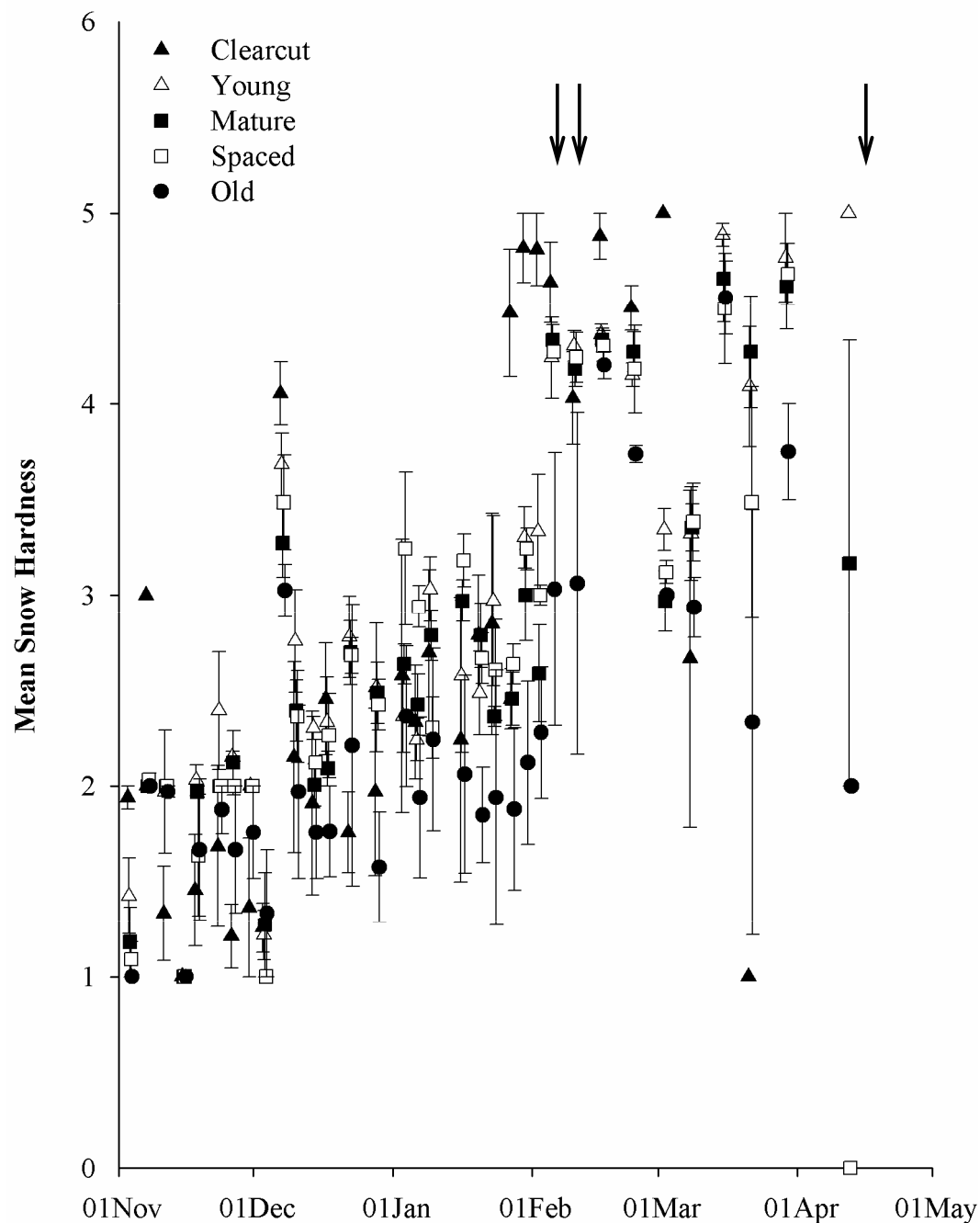


Figure 3.6. Snow hardness ($\bar{x} \pm SE$) for permanent transects, by stand type during winter 2004/2005, within the Kennedy Siding UWR in central British Columbia. See categorical definitions of hardness in text. Snow hardness was calculated for each stand type from measurements ($n = 11$) taken along each permanent transect ($n = 3$) within a stand. The arrows show the final dates of departure by collared caribou from Kennedy Siding: 7 February ($n = 3$), 11 February ($n = 2$), and 18 April ($n = 2$). Measurements among stands were taken on the same day, but slightly offset for improved readability.

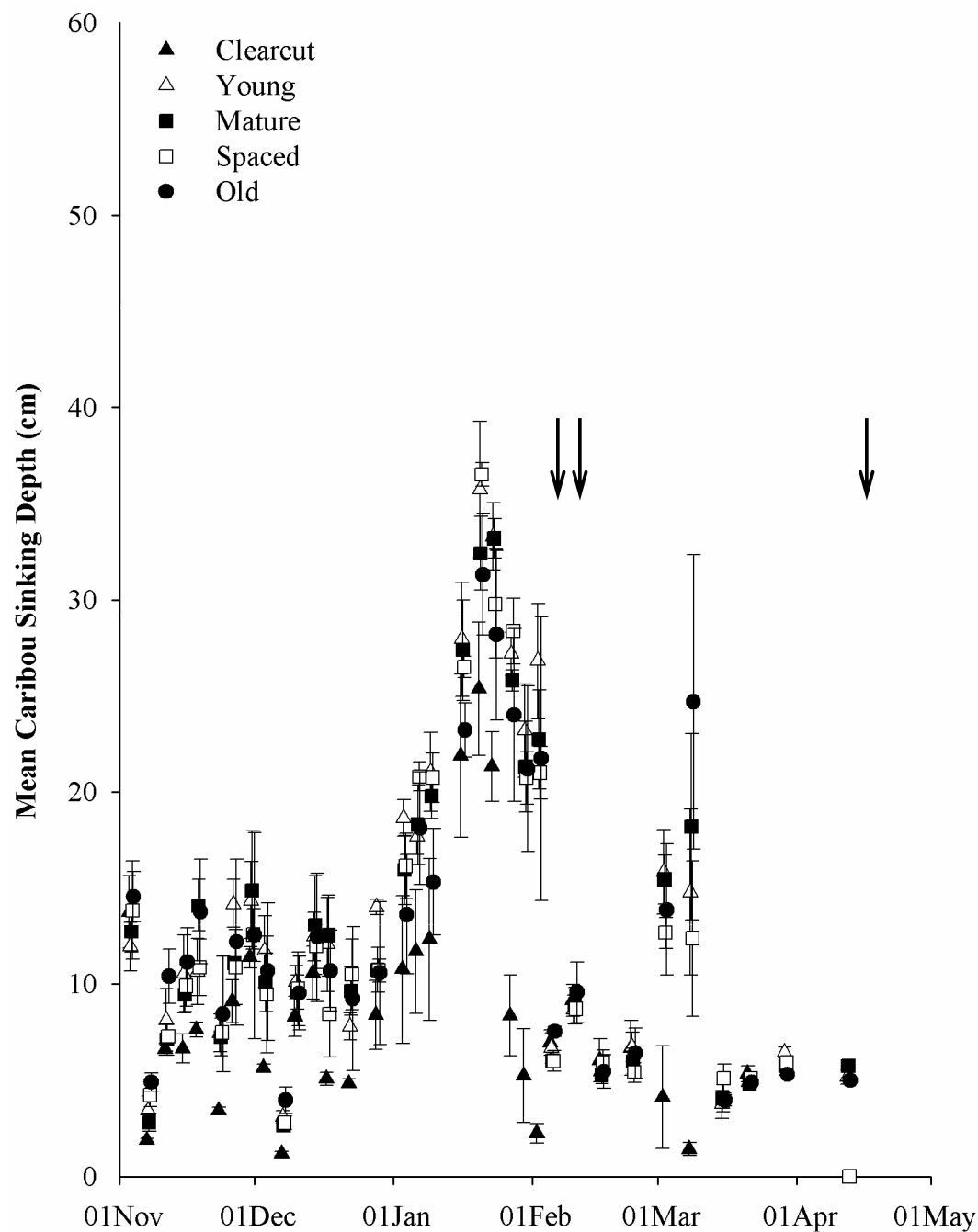


Figure 3.7. Caribou sinking depths ($\bar{x} \pm SE$) for permanent transects, by stand type during winter 2003/2004, within the Kennedy Siding UWR in central British Columbia. Caribou sinking depths were calculated for each stand type from measurements ($n = 5$) taken along each permanent transect ($n = 3$) within a stand. Caribou sinking depth was derived for each measurement using observer-specific regression equations (see text) between biologist and caribou sinking depth. The arrows show the final dates of departure by collared caribou from Kennedy Siding: 7 February ($n = 3$), 11 February ($n = 2$), and 18 April ($n = 2$). Measurements among stands were taken on the same day, but slightly offset for improved readability.

Table 3.2. Percent cover ($\bar{x} \pm \text{SE}$) of different ground lichens or vegetation types, by stand type (2003 to 2005), within the Kennedy Siding UWR in central British Columbia. Percent cover was calculated by averaging the percent cover of each ground lichen or vegetation type across all transects within a stand. There were significant differences among stand types for all ground lichens and vegetation types (all $P < 0.003$). Stands sharing the same superscript letters were not significantly different from each other (Kruskal-Wallis; $P \geq 0.0025$, adjusted for multiple comparisons).

| Vegetation Type | Clearcut ($n = 55$) | Young ($n = 63$) | Mature ($n = 13$) | Spaced ($n = 13$) | Old ($n = 15$) |
|--------------------------|--------------------------|-----------------------|------------------------|------------------------|---------------------|
| <i>Cladina</i> spp. | 28 ± 1.7^a | 37 ± 3.9^a | 29 ± 1.4^a | 35 ± 2.9^a | 9 ± 2.9^b |
| <i>Cladonia</i> spp. | 0 ± 0.1^a | 1 ± 0.3^{ab} | 1 ± 0.2^b | 1 ± 0.2^{ab} | 0 ± 0.1^{ab} |
| <i>Peltigera</i> spp. | 1 ± 0.1^a | 4 ± 1.0^b | 3 ± 0.2^b | 3 ± 0.7^b | 4 ± 0.6^b |
| <i>Stereocaulin</i> spp. | 2 ± 1.3^a | 9 ± 2.6^a | 2 ± 0.3^a | 1 ± 0.3^{ab} | 1 ± 0.2^b |
| <i>Thamnolia</i> spp. | 0 | 0 | 0 | 0 | 0 |
| Forbs | 5 ± 1.0^a | 6 ± 1.4^{ac} | 1 ± 0.3^b | 3 ± 0.8^{abc} | 12 ± 2.4^c |
| Grasses/Sedges | 3 ± 0.6^a | 1 ± 0.3^{ab} | 0 ± 0.0^b | 0 ± 0.1^{ab} | 0 ± 0.2^{ab} |
| Dwarf Shrubs | 31 ± 1.4^b | 15 ± 2.2^a | 17 ± 0.9^a | 15 ± 1.2^a | 14 ± 1.8^a |
| Mosses | 14 ± 1.0^a | 3 ± 3.0^{ac} | 38 ± 1.8^b | 30 ± 3.7^{bc} | 53 ± 3.7^b |
| Clubmosses | 0 ± 0.0^a | 0 ± 0.3^a | 0 ± 0.2^a | 1 ± 0.3^{ab} | 4 ± 1.1^b |

indicating that lichens, particularly *Cladina* spp., may not be as abundant in older-pine stands. The percent cover of *Cladonia* spp. and *Peltigera* spp. was lowest in the clearcut (Table 3.2), but cover of these species was <5% in all stands and so did not account for a large amount of overall lichen abundance.

There were significant differences among stand types for all types of ground vegetation measured (Table 3.2), but the percent cover of forbs, grasses/sedges and clubmosses were essentially negligible (<5%) in most stand types, with the exception of forbs in old stands. The percent cover of dwarf shrubs was highest in the clearcut and the percent cover of moss was lower in the clearcut than in mature, spaced and old stands.

Response of caribou to potential differences in forage abundance and accessibility

Use of stand types by caribou

We determined that caribou used all identified stand types within the Kennedy Siding UWR, based on visual observations of caribou and caribou tracks during fieldwork. We did not see caribou or caribou tracks as frequently in young, spaced and old stands, compared to clearcut and mature stands (as also reflected by sample sizes of caribou-track transects in stand types). Visual observations of caribou and caribou tracks within the Kennedy Siding UWR, and telemetry and GPS locations of collared caribou in winters 2003/2004 and 2004/2005, indicated that caribou stopped using the clearcut by 11 December in winter 2003/2004 (when snow depths were typically >40 cm), but did not stop using the clearcut in winter 2004/2005 (when snow depths were typically <40 cm).

Selection of feeding trees by caribou

Abundance of *Bryoria* spp. on a tree influenced whether individual trees were fed on or not

fed on by caribou (Table 3.3), though, we were unable to determine whether abundance in young and spaced pine stands influenced arboreal-lichen feeding because small sample sizes for young and spaced models resulted in large standard errors (SEs), and the results from these models were not significant ($P > 0.05$). Models for mature and old stands were significant, but the receiver operating characteristic (ROC) curves indicated that the models were slightly below levels of acceptable discrimination (<0.70 , Manel *et al.*, 2001). In mature and old stands, caribou selected feeding trees that were highest in *Bryoria* spp. abundance (class 3) and avoided feeding on trees that were lowest in *Bryoria* spp. abundance (class 1). Trees that had mid-range *Bryoria* spp. abundance (class 2) were neither selected nor avoided.

Ground lichens and vegetation types in craters excavated by caribou

The frequency of all ground lichens and vegetation types identified in craters (Table 3.4) differed significantly among stand types. *Cladina* spp. were found in fewer craters in old stands than in all other stand types. Percent frequency of occurrence of *Cladina* spp. in craters was $>94\%$ in clearcut, young, mature and spaced stands suggesting that caribou were primarily foraging on *Cladina* spp. in these stand types. *Cladonia* spp. and *Peltigera* spp. were found in more craters in young and mature than in the clearcut, spaced and old stands, and *Stereocaulin* spp. were found in more craters in young than in all other stand types (Table 3.4). In old stands, more craters contained forbs and clubmosses than clearcut, young and mature stands.

Method of foraging (ground versus arboreal)

Snow hardness influenced the method of foraging by caribou in both the multinomial logistic regression models (ground, ground/arboreal, arboreal) and logistic regression models

Table 3.3. Selection coefficients (β_i) \pm SEs for *Bryoria* spp. abundance from models for trees that were fed on and not fed on by caribou, by stand type (2003 to 2005), within the Kennedy Siding UWR in central British Columbia. ^a indicates that the abundance class of *Bryoria* spp. was significant ($P < 0.01$) in the model. *Bryoria* spp. abundance on each tree was determined using a categorical classification system (Stevenson *et al.*, 1998). Models were run for each stand type using case-control logistic regression (by transect) and *Bryoria* spp. abundance was pooled into three classes; Class 1 = 0, 1 and 2, Class 2 = 3, Class 3 = 4 and 5 to adjust for rare or zero cell counts (Menard, 2002).

| Stand Type | <i>P</i> | ROC | <i>n</i> transect (trees) | <i>Bryoria</i> spp. Abundance Class | Coefficient (β) | SE |
|------------|----------|--------|---------------------------------|---|----------------------------|-------|
| Mature | <0.001 | 0.6677 | 26 (885) | 1 | -1.215 ^a | 0.152 |
| | | | | 2 | 0.237 | 0.142 |
| | | | | 3 | 0.978 ^a | 0.218 |
| Old | <0.001 | 0.6766 | 8 (275) | 1 | -1.747 ^a | 0.344 |
| | | | | 2 | 0.013 | 0.302 |
| | | | | 3 | 1.733 ^a | 0.513 |

Table 3.4. Percent frequency of occurrence of different ground lichens and vegetation types in craters excavated by caribou, by stand type (2003 to 2005), within the Kennedy Siding UWR in central British Columbia. Percentages were obtained by dividing the frequency of occurrence of ground lichens or vegetation types in each crater by the total number of craters (n) examined in each stand type (multiplied by 100). A χ^2 contingency table was used to compare frequencies (all $P < 0.04$) and data were converted to proportions for multiple comparisons (Zar, 1999). Stands sharing the same superscript letters were not significantly different from each other (q adjusted for multiple comparisons).

| Vegetation Type | Clearcut ($n = 371$) | Young ($n = 63$) | Mature ($n = 157$) | Spaced ($n = 31$) | Old ($n = 67$) |
|--------------------------|---------------------------|-----------------------|-------------------------|------------------------|---------------------|
| <i>Cladina</i> spp. | 94.3 ^a | 96.8 ^a | 97.5 ^a | 100.0 ^a | 44.8 ^b |
| <i>Cladonia</i> spp. | 7.8 ^a | 25.4 ^{bc} | 24.2 ^{bc} | 12.9 ^{ac} | 1.5 ^a |
| <i>Peltigera</i> spp. | 8.9 ^a | 30.2 ^{bc} | 19.7 ^{bc} | 9.7 ^{ac} | 6.0 ^a |
| <i>Stereocaulin</i> spp. | 3.8 ^a | 14.3 ^b | 2.5 ^a | 0.0 ^a | 0.0 ^a |
| <i>Thamnolia</i> spp. | 0.3 ^a | 1.6 ^{ab} | 7.6 ^b | 3.2 ^{ab} | 0.0 ^a |
| Forbs | 1.3 ^a | 0.0 ^a | 0.0 ^a | 0.0 ^{ab} | 10.4 ^b |
| Grasses/Sedges | 12.7 ^a | 6.3 ^{ab} | 0.6 ^b | 3.2 ^{ab} | 14.9 ^a |
| Dwarf Shrubs | 76.5 ^a | 65.1 ^a | 75.2 ^a | 96.8 ^b | 85.1 ^{ab} |
| Mosses | 64.7 ^a | 46.0 ^b | 66.2 ^a | 58.1 ^{ab} | 77.6 ^a |
| Clubmosses | 0.8 ^a | 0.0 ^a | 0.6 ^a | 3.2 ^{ab} | 10.4 ^b |

(ground and ground/arboreal versus arboreal only), but snow depth and percent cover of *Cladina* spp. were not significant in any model (Table 3.5 and Table 3.6). In the multinomial model, snow hardness was not significant only when comparing ground with ground/arboreal feeding, suggesting that snow hardness may not influence arboreal feeding by caribou along a transect but does influence whether caribou crater. Both minimum and mean snow hardness were significant in the models and snow hardness was significant and positive for arboreal feeding only, indicating that as snow hardness increased caribou were less likely to crater.

Because snow hardness was significant in both models, we examined the predicted probabilities of foraging method by caribou for each category of snow hardness (Table 3.7). The probability of ground feeding only (synonymous with not feeding on arboreal lichens) decreased somewhat with increasing snow hardness (0 to 23%, Table 3.7), whereas the probability of arboreal feeding only (synonymous with not feeding on the ground) increased substantially with increasing snow hardness (0 to 99%, Table 3.7). These probabilities indicate that snow hardness acts to influence ground feeding by caribou, but may have little influence on whether caribou also feed on arboreal lichens. When snow hardness (\bar{x} or minimum) = 4, the probability of arboreal feeding only was >95% for both the multinomial logistic regression and logistic regression models. When snow hardness (\bar{x}) = 3 along a caribou-track transect, the probability of feeding on arboreal lichens only was considerably lower (>46%), but if snow hardness (minimum) = 3 along the entire caribou-track transect, the probability of feeding on arboreal lichens only was much higher (>82%). These results suggest that there is a hardness threshold for ground feeding by caribou and that foraging methods by caribou are also influenced by snow conditions at smaller scales (variation in snow hardness within a caribou-track transect).

Table 3.5. Multinomial logistic regression coefficients (β_i) \pm SEs from models of foraging method (ground, arboreal or ground/arboreal) by caribou along transects in mature stands (2003 to 2005), within the Kennedy Siding UWR in central British Columbia. ^a indicates that the variable was significant ($P < 0.05$) in the model. Models were run using multinomial logistic regression; coefficients for ground and arboreal feeding are in comparison to ground/arboreal feeding. Model name refers to how snow depth and hardness were entered into the model for each caribou track-transect (n).

| Model | P | -2LL | n | Foraging Method | Variable | Coefficient (β) | SE |
|---------|--------|-----------|-----|-----------------|-----------------------------------|-------------------------|--------|
| Mean | 0.0009 | 52.860914 | 42 | Ground | Snow depth (\bar{x}) | -0.0407 | 0.0346 |
| | | | | | Snow hardness (\bar{x}) | -0.5609 | 0.7532 |
| | | | | | Percent <i>Cladina</i> spp. cover | -2.7424 | 4.8143 |
| | | | | Arboreal | Snow depth (\bar{x}) | 0.0522 | 0.0375 |
| | | | | | Snow hardness (\bar{x}) | 3.0459 ^a | 1.1921 |
| | | | | | Percent <i>Cladina</i> spp. cover | -8.5131 | 5.8480 |
| Minimum | 0.0068 | 57.67573 | 42 | Ground | Snow depth (min) | -0.0418 | 0.0424 |
| | | | | | Snow hardness (min) | -0.4116 | 1.0802 |
| | | | | | Percent <i>Cladina</i> spp. cover | -3.9801 | 5.1534 |
| | | | | Arboreal | Snow depth (min) | -0.0097 | 0.0344 |
| | | | | | Snow hardness (min) | 2.8648 ^a | 1.2059 |
| | | | | | Percent <i>Cladina</i> spp. cover | -5.3618 | 4.9189 |

Table 3.6. Regression coefficients ($\beta_i \pm$ SEs) from models of foraging method (ground or arboreal only) by caribou in mature stands (2003 to 2005), within the Kennedy Siding UWR in central British Columbia. ^a indicates that variable was significant ($P < 0.05$) in the model. Models were run using logistic regression. Model name refers to how snow depth and hardness were entered into the model for each caribou track-transect (n).

| Model | P | ROC | n | Variable | Coefficient (β) | SE | Odds Ratio |
|-----------|--------|--------|-----|-----------------------------------|-------------------------|--------|------------|
| \bar{x} | 0.0003 | 0.9191 | 42 | Snow depth (\bar{x}) | 0.0571 | 0.0372 | 1.0588 |
| | | | | Snow hardness (\bar{x}) | 3.1329 ^a | 1.1911 | 22.9412 |
| | | | | Percent <i>Cladina</i> spp. cover | -8.3411 | 5.8178 | 0.0002 |
| Minimum | 0.0021 | 0.8603 | 42 | Snow depth (min) | -0.0036 | 0.0338 | 0.9963 |
| | | | | Snow hardness (min) | 2.9212 ^a | 1.1910 | 18.5652 |
| | | | | Percent <i>Cladina</i> spp. cover | -4.9013 | 4.8706 | 0.0074 |

Table 3.7. Predicted probabilities for foraging method by caribou (post-estimation) based on the minimum or mean snow hardness class in mature stands (2003 to 2005), within the Kennedy Siding UWR in central British Columbia. Three foraging categories refers to the multinomial logistic regression model; two foraging categories refers to the logistic regression model.

| Description | Snow Hardness Class | Ground Only | Ground/ Arboreal | Arboreal Only |
|-----------------------------|---------------------|-------------|------------------|---------------|
| Three Foraging Categories | | | | |
| Snow Hardness (Minimum) | 1 | 0.193 | 0.793 | 0.014 |
| | 2 | 0.109 | 0.676 | 0.215 |
| | 3 | 0.016 | 0.149 | 0.835 |
| | 4 | 0.001 | 0.010 | 0.989 |
| Snow Hardness (\bar{x}) | 1 | 0.229 | 0.769 | 0.002 |
| | 2 | 0.140 | 0.821 | 0.039 |
| | 3 | 0.047 | 0.478 | 0.475 |
| | 4 | 0.003 | 0.046 | 0.952 |
| Two Foraging Categories | | | | |
| Snow Hardness (Minimum) | 1 | | | 0.014 |
| | 2 | | | 0.206 |
| | 3 | | | 0.828 |
| | 4 | | | 0.989 |
| Snow Hardness (\bar{x}) | 1 | | | 0.002 |
| | 2 | | | 0.037 |
| | 3 | | | 0.470 |
| | 4 | | | 0.953 |

Discussion

For caribou in winter, the energetic costs of obtaining forage are influenced by snow depths, snow hardness and sinking depths, and as such, caribou may use areas or methods of foraging (ground versus arboreal) where the energetic demands of foraging and movement are lowest. Kennedy caribou responded to changes in forage accessibility or cost of movement by abandoning stand types (clearcut), using different methods of foraging (ground versus arboreal), or leaving Kennedy Siding to return to subalpine forest/alpine. Snow hardness had the largest influence on these responses.

In winter 2003/2004, we observed that caribou did not use the clearcut once mean snow depths were >40 cm and snow hardness was >1 . Similarly, other studies have noted that caribou occupying low-elevation pine stands moved from more open areas into forested areas when snow exceeded 50 cm (Cichowski, 1993). At lower snow depths and hardness values, however, visual observations and locations (GPS and telemetry) indicated that caribou used the clearcut. In winter 2004/2005, snow depths were typically lower in the clearcut than in other stand types, though differences were not statistically significant. Variation in snow depths among permanent transects in forested stands may have resulted in our result of no statistical difference between the clearcut and forest. Because lichen abundance (combined ground and arboreal) was higher in mature stands than the clearcut, we speculate that the clearcut may also have been used by caribou to more easily spot predators (Helle *et al.*, 1990). Alternately, we found that forbs and sedge/grass were significantly more abundant in the clearcut, and may have provided an additional source of protein (Klein, 1990; Danell *et al.*, 1994) that was not as available to caribou in mature stands. Caribou may have abandoned the clearcut once snow depths and hardness exceeded a certain threshold, as these alternative benefits may not have outweighed access to arboreal lichens when energetic costs

of cratering increased.

In mature stands, snow hardness influenced the method of foraging (ground versus arboreal) by caribou. Other studies have found that snow depths or abundance of ground lichens also influenced method of foraging (Edmonds & Bloomfield, 1984; Cichowski, 1993; Johnson *et al.*, 2001). In our study, snow depths may not have been influential in the models of foraging method because snow depths did not exceed cratering thresholds reported by other studies (Edmonds & Bloomfield, 1984; Brown & Theberge, 1990), and *Cladina* spp. may not have been influential in the models because percent cover of *Cladina* spp. along transects was similar within mature stands.

Snow hardness influenced whether caribou fed on ground vegetation, but had little influence on whether caribou fed on arboreal lichens. In fact, we saw caribou feeding on arboreal lichens in the absence of snow cover. Previous field studies have suggested that ground lichens are favored over arboreal lichens when snow conditions do not limit cratering, and that foraging on arboreal lichens increases or only occurs when snow depth and hardness levels inhibit cratering (Edmonds & Bloomfield, 1984; Johnson *et al.*, 2001). Research using feeding trials, however, indicated that there was no difference in preference by semi-domestic reindeer between *Bryoria* spp. and *Cladina* spp. (Danell *et al.*, 1994). Our analyses examined the presence or absence of a feeding activity only along a transect, and did not consider the influence of snow and forage variables on increases in specific feeding activities. Our results and observations do indicate, however, that snow hardness in mature forests may influence whether caribou stop cratering, but has little effect on whether or not caribou feed on arboreal lichens.

Although snow depths, snow hardness and caribou sinking depths did not differ among stand types, snow conditions differed at different time periods throughout both winters. The

lack of overall differences in snow conditions among stand types (in part due to large variation among permanent transects within a stand type) precluded examining date-specific contrasts in snow conditions among different stand types. This result, however, does not mean that caribou could not select areas where snow depths were lower or snow was less hard than other areas (e.g., the clearcut during February and March in 2004/2005, Figure 3.5). The overall results suggest that the energetic cost of movement or forage accessibility for caribou varies throughout the winter. The migration of caribou from Kennedy Siding to the subalpine on 25 January in winter 2003/2004, appeared to be influenced by differences in snow hardness and sinking depths of caribou. On the day of caribou departure, snow became very difficult for a person to kick through (snow hardness >3.5) in all stand types and caribou sinking depths were significantly lower than previous time periods. The departure of caribou from Kennedy Siding in winter 2003/2004 occurred when snow hardness reached levels across the entire range that likely inhibited cratering for ground vegetation by caribou (as indicated by the influence of snow hardness on method of foraging by caribou). Migration by caribou may be in response to inaccessible ground vegetation, and availability of arboreal lichens alone may not be adequate to ensure occupancy of a pine-dominated range by caribou in winter. Alternatively, caribou may return to the mountains when the energetic cost of migration is lowest (synonymous with low sinking depths of caribou).

Forage abundance was significantly different among stand types in the Kennedy Siding UWR. The combination of highly used or selected *Cladina* spp. (Danell *et al.*, 1994; Johnson *et al.*, 2000) and *Bryoria* spp. (Danell *et al.*, 1994) was most abundant in mature-pine stands. Similarly, we observed that *Cladina* spp. were used by caribou (implied by frequency of occurrence in craters) more often than available, although use (within a 10- x 10-cm area) and availability (at a point) were measured differently. In forested stands, we

found that when caribou chose to feed on arboreal lichens, they selected trees to feed on with a higher abundance of *Bryoria* spp. compared to other trees, as did other studies (Rominger *et al.*, 1996; Terry *et al.*, 2000; Johnson *et al.*, 2001; Kinley *et al.*, 2003). Intake rate (g/min) by caribou increases when feeding on trees containing more arboreal lichens (Rominger *et al.*, 1996). This implies that caribou may maximize energetic gains by selecting trees with higher *Bryoria* spp. abundance, and as such, foraging in stands containing more *Bryoria* spp. (e.g., mature pine) compared to other stands (e.g., young) probably results in increased forage intake for caribou.

As management regimes are typically applied at a forest-stand level, the objectives of this study were to compare forage abundance and accessibility among different pine stands. Discrepancies between methods used to collect data along caribou-track transects in this study and those of similar studies examining winter-foraging patterns of woodland caribou (Antifeau, 1987; Terry *et al.*, 1996; Johnson *et al.*, 2000) are mainly because of differences in the scale of analysis. By limiting our sampling and analysis to stand-level comparisons we may have failed to identify important variables that influence use of habitats or differences in smaller-scale foraging activities by caribou. Previous studies, for example, have found that snow depths, snow hardness and lichen abundances differed among sites cratered and not cratered by caribou within a homogenous stand (Johnson *et al.*, 2000). Indeed, we often observed caribou cratering in stands where snow depths and snow hardness were lower compared to the rest of the stand (e.g., tree wells, forest/road ecotones). Similarly, by measuring snow conditions and ground-lichen abundance at a stand-level scale, we may have failed to identify variables that influenced feeding-site selection. For example, *Bryoria* spp. abundance may not be the sole influence for selection of feeding trees, but not measuring other variables at fed-on and non-fed-on trees (e.g., snow, ground lichens) precluded

examining other variables that may have influenced feeding-tree selection by caribou.

Despite higher abundances of lichens in mature stands compared to other stand types, caribou used all stand types within the winter range suggesting that abundance of *Cladina* spp. and *Bryoria* spp. may not entirely be governing use of stands in pine-dominated winter ranges. Potentially, caribou may be responding to differences in lichen accessibility at a smaller scale (within-stand) and it may be important to maintain a proportion of different stand types that enhance micro-site lichen accessibility under different snow conditions. Although not used exclusively by caribou, mature forests were consistently used by caribou throughout both winters and contained the highest combined abundance of lichens typically used by caribou in winter. In particular, mature forests may become critical during winters of deep and heavy snow accumulation as abundant and accessible arboreal lichens may offset increasing energetic costs of obtaining ground forage by caribou. Although the current mountain-pine beetle epidemic will likely result in large losses of mature-pine forest, we recommend that all attempts be made to maintain or perpetuate mature-pine forests in pine-dominated winter ranges used by caribou.

Our data demonstrate that caribou used different wintering areas, stand types and foraging methods in response to forage accessibility (primarily snow hardness) and selected feeding sites in response to distribution of forage species and abundance. Our data also suggest that the general pattern for the Kennedy herd is to migrate to the low-elevation pine forests prior to snow accumulation and forage for ground lichens in the clearcut, as well as ground and arboreal lichens in the forest when snow is shallow and light. When snow exceeds a certain depth or hardness throughout the clearcut, caribou move into the forest and feed on ground and arboreal lichens. When snow conditions are variable throughout the pine forest, caribou forage exclusively on arboreal lichens where snow is difficult for a person to

kick through, or feed on ground vegetation at microsites where snow is softer and shallower. When snow becomes very difficult for a person to kick through across the entire UWR and the snowpack supports the weight of a caribou, Kennedy caribou abandon the UWR and return to the alpine/subalpine forest.

These findings imply that caribou are capable of altering habitat use and foraging methods in response to varying snow conditions and disturbances that mimic natural patterns (e.g., clearcuts within pine forests) across the landscape. Although we did not measure caribou energetics it appears that stands and foraging methods used by caribou are associated with decreasing energetic costs and increasing energetic gains. It may well be that the ability of caribou to forage in a variety of stand types, and employ different foraging methods allows them to maximize net energetic gains across a variable landscape and under different climatic conditions. Scenarios that result in an atypical level of forest alteration (e.g., epidemic pine-beetle outbreaks) or changes to climatic patterns (e.g., increased frequency of melt/freeze or rain-on-snow events that harden snow) may result in winter ranges that are inhospitable to caribou. Reduction in winter range or foraging options may ultimately reduce the fitness and survival of northern caribou herds that use low-elevation pine forests. This research provides baseline information on use and foraging methods by caribou of stand types within a low-elevation pine forest prior to extreme disturbance or climatic change.

Chapter 4: Management of woodland caribou herds in central British Columbia: recommendations for land-management practices

Introduction

In British Columbia, woodland caribou inhabit less than 80% of their historic range (Spalding, 2000). Initial declines in caribou populations are believed to be related to liberal hunting regulations prior to the early 1970s, and increasing moose (*Alces alces*) populations throughout British Columbia in the early 1900s (Seip & Cichowski, 1996). An increase in moose populations may support an increasing number of wolves (*Canis lupus*), resulting in higher predation pressure on caribou (Bergerud & Elliot, 1986; Seip, 1992a). Currently, logging, mining, oil and gas exploration and associated roads likely contribute to reducing woodland caribou populations and ranges (Heard & Vagt, 1998). These activities create early-seral staged forests that may support the increase or presence of alternative prey (e.g., moose), and consequently predator numbers (Heard & Vagt, 1998, Seip & Cichowski, 1996). Predation is considered to be the primary factor contributing to population declines of caribou (Bergerud & Elliot; Seip; 1992a, Wittmer *et al.*, 2005). Caribou mortality may also be related to increased disturbance, barriers to movement, or displacement and avoidance of altered habitat by caribou (Dyer *et al.*, 2001).

Current land-management guidelines in British Columbia recommend that forest-harvesting practices should attempt to mimic natural forest-alteration events, specifically fire, insect and disease (Seip & Cichowski, 1996). The natural-disturbance pattern in forests used by mountain caribou consists of small, low-frequency fires, which create small patches of early-seral habitat within a large matrix of contiguous old-growth forest (Seip, 1998). Land-use conflicts in mountain caribou range focus primarily on logging in subalpine forests (Seip,

1998) or disturbance from motorized or non-motorized recreation (Hart and Cariboo Mountains Recovery Implementation Group, 2005). In mountain-caribou habitat, it is important to maintain large areas of uninterrupted old-growth forest stands that support arboreal lichens (Seip & Cichowski, 1996; Stevenson *et al.*, 2001), reduce the number of early-seral ungulates and their predators, and minimize disturbance to caribou from recreational activities (Hart and Cariboo Mountains Recovery Implementation Group, 2005).

In contrast, the natural-disturbance regime in northern-caribou habitat consists of large, stand-destroying fires that regenerate into pine forests that can contain large quantities of ground lichens. Forest alteration within northern-caribou ranges mainly involves clear-cutting in lower-elevation pine and black-spruce forests containing ground lichens (Seip, 1998), and epidemic levels of mountain-pine beetle (Cichowski & Williston, 2005). Creating early-seral habitat in areas adjacent to mature-pine forests used by caribou may increase predation risk to caribou, and increase disturbance and poaching by allowing areas to be more accessible to human activity (Seip, 1998). In addition, logging in low-elevation pine or black-spruce forests may reduce ground-lichen abundance and accessibility. Low-elevation pine forests used by caribou in winter should consist of large expanses of mature-pine trees containing an abundance of ground lichens (Cichowski, 1993; Seip & Cichowski, 1996).

In order to apply appropriate land-management strategies in woodland caribou habitat, it is essential to understand the spatial distribution, habitat use and selection of caribou herds and the variables that influence use of vegetation-cover and forage types by woodland caribou. This chapter focuses on management recommendations for the Parsnip, Moberly, Kennedy and Quintette herds based on a summary of the spatial distribution of herds, differences in habitat use and selection among herds, and foraging patterns across the geographical range of each herd and within a pine-dominated winter range.

Spatial distribution

I found evidence of spatial overlap among herds and ecotypes of woodland caribou in central British Columbia in all seasons except early winter (see Chapter 2). Differences in use and selection among herds, therefore, can not be completely attributed to spatial separation. Spatial overlap was apparent in summer/fall, suggesting that genetic exchange may occur among some herds in this study. Genetic analysis of these caribou herds may be a more definitive way of determining how herds were distinct, although sample sizes obtained in this study were likely inadequate to detect genetic differences or similarities among herds (Michael Procter, pers. comm.), so these analyses were not attempted. Further research is required to determine whether herds are genetically isolated, and to identify other areas where spatial overlap may occur. To facilitate potential gene flow among herds, areas where spatial overlap occurs should remain undeveloped.

Spatial overlap among the northern and mountain-ecotype herds indicates that there is not a clear boundary separating mountain from northern herds at the transition zone from northern to mountain ecotype. The outermost boundaries for the range of the mountain ecotype, however, can be delineated and I recommend that the management boundary for mountain caribou be extended to incorporate the new information on the distribution of mountain caribou resulting from this study.

My results suggest that Highway 97 may act as a barrier between northern and southern Moberly caribou groups, but caribou in the Kennedy herd cross this highway. The Kennedy herd winters in a low-elevation pine forest containing a network of roads and railways and may be less wary of roads than Moberly caribou. More individuals may need to be collared within the northern and southern Moberly groups to determine whether caribou in these two

groups are spatially (and as a result genetically) isolated from each other. In the absence of these data, I suggest that the Moberly herd actually be grouped into 2 separate herds for the purpose of monitoring population status. In broader terms of recovery planning for woodland caribou, I recommend that all efforts be made to establish or maintain connectivity among separate herds in order to facilitate genetic exchange.

Habitat use and selection

Differences in seasonal habitat use and selection were evident among all caribou herds, with the northern-ecotype herds on the eastern side of the Rockies (Moberly and Quintette) being most similar, and differing from the Kennedy (northern ecotype) and Parsnip (mountain ecotype) herds on the western side of the Rockies (see Chapter 2). Although use and selection varied among seasons, the Moberly and Quintette caribou typically used and selected alpine at elevations above 1600 m and were never located below 1200 m. The Kennedy herd typically selected alpine and pure fir stands at elevations above 1400 m, with the exception of early and late winter when they commonly used low-elevation pine forests. Fir-leading stands were generally avoided or not used by all northern-ecotype herds. The Parsnip herd used and selected fir stands and in contrast to the northern ecotype herds, selected fir-leading stands at elevations between 1150 and 1800 m.

Caribou herds that showed the most similarity in use and selection were spatially separated (Moberly and Quintette), whereas differences were apparent among spatially overlapping herds (Moberly and Kennedy, Kennedy and Parsnip, Parsnip and Quintette). Spatial overlap and similarities in use of vegetation-cover type were most apparent among herds during the rut (summer/fall) suggesting that these caribou may be part of a meta-population in that genetic exchange may occur. Spatial separation between the Moberly and

Quintette herds may have been an artifact of the ranges of individual caribou that we collared within the Moberly and Quintette regions. During caribou captures, however, we did not find caribou in the area between these two regions and other surveys (Seip, 2002) suggest that caribou may be absent from this region.

Distinct differences among herds in the same climatic region (e.g., Parsnip and Kennedy) may be the result of differences in availability of selected vegetation-cover types. For example, at our scale of analysis, pine forests were not available to the Parsnip caribou. Although alpine was available to Parsnip caribou, observations during telemetry flights indicated that mountain tops in the Parsnip range were more treed and less wind-swept than those available to the northern ecotypes and may not have been suitable for winter foraging.

Because climatic regimes vary distinctly between the eastern and western side of the Rockies, differences among herds in these different regions may be due to differences in forage quality, forage abundance and risk of predation between the eastern and western sides of the Rockies. Differences in use and selection within and between ecotypes, however, occurred even when some range overlap was apparent. Observations of Quintette caribou during telemetry flights indicated that these caribou were more commonly located in the alpine even when they were located within the seasonal MCP of the Parsnip herd. Such observations suggest that there may be a predisposition by caribou to use specific vegetation types independent of environmental variation.

Despite some spatial and ecological overlap, all herds in this study exhibited seasonal differences in geographical range, use and selection. I recommend that land-management strategies are herd-specific, in that used and selected vegetation-cover types are maintained within the range of each herd. In particular, in areas where spatial overlap occurs among herds, vegetation-cover types used and selected by both herds (e.g., Quintette - alpine,

Parsnip - fir and fir-leading) should be maintained.

Because the spatial distribution for herds in this study were constrained by locations on a small number of individuals during a relatively short time period, I suggest that land-management strategies for each of these herds focus on, but not be limited to, the extent of these areas. Boundaries created using this location data will be largely dependent on the number of caribou that were collared for this study and the individual ranges of each collared caribou. Areas without caribou locations may still be inhabited by woodland caribou.

Despite differences in use and selection within and among ecotypes, some commonalities were evident for all herds. Caribou typically avoided or did not use deciduous/shrub, spruce-leading and young-coniferous stands in all seasons. Caribou may avoid deciduous/shrub and young-coniferous stands because of a higher risk of predation in these areas compared to other vegetation types (Schwartz & Franzmann, 1989; Johnson *et al.*, 2002; Kuzyk *et al.*, 2004). I recommend that management strategies for woodland caribou focus on reducing the amount of early-seral vegetation types (deciduous/shrub, young-coniferous) in areas identified as caribou range, and as a cautious measure in areas adjacent to caribou range.

Use locations indicated that individual caribou, regardless of herd or ecotype, calved in fir, fir-leading or spruce-leading stands. Despite extensive use and selection of alpine by the northern-ecotype herds on the eastern side of the Rockies, the subalpine forest may be an important vegetation-cover type during parturition for caribou in all herds. I recommend that management strategies for both northern and mountain caribou recognize that subalpine forests may be important during the calving period, even for herds that typically use or select alpine during that season.

Models that describe selection by these caribou herds were created using locations from

only a few GPS-collared caribou from each herd (<3 in some seasons) and selection was examined at only one spatial scale. Although these models discriminated between used and available locations of caribou at the scale of approximate daily movement capability, a broader scale of analysis combined with data on more individuals may be necessary to identify other variables selected by caribou across their range. Additionally, quantification of forage quality, abundance, accessibility and risk of predation within the seasonal range of each herd would be instrumental to explaining selection by caribou in these herds. Selection models were constrained by sample size, limited variables and scale of analyses, so it may also be prudent to incorporate use of vegetation-cover types by caribou into land-use planning. Additionally, low occurrences of use of vegetation-cover types by caribou do not imply that those vegetation-cover types are not important.

Foraging by caribou across northern and mountain caribou range

Regardless of differences in use and selection among all caribou herds, I determined that northern and mountain caribou using similar vegetation-cover types also used similar methods of foraging (Figure 4.1). During winter telemetry flights, I rarely observed Parsnip caribou in alpine and I did not see any evidence of cratering in alpine by Parsnip caribou. In contrast, all northern herds cratered in alpine, while Quintette and Moberly caribou commonly used windswept alpine where snow was negligible. Caribou in all herds foraged on arboreal lichens in the subalpine parkland and subalpine forest.

I occasionally found craters (ground feeding) along caribou-track transects in the subalpine forest for Moberly and Quintette caribou when snow depths were in the 50-cm range (Figure 4.1). I did not observe cratering in the subalpine forest by either the Kennedy or Parsnip herds, although during our foraging investigations snow depths were typically

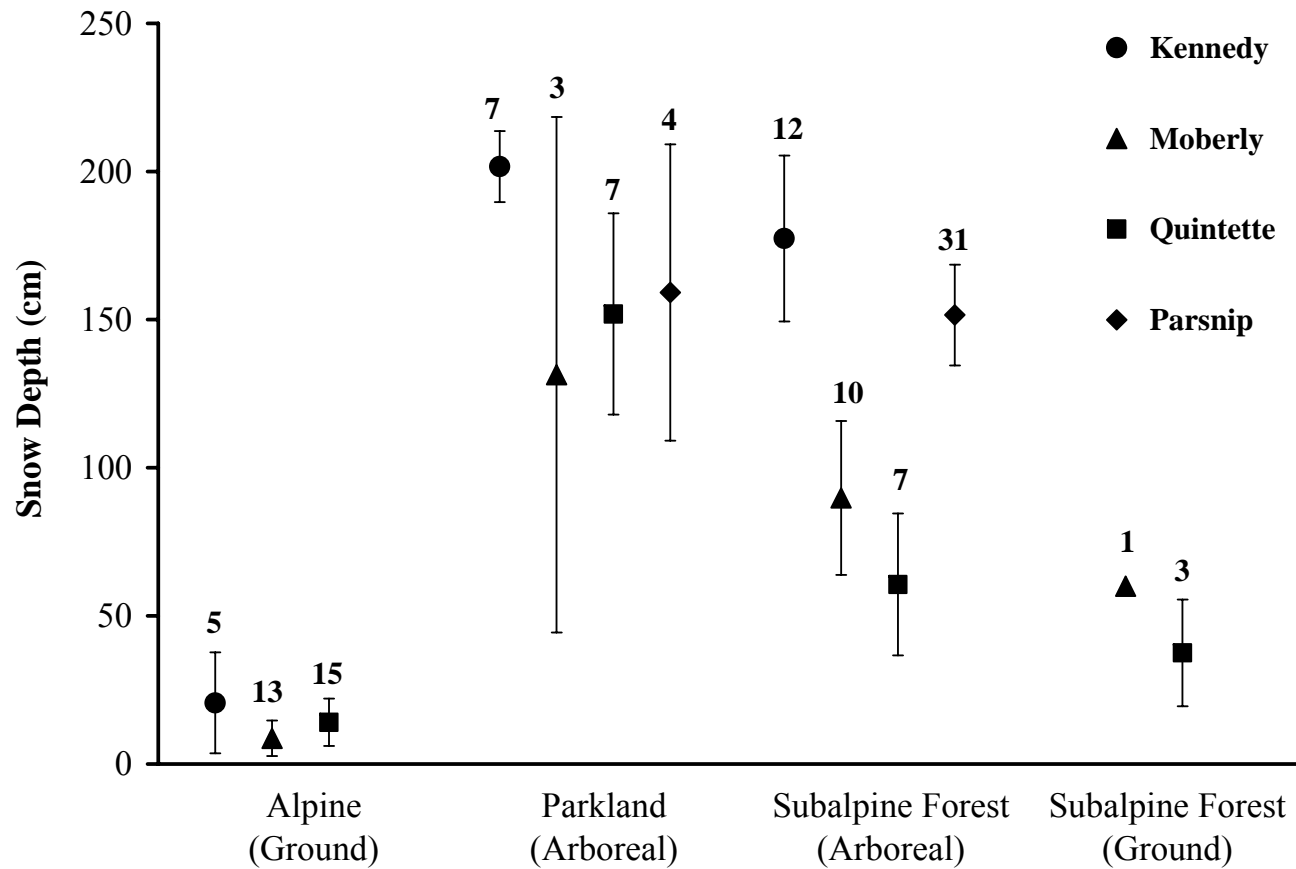


Figure 4.1. Snow depths ($\bar{x} \pm SE$) on 100-m caribou-track transects in relation to foraging method (ground versus arboreal) in alpine, parkland, and the subalpine forest (winter 2003/2004 and 2004/2005) for woodland caribou herds in central British Columbia. Number of caribou-track transects (n) are shown above each vegetation type for each herd. Methods for measuring snow depths and defining foraging method are presented in Chapter 3. Sites were accessed by helicopter following telemetry flights of collared caribou and chosen based on helicopter accessibility and proximity.

greater than the highest mean snow depths (≤ 123 cm) reported for cratering by caribou (Brown & Theberge, 1990).

Regardless of herd or ecotype, I observed that most collared caribou foraged on arboreal lichens in the subalpine forest in winter, suggesting that this behavior was not unique to only a few individuals. Northern caribou and particularly the northern herds on the eastern side of the Rockies, however, typically foraged in high-elevation parkland or fir stands in contrast to mountain caribou that primarily foraged in fir and fir-leading stands. I recommend that forested areas within these caribou ranges be maintained as old-growth forest stands that are capable of supporting an abundance of arboreal lichens (Stevenson *et al.*, 2001). Land-use conflicts between caribou and forestry within northern caribou ranges should be minimal, as use and foraging by northern caribou in this study typically occurred in high-elevation forests of low productivity.

Foraging by caribou in pine-dominated forests

Kennedy caribou foraged in each of five identified stand types (clearcuts, young, mature, spaced and old pine) within their pine-dominated winter range, but most frequently used clearcuts and mature-pine stands. Caribou did not use the clearcut once snow depths exceeded 40 cm and snow became moderately difficult to kick through (by a person). There were no significant differences in snow depths, snow hardness, or caribou sinking depths among stand types during the same time period, so there may be no differences in energetic costs of cratering or movement by caribou in different stand types on a given day. Differences in snow conditions seemed to occur at a finer scale than stand type (e.g., forest opening, road edge, tree wells).

Cladina spp. and *Bryoria* spp. were the main forage species, although examination of

vegetation remaining in craters indicated that grasses and sedges were commonly grazed by caribou. *Cladina* spp. were equally or more abundant in clearcut compared to forested stands, but mature-pine stands were significantly higher in overall principal food abundance (*Cladina* spp. and *Bryoria* spp. combined), indicating that mature-pine stands may contain the most abundant forage for caribou compared to other stand types.

The absence of *Bryoria* spp. in the clearcut indicates that there may have been some other advantage to foraging in the clearcut compared to the forest. Potentially, visibility of predators improves in clearcuts compared to the forest (Helle *et al.*, 1990), and use of clearcuts by caribou may be related to predator vigilance. Forbs and grasses/sedges were also more abundant in the clearcut and use of clearcuts by caribou may be related to increased access to these food sources which are higher in protein than lichens (Klein 1990, Danell *et al.*, 1994). Once energetic costs of cratering for caribou reach a certain threshold these benefits may not outweigh access to arboreal lichens in the forest.

In the mature-pine forest, snow hardness was the only factor that influenced whether caribou fed on ground vegetation or arboreal lichens. Contrary to most studies (but see Stardom, 1975), I observed that caribou fed on arboreal lichens even when snow conditions were ideal for ground-lichen feeding (none, or soft and shallow snow), and that caribou may not switch to arboreal feeding as a result of snow conditions, but that snow conditions act only to prohibit cratering. My results imply that cratering for *Cladina* spp., is not favored by caribou over foraging on *Bryoria* spp.

Snow hardness also influenced migration from the pine-dominated winter range. In winter 2003/2004, caribou returned to the mountains following a hardening of snow in all stand types in the pine-dominated range. This departure indicates that although caribou forage on arboreal lichens irrespective of snow conditions, when snow hardness inhibits

cratering for ground lichens, caribou may abandon pine-dominated winter ranges. Increased frequencies of melt/freeze or rain-on-snow events because of global warming may result in earlier abandonment by caribou of the Kennedy Siding UWR.

Management strategies in low-elevation pine forests should focus on providing a mixture of mature-pine forest and clearcuts, as both stand types are used concurrently and at different times throughout the winter. Because creation of early-seral areas may enhance alternative prey and consequently predator numbers, clearcut areas in pine-dominated winter ranges used by caribou should perpetuate forage for caribou (e.g., ground lichens) and restrict forage for moose (e.g., shrubs). The clearcut in the Kennedy Siding UWR was logged during winter, so ground lichens may have been maintained because of protective snow cover. Harvesting in pine-dominated stands used by caribou should occur in the winter (ultimately after caribou have returned to the mountains to reduce disturbance) to mimic the conditions that produced the clearcut used by caribou at Kennedy Siding. As pine-dominated winter ranges continue to be attacked and killed by mountain-pine beetle, management strategies aimed at maintaining mature-pine stands may be futile. Efforts should be made, however, to cultivate mature-pine stands as beetle-killed stands regenerate.

Ecotype classification

Kennedy, Moberly and Quintette caribou were previously classified as northern caribou, whereas the Parsnip caribou were classified as mountain caribou. My data suggest that generally these classifications are correct. In winter, Moberly and Quintette caribou typically foraged on ground vegetation in wind-swept alpine areas and Kennedy caribou foraged for ground vegetation and arboreal lichens in a low-elevation pine forest. In contrast, the Parsnip caribou foraged on arboreal lichens in subalpine forests.

Ecotype classifications are adequate to describe general differences among caribou herds in winter. It should be recognized, however, that seasonal use, selection and methods of foraging by these herds were more variable than ecotype descriptions. Different ecotypes and herds showed some spatial overlap despite distinct seasonal differences in use and selection within herds of the same ecotype, and between ecotypes. All northern-ecotype herds used subalpine forests in winter where they foraged for arboreal lichens. Northern-ecotype herds calved in subalpine forests and the mountain-ecotype herd selected alpine in spring. Discrepancies between ecotype classifications and actual use of vegetation-cover and forage types by caribou herds illustrate the importance of determining seasonal use, selection and foraging habits for woodland caribou herds across their range.

Caribou herds in this study (particularly northern-ecotype herds) appear to be capable of using a variety of vegetation-cover types and foraging methods across their range. The ability of caribou to use a variety of different vegetation-cover types and foraging methods may be a strategy that enables them to increase energetic gains and reduce energetic costs of foraging under different climatic conditions and across variable terrain. Caribou may require habitat variety in order to ensure adequate nutrition, particularly during winter, when forage accessibility differs across the landscape. Maintaining all vegetation-cover types (e.g., alpine, fir-dominated and pine-dominated stands) predominantly used and selected by caribou will ensure that caribou have options when making trade-off decisions between forage quality and abundance, and risk of predation. Activities or events that alter the natural state of vegetation-cover types, snow conditions or forage distribution and abundance (e.g., epidemic pine-beetle outbreaks, climate change, forestry or industrial development) may limit habitat and foraging options for caribou and consequently reduce the success of these caribou herds.

Literature Cited

- Adams, L. G. & Dale, B. W.** 1998a. Reproductive performance of female Alaskan caribou. – *Journal of Wildlife Management* 62: 1184–1195.
- Adams, L. G. & Dale, B. W.** 1998b. Timing and synchrony of parturition in Alaskan caribou. – *Journal of Mammalogy* 79: 287–194.
- Antifeau, T. D.** 1987. *The significance of snow and arboreal lichen in the winter ecology of mountain caribou (Rangifer tarandus caribou) in the North Thompson watershed of British Columbia*. M.Sc. Thesis. University of British Columbia. Vancouver, BC, Canada. 142pp.
- Apps, C. D., McLellan, B. N., Kinley, T. A. & Flaa, K. J.** 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. – *Journal of Wildlife Management* 65: 65–77.
- Arthur, S. M., Manly, F. J., McDonald, L. L. & Garner, G. W.** 1996. Assessing habitat selection when availability changes. – *Ecology* 77: 215–227.
- Arthur, W. R.** 2002. *Kennedy Siding ungulate winter range (UWR) (U-7-001) report*. BC Ministry of Land, Water and Air Protection. Prince George, BC, Canada. 13pp.
- Banfield, A. W. F.** 1961. *A Revision of the Reindeer and Caribou, Genus Rangifer*. National Museum of Canada, Department of Northern Affairs and Natural Resources. Ottawa, ON, Canada. 137pp.
- Barten, N. L., Bowyer, T. R. & Jenkins, K. J.** 2001. Habitat use by female caribou: tradeoffs associated with parturition. – *Journal of Wildlife Management* 65: 77–92.
- Bergerud, A. T.** 1978. *The status and management of caribou in British Columbia*. Report to the Minister of Recreation and Conservation. BC Ministry of Recreation and Conservation. Victoria, BC, Canada. 150pp.
- Bergerud, A. T.** 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? – *Rangifer* Special Issue No. 9: 95–118.
- Bergerud, A. T., Butler, H. E. & Miller, D. R.** 1984. Antipredator tactics of calving caribou: dispersion in mountains. – *Canadian Journal of Zoology* 62: 1566–1575.
- Bergerud, A. T. & Elliot, J. P.** 1986. Dynamics of caribou and wolves in northern British Columbia. – *Canadian Journal of Zoology* 64: 1515–1519.
- Bergerud, A. T., Ferguson, R. & Butler, H. E.** 1990. Spring migration and dispersion of woodland caribou at calving. – *Animal Behavior* 39: 360–368.

- Bergerud, A. T. & Page, R. E.** 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. – *Canadian Journal of Zoology* 65: 1597–1606.
- Boulanger, J. G. & White, G. C.** 1990. A comparison of home-range estimators using Monte Carlo simulation. – *Journal of Wildlife Management* 54: 310–315.
- Bowyer, R. T.** 1986. Habitat selection by southern mule deer. – *California Fish and Game* 72: 138–145.
- Boyce, M. S., Vernier, P. R., Nielson, S. E. & Schmiegelow, F. K. A.** 2002. Evaluating resource selection functions. – *Ecological Modeling* 157: 281–300.
- Bradshaw, C. J. A., Herbert, D. M., Rippin, A. B. & Boutin, S.** 1995. Winter peatland habitat selection by woodland caribou in northeastern Alberta. – *Canadian Journal of Zoology* 73: 1567–1574.
- British Columbia Ministry of Forests and Range.** 2005. *VRI Relational Data Dictionary. Version 1.0d – Draft*. Available at: <http://www.for.gov.bc.ca/hts/vridata/standards/>. Date accessed: 18 October 2005.
- British Columbia Ministry of Sustainable Resource Management, Base Mapping and Geomatic Services Branch.** 2005. *BC DEM*. <http://ilmbwww.gov.bc.ca/bmgs/>. Date accessed: 12 December 2005.
- British Columbia Ministry of Sustainable Resource Management, Land and Resource Data Warehouse.** 2005a. *TRIM Transportation Lines*. <http://www.lrdw.ca/>. Date accessed: 11 October 2005.
- British Columbia Ministry of Sustainable Resource Management, Land and Resource Data Warehouse.** 2005b. *Vegetation Resource Inventory*. <http://www.for.gov.bc.ca/hts/vri/>. Date accessed: 12 October 2005.
- Brown, W. K. & Theberge, J. B.** 1990. The effect of extreme snowcover on feeding-site selection by woodland caribou. – *Journal of Wildlife Management* 54: 161–168.
- Bunnell, F. L., Hovey, F. W., McNay, R. S. & Parker, K. L.** 1990a. Forest cover, snow conditions, and black-tailed deer sinking depths. – *Canadian Journal of Zoology* 68: 2403–2408.
- Bunnell, F. L., Parker, K. L., McNay, R. S. & Hovey, F. W.** 1990b. Sinking depths of black-tailed deer in snow, and their indices. – *Canadian Journal of Zoology* 68: 917–922.
- Burnham, K. P. & Anderson, D. R.** 2002. *Model selection and inference: a practical information-theoretic approach*. 2nd Edition. Springer-Verlag. New York, NY, USA. 353pp.

- Cameron, R. D., Smith, W. T., Fancy, S. G., Gerhart, K. L. & White, R. G.** 1993. Calving success of female caribou in relation to body weight. – *Canadian Journal of Zoology* 71: 480–486.
- Casi, H. M.** 1999. *KWALLIS2: Stata module to perform Kruskal-Wallis Test for equality of populations*. Statistical Software Components S379201, Boston College Department of Economics, Chestnut Hill, MA, USA.
- Cichowski, D. B.** 1993. *Seasonal movements, habitat use, and winter feeding ecology of woodland caribou in west-central British Columbia*. Land Management Report No. 79. BC Ministry of Forests. Victoria, BC, Canada. 54pp.
- Cichowski, D. B. & Williston, P.** 2005. Mountain pine beetles and emerging issues in the management of woodland caribou in westcentral British Columbia. – *Rangifer* Special Issue No. 16: 97–104.
- Compton, B. W., Rhymer, J. M. & McCollough, M.** 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. – *Ecology* 83: 833–843.
- COSEWIC.** 2002. COSEWIC assessment and update status report on the woodland caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, ON, Canada. 106pp.
- Coxson, D. S. & Marsh, J.** 2001. Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. – *Canadian Journal of Botany* 79: 1449–1464.
- Culling, D. E., Culling, B. A. & Raabis, T.** 2005. *Seasonal habitat use and movements of Graham caribou, 2001 to 2003*. Final report prepared for Canadian Forest Products, Ltd. & BC Ministry of Water, Land and Air Protection. Fort St. John, BC, Canada. 88pp.
- Danell, K., Utsi, P. M., Palo, R. T. & Eriksson, O.** 1994. Food plant selection by reindeer during winter in relation to plant quality. – *Ecography* 17: 153–158.
- Delong, C.** 1994. *A field guide to site identification and interpretation for the northern Rockies portion of the Prince George forest region*. Land Management Handbook Number 29. BC Ministry of Forests. Victoria, BC, Canada. 141pp.
- Demarchi, D.** 1996. *An introduction to the ecoregions of British Columbia*. BC Ministry of Water, Land and Air Protection, Wildlife Branch. Victoria, BC, Canada. 47pp. Available at: http://srmwww.gov.bc.ca/ecology/ecoregions/title_author.html. Date accessed: January 15, 2006.
- Dussault, C., Courtois, R., Ouellet, J. & Huot, J.** 2001. Influence of satellite geometry and differential correction on GPS location accuracy. – *Wildlife Society Bulletin* 29: 171–179.

- Dyer, S. J., O'Neill, J. P., Wasel, S. M. & Boutin, S.** 2001. Avoidance of industrial development by woodland caribou. – *Journal of Wildlife Management* 65: 531–542.
- Edmonds, E. J.** 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. – *Canadian Journal of Zoology* 66: 817–826.
- Edmonds, E. J. & Bloomfield, M.** 1984. *A study of woodland caribou (Rangifer tarandus caribou) in west central Alberta, 1979 to 1983*. Alberta Energy and Natural Resources, Fish and Wildlife Division. Edmonton, AB, Canada. 203pp.
- ESRI.** 2003. *ArcMap 8.3*. Environmental Systems Research Institute. Redlands, CA, USA.
- Fancy, S. G. & White, R. G.** 1985. Energy expenditures by caribou while cratering in snow. – *Journal of Wildlife Management* 49: 987–993.
- Fancy, S. G. & White, R. G.** 1987. Energy expenditures for locomotion by barren-ground caribou. – *Canadian Journal of Zoology* 65: 122–128.
- Fuller, T. K. & Keith, L. B.** 1981. Woodland caribou population dynamics in northeastern Alberta. – *Journal of Wildlife Management* 45: 197–213.
- Girard, I., Ouellet, J., Courtois, R., Dussault, C. & Breton, L.** 2002. Effects of sampling effort based on GPS telemetry on home-range size estimations. – *Journal of Wildlife Management* 65: 531–542.
- Girden, E. R.** 1992. *ANOVA Repeated Measures*. Sage University Paper series on Quantitative Applications in the Social Sciences, Series No. 07–022. Sage Publications, Inc. Newbury Park, CA, USA. 77pp.
- Gustine, D. D., Parker, K. L., Lay, R. J., Gillingham, M. P. & Heard, D. C.** 2006a. Calf survival of woodland caribou in a multi-predator ecosystem. – *Wildlife Monographs* 165: 1–32.
- Gustine, D. D., Parker, K. L., Lay, R. J., Gillingham, M. P. & Heard, D. C.** 2006b. Interpreting resource selection at different scales for woodland caribou in winter. – *Journal of Wildlife Management* 70: 1601–1614.
- Hart and Cariboo Mountains Recovery Implementation Group.** 2005. *Recovery implementation plan for threatened woodland caribou (Rangifer tarandus caribou) in the Hart and Cariboo Mountains Recovery Area, British Columbia*. Available at: <http://www.centralbccaribou.ca/>. Date accessed: 30 December 2006.
- Hatter, I. W.** 2002. *A Strategy for the recovery of mountain caribou in British Columbia*. Version 1.0. BC Ministry of Water, Land and Air Protection. Victoria, BC, Canada. 73pp.
- Heard, D. C. & Vagt, K. L.** 1998. Caribou in British Columbia: a 1996 status report. – *Rangifer* Special Issue No. 10: 159–172.

- Helle, T., Aspi, J. & Kilpela, S. S.** 1990. The effects of stand characteristics on reindeer lichens and range use by semi-domesticated reindeer. – *Rangifer* Special Issue No. 3: 107–114.
- Hendrickx, J.** 2001. Contrasts for categorical variables: update. – *Stata Technical Bulletin Reprints* 10: 14–15.
- Holleman, D. F., Luick, J. R. & White, R. G.** 1979. Lichen intake estimates for reindeer and caribou during winter. – *Journal of Wildlife Management* 43: 192–201.
- Hosmer, D. W. Jr. & Lemeshow, S.** 2000. *Applied logistic regression*. 2nd Edition. J. Wiley and Sons, Inc. New York, NY, USA. 392pp.
- Johnson, C. J., Parker, K. L. & Heard, D. C.** 2000. Feeding site selection by woodland caribou in north-central British Columbia. – *Rangifer* Special Issue No. 12: 159–172.
- Johnson, C. J., Parker, K. L. & Heard, D. C.** 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. – *Oecologia* 127: 590–602.
- Johnson, C. J., Parker, K. L., Heard, D. C. & Gillingham, M. P.** 2002. A multiscale behavioral approach to understanding the movements of woodland caribou. – *Ecological Applications* 12: 1840–1860.
- Johnson, C. J., Parker, K. L., Heard, D. C. & Seip, D. R.** 2004. Movements, foraging habits and habitat use strategies of northern woodland caribou: implications for forest practices. – *British Columbia Journal of Ecosystems and Management* 5: 22–35.
- Kelsall, J. P.** 1968. *The migratory barren-ground caribou of Canada*. Queen's Printer. Ottawa, ON, Canada. 340pp.
- Kelsall, J. P.** 1983. *Status report on woodland caribou, Rangifer tarandus caribou, in Canada in 1982*. Committee on the Status of Endangered Wildlife in Canada. Ottawa, ON, Canada. 106pp.
- Kinley, T. A., Bergenske, J., Davies, J. & Quinn, D.** 2003. Characteristics of early-winter caribou, *Rangifer tarandus caribou*, feeding sites in the Southern Purcell Mountains, British Columbia. – *Canadian Field-Naturalist* 117: 352–359.
- Klein, D. R.** 1990. Variation in quality of caribou and reindeer forage plants associated with season, plant part, and phenology. – *Rangifer* Special Issue No. 3: 123–130.
- Kojola, I. & Eloranta, E.** 1990. Reproductive investment by females in semi-domesticated reindeer. – *Rangifer* Special Issue No. 3: 343–350.
- Kuzyk, G. W., Kneteman, J. & Schmiegelow, F. K. A.** 2004. Winter habitat use by wolves, *Canis lupus*, in relation to forest harvesting in west-central Alberta. – *Canadian Field-Naturalist* 118: 368–375.

- LaPerriere, A. J. & Lent, P. C.** 1977. Caribou feeding sites in relation to snow characteristics in northeastern Alaska. – *Arctic* 30: 101–108.
- Manel, S., Williams, H. C. & Ormerod, S. J.** 2001. Evaluating presence-absence models in ecology: the need to account for prevalence. – *Journal of Applied Ecology* 38: 921–931.
- Meidinger, D. & Pojar, J. (eds).** 1991. *The ecosystems of British Columbia*. Special Report Series No. 6. BC Ministry of Forests. Victoria, BC, Canada. 330pp.
- Menard, S.** 2002. *Applied logistic regression analysis*. Sage publications, Inc. Thousand Oaks, CA, USA. 111pp.
- Mosnier, A., Ouellet, J., Sirois, L. & Fournier, N.** 2003. Habitat selection and home-range dynamics of the Gaspé caribou: a hierarchical analysis. – *Canadian Journal of Zoology* 81: 1174–1184.
- Natural Resources Canada.** 2005. *Mountain Pine Beetle Initiative Interim Report 2005*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre. Victoria, BC, Canada. 64pp.
- Parker, K. L., Barboza, P. S. & Stephenson, T. R.** 2005. Protein conservation in female caribou (*Rangifer tarandus*): effects of decreasing diet quality during winter. – *Journal of Mammalogy* 86: 610–622.
- Parker, K. L., Gillingham, M. P., Hanley, T. A & Robbins, C. T.** 1999. Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. – *Wildlife Monographs* 143: 1–48.
- Parker, K. L., Robbins, C. T. & Hanley, T. A.** 1984. Energy expenditures for locomotion by mule deer and elk. – *Journal of Wildlife Management* 48: 474–488.
- PCI Geomatics.** 2003. *PCI Imageworks 9.1*. PCI Geomatics. Richmond Hill, ON, Canada.
- Pharo, E. J. & Vitt, D. H.** 2000. Local variation in bryophyte and macro-lichen cover and diversity in montane forests of western Canada. – *The Bryologist* 103: 455–466.
- Poole, K. G., Heard, D. C. & Mowat, G.** 2000. Habitat use by woodland caribou near Takla Lake in central British Columbia. – *Canadian Journal of Zoology* 78: 1552–1561.
- Rempel, R. S. & Rodgers, A. R.** 1997. Effects of differential correction on accuracy of a GPS animal location system. – *Journal of Wildlife Management* 61: 525–530.
- Rettie, W. J. & Messier, F.** 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. – *Ecography* 23: 466–478.
- Rominger, E. M. & Oldemeyer, J. L.** 1989. Early-winter habitat of woodland caribou, Selkirk Mountains, British Columbia. – *Journal of Wildlife Management* 53: 238–243.

- Rominger, E. M., Robbins, C. T. & Evans, M. A.** 1996. Winter foraging ecology of woodland caribou in northeastern Washington. – *Journal of Wildlife Management* 60: 719–728.
- Saher, J.** 2005. *Woodland caribou habitat selection during winter and along migratory routes in west-central Alberta*, M.Sc. Thesis. University of Alberta. Edmonton, AB, Canada. 125pp.
- Saher, D. J. & Schmiegelow, F. K. A.** 2005. Movement pathways and habitat selection by woodland caribou during spring migration. – *Rangifer* Special Issue No. 16: 11–18.
- SAS Institute Inc.** 2003. *SAS 9.1*. SAS Institute Inc. Cary, NC, USA.
- Schaefer, J. A.** 1996. Canopy, snow, and lichens on woodland caribou range in southeastern Manitoba. – *Rangifer* Special Issue No. 9: 239–244.
- Schwartz, C. C. & Franzmann, A. W.** 1989. Bears, wolves, moose and forest succession: some management considerations on the Kenai Peninsula, Alaska. – *Alces* 25: 1–10.
- Seip, D. R.** 1990. *Ecology of woodland caribou in Wells Gray Provincial Park*. Wildlife Bulletin No. B-68. BC Ministry of Environment, Wildlife Branch. Victoria, BC, Canada. 41pp.
- Seip, D. R.** 1991. Predation and caribou populations. – *Rangifer* Special Issue No. 7: 46–52.
- Seip, D. R.** 1992a. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. – *Canadian Journal of Zoology* 70: 1494–1503.
- Seip, D. R.** 1992b. *Habitat use and population status of woodland caribou in the Quesnel Highlands, British Columbia*. Wildlife Bulletin No. B-71. BC Ministry of Environment, Lands and Parks. Williams Lake, BC, Canada. 50pp.
- Seip, D. R.** 1998. Ecosystem management and the conservation of caribou habitat in British Columbia. – *Rangifer* Special Issue No. 10: 203–211.
- Seip, D. R.** 2002. *Ecological relationships between threatened caribou herds and their habitat in the Central Rocky Mountains ecoregion*. BC Ministry of Forests. Prince George, BC, Canada. 15pp.
- Seip, D. R. & Cichowski, D. B.** 1996. Population ecology of caribou in British Columbia. – *Rangifer* Special Issue No. 9: 73–80.
- Servheen, G. & Lyon, J. L.** 1989. Habitat use by woodland caribou in the Selkirk Mountains. – *Journal of Wildlife Management* 53: 230–237.
- Skogland, T.** 1980. Comparative summer feeding strategies of arctic and alpine *Rangifer*. – *Journal of Animal Ecology* 49: 81–98.

- Skogland, T.** 1984. The effects of food and maternal conditions on fetal growth and size in wild reindeer. – *Rangifer* Special Issue No. 4: 39–46.
- Soppela, P., Heiskari, U., Nieminen, M., Salminen, I., Sankari, S. & Kindahl, H.** 2000. The effects of prolonged undernutrition on serum lipids and fatty acid composition of reindeer calves during winter and spring. – *Acta Physiologica Scandinavia* 168: 337–350.
- Spalding, D. J.** 2000. *The early history of woodland caribou (Rangifer tarandus caribou) in British Columbia*. Wildlife Bulletin No. B-100. BC Ministry of Environment, Lands and Parks, Wildlife Branch. Victoria, BC, Canada. 61pp.
- Stardom, R. P.** 1975. *Woodland caribou and snow conditions in southeast Manitoba*. Proceedings of the First International Reindeer and Caribou Symposium, Biological Papers of the University of Alaska, Special Report Number 1: 324–341. University of Alaska. Fairbanks, AK, USA.
- StataCorp.** 2005. *Intercooled STATA 8.0 for Windows*. StataCorp. College Station, TX, USA.
- Stevenson, S. K., Armleder, H. M., Jull, M. J., King, D. G., McLellan, B. N. & Coxson, D. S.** 2001. *Mountain caribou in managed forests: recommendations for managers*. 2nd Edition. Wildlife Report No. R-26. BC Ministry of Environment, Lands and Parks, Wildlife Branch. Victoria, BC, Canada. 58pp.
- Stevenson, S. K. & Hatler, D. F.** 1985. *Woodland caribou and their habitat in southern and central British Columbia*. Volume 1. Land Management Report No. 23. BC Ministry of Forests. Victoria, BC, Canada. 355pp.
- Stevenson, S. K., Lance, A. N. & Armleder, H. A.** 1998. *Estimating the abundance of arboreal forage lichens: user's guide*. Land Management Handbook No. 43. BC Ministry of Forests. Victoria, BC, Canada. 35pp.
- Terry, E. L., McLellan, B. N. & Watts, G. S.** 2000. Winter habitat ecology of mountain caribou in relation to forest management. – *Journal of Applied Ecology* 37: 589–602.
- Terry, E. L., McLellan, B. N., Watts, G. S. & Flaa, J.** 1996. Early winter habitat use by mountain caribou in the North Cariboo and Columbia Mountains, British Columbia. – *Rangifer* Special Issue No. 9: 133–140.
- Thomas, D. C., Kroeger, P. & Hervieux, D.** 1984. *In vitro* digestibilities of plants utilized by barren-ground caribou. – *Arctic* 37: 31–36.
- Tveraa, T., Fauchald, P., Henaug, C. & Yoccoz, N. G.** 2003. An examination of a compensatory relationship between food limitation and predation in semi-domestic reindeer. – *Oecologia* 137: 370–376.
- White, R. G.** 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. – *Oikos* 40: 377–384.

- Wittmer, H. U., McLellan, B. N., Seip, D. R., Young, J. A., Kinley, T. A., Watts, G. S. & Hamilton, D.** 2005. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. – *Canadian Journal of Zoology* 83: 407–418.
- Wood, M. D.** 1996. Seasonal habitat use and movements of woodland caribou in the Omineca Mountains, north central British Columbia, 1991-1993. – *Rangifer* Special Issue No. 9: 365–377.
- Zar, J. H.** 1999. *Biostatistical Analysis*. 4th Edition. Prentice-Hall International Inc. Upper Saddle River, NJ, USA. 663pp.

Appendix A. Collar status and history for woodland caribou in central British Columbia, from April 2002 to January 2006. Collar status was defined as follows: active - collar was monitored after January 2006, mortality - collar was removed after death of caribou, recovered - collar was removed from live caribou using drop-off mechanism, and lost - collar could not be removed or monitored due to VHF signal failure.

| ID | Capture Date | Collar Type | Collar Status | Herd | Ecotype | Age | Sex |
|----|--------------|---------------------------|---------------|-----------|----------|----------|--------|
| 1 | 8-Apr-02 | VHF | Active | Parsnip | Mountain | Adult | Female |
| 2 | 8-Apr-02 | VHF | Active | Parsnip | Mountain | Adult | Female |
| 3 | 8-Apr-02 | VHF | Mortality | Kennedy | Northern | Adult | Female |
| 4 | 8-Apr-02 | VHF | Active | Kennedy | Northern | Adult | Female |
| 5 | 8-Apr-02 | VHF | Active | Moberly | Northern | Adult | Female |
| 6 | 8-Apr-02 | VHF | Active | Moberly | Northern | Adult | Female |
| 7 | 9-Apr-02 | VHF | Active | Quintette | Northern | Adult | Female |
| 8 | 9-Apr-02 | VHF | Mortality | Quintette | Northern | Adult | Female |
| 9 | 2-Dec-02 | Televilt/VHF ^a | Active | Moberly | Northern | Adult | Female |
| 10 | 2-Dec-02 | Televilt/ATS ^a | Removed | Moberly | Northern | Adult | Female |
| 11 | 4-Feb-03 | Televilt/VHF ^a | Active | Kennedy | Northern | Adult | Female |
| 12 | 12-Feb-03 | Televilt/ATS ^a | Removed | Quintette | Northern | Adult | Female |
| 13 | 12-Feb-03 | Televilt | Lost | Quintette | Northern | Adult | Female |
| 14 | 12-Feb-03 | Televilt | Lost | Quintette | Northern | Adult | Female |
| 15 | 12-Feb-03 | Televilt | Lost | Parsnip | Mountain | Adult | Female |
| 16 | 6-Mar-03 | Televilt/VHF ^a | Mortality | Parsnip | Mountain | Adult | Female |
| 17 | 6-Mar-03 | Televilt | Lost | Parsnip | Mountain | Yearling | Female |
| 18 | 6-Mar-03 | Televilt | Lost | Kennedy | Northern | Adult | Female |
| 19 | 6-Mar-03 | Televilt/ATS ^a | Mortality | Parsnip | Mountain | Adult | Female |
| 20 | 23-Mar-03 | Televilt/ATS ^a | Removed | Moberly | Northern | Adult | Female |
| 21 | 24-Mar-03 | VHF | Mortality | Moberly | Northern | Adult | Female |
| 22 | 24-Mar-03 | VHF | Active | Moberly | Northern | Adult | Female |
| 23 | 24-Mar-03 | VHF | Mortality | Moberly | Northern | Adult | Female |
| 24 | 1-Dec-03 | ATS | Removed | Kennedy | Northern | Adult | Female |
| 25 | 1-Dec-03 | ATS | Removed | Kennedy | Northern | Adult | Female |
| 26 | 2-Dec-03 | VHF | Active | Kennedy | Northern | Juvenile | Male |
| 27 | 2-Dec-03 | VHF | Mortality | Kennedy | Northern | Adult | Female |

^a Removed and replaced Televilt GPS collar

Appendix A. Continued.

| ID | Capture Date | Collar Type | Collar Status | Herd | Ecotype | Age | Sex |
|----|--------------|-------------|---------------|-----------|----------|-------|--------|
| 28 | 2-Dec-03 | VHF | Mortality | Kennedy | Northern | Adult | Female |
| 29 | 10-Dec-03 | ATS | Recovered | Parsnip | Mountain | Adult | Female |
| 30 | 10-Dec-03 | ATS | Recovered | Parsnip | Mountain | Adult | Female |
| 31 | 10-Dec-03 | ATS | Recovered | Quintette | Northern | Adult | Female |
| 32 | 11-Dec-03 | ATS | Recovered | Moberly | Northern | Adult | Female |
| 33 | 11-Dec-03 | VHF | Active | Parsnip | Mountain | Adult | Female |
| 34 | 11-Dec-03 | VHF | Mortality | Parsnip | Mountain | Adult | Female |
| 35 | 13-Feb-04 | VHF | Active | Quintette | Northern | Adult | Female |
| 36 | 24-Mar-04 | VHF | Active | Quintette | Northern | Adult | Female |
| 37 | 24-Mar-04 | VHF | Active | Quintette | Northern | Adult | Female |
| 38 | 24-Mar-04 | VHF | Active | Quintette | Northern | Adult | Female |
| 39 | 24-Mar-04 | VHF | Active | Kennedy | Northern | Adult | Female |
| 40 | 4-Apr-05 | ATS | Active | Quintette | Northern | Adult | Female |
| 41 | 4-Apr-05 | ATS | Active | Quintette | Northern | Adult | Female |
| 42 | 4-Apr-05 | ATS | Active | Quintette | Northern | Adult | Female |
| 43 | 4-Apr-05 | ATS | Active | Moberly | Northern | Adult | Female |
| 44 | 4-Apr-05 | ATS | Active | Kennedy | Northern | Adult | Female |
| 45 | 22-Dec-05 | ATS | Active | Quintette | Northern | Adult | Female |
| 46 | 22-Dec-05 | ATS | Active | Quintette | Northern | Adult | Female |

Appendix B. Classification criteria used to define vegetation-cover types using VRI (Vegetation Resource Inventory) and elevation for woodland caribou in central British Columbia. A description of the land cover VRI variables can be found in the VRI Data Dictionary (British Columbia Ministry of Forests and Range, 2005).

| Vegetation Type | Conditions |
|-----------------|---|
| Alpine | <ol style="list-style-type: none"> 1. bclcs_level_3 = alpine 2. bclcs_level_1 = non-vegetated and elevation >1599 m 3. bclcs_level_1 = vegetated and bclcs_level_2 = non-treed and elevation >1599 m 4. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_5 = sparse and elevation >1599 m |
| Parkland | <ol style="list-style-type: none"> 1. non_productive_cd = alpine forest |
| Fir | <ol style="list-style-type: none"> 1. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = sparse and species_cd_1 = fir or subalpine fir and species_pct_1 = 100 and age >40 and elevation <1600 m 2. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = open and species_cd_1 = fir or subalpine fir and species_pct_1 = 100 and age >40 3. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = dense and species_cd_1 = fir or subalpine fir and species_pct_1 = 100 and age >40 |
| Fir-leading | <ol style="list-style-type: none"> 1. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = sparse and species_cd_1 = fir or subalpine fir and species_pct_1 <100 and age >40 and elevation <1600 m 2. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = open and species_cd_1 = fir or subalpine fir and species_pct_1 <100 and age >40 3. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = dense and species_cd_1 = fir or subalpine fir and species_pct_1 <100 and age >40 |

Appendix B. Continued.

| Vegetation Type | Conditions |
|----------------------------|---|
| Fir-leading (continued) | <ol style="list-style-type: none"> 4. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = sparse and elevation <1600m and species_cd_1 = fir or subalpine fir and age >40 and species_pct_1 >49 5. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = open and species_cd_1 = fir or subalpine fir and age >40 and species_pct_1 >49 6. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = dense and species_cd_1 = fir or subalpine fir and age >40 and species_pct_1 >49 |
| Spruce-leading | <ol style="list-style-type: none"> 1. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = sparse and species_cd_1 = spruce or spruce hybrid or white spruce or Engelmann spruce or Sitka spruce or black spruce and age >40 and elevation <1600 m 2. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = open and species_cd_1 = spruce or spruce hybrid or white spruce or Engelmann spruce or Sitka spruce or black spruce and age >40 3. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = dense and species_cd_1 = spruce or spruce hybrid or white spruce or Engelmann spruce or Sitka spruce or black spruce and age >40 4. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = sparse and elevation <1600m and species_cd_1 = spruce or spruce hybrid or white spruce or Engelmann spruce or Sitka spruce or black spruce and age >40 and species_pct_1 >49 5. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = open and species_cd_1 = spruce or spruce hybrid or white spruce or Engelmann spruce or Sitka spruce or black spruce and age >40 and species_pct_1 >49 6. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = dense and species_cd_1 = spruce or spruce hybrid or white spruce or Engelmann spruce or Sitka spruce or black spruce and age >40 and species_pct_1 >49 |

Appendix B. Continued.

| Vegetation Type | Conditions |
|--------------------|--|
| Pine-leading | <ol style="list-style-type: none"> 1. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = sparse and species_cd_1 = lodgepole pine and age >40 and elevation <1600 m 2. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = open and species_cd_1 = lodgepole pine and age >40 3. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = dense and species_cd_1 = lodgepole pine and age >40 4. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = sparse and elevation <1600 m and species_cd_1 = lodgepole pine and age >40 and species_pct_1 >49 5. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = open and species_cd_1 = lodgepole pine and age >40 and species_pct_1 >49 6. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = dense and species_cd_1 = lodgepole pine and age >40 and species_pct_1 >49 |
| Coniferous-unknown | <ol style="list-style-type: none"> 1. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = sparse and species_cd_1 = douglas fir or western hemlock or not specified and age >40 and elevation <1600 m 2. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = open and species_cd_1 = douglas fir or western hemlock or not specified and age >40 3. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and bclcs_level_5 = dense and species_cd_1 = douglas fir or western hemlock or not specified and age >40 4. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = sparse and elevation <1600 m and species_cd_1 = douglas fir or western hemlock or not specified and age >40 and species_pct_1 >49 |

Appendix B. Continued.

| Vegetation Type | Conditions |
|-----------------------------------|---|
| Coniferous-unknown (continued) | <ol style="list-style-type: none"> 5. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = open and species_cd_1 = douglas fir or western hemlock or not specified and age >40 and species_pct_1 >49 6. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = dense and species_cd_1 = douglas fir or western hemlock or not specified and age >40 and species_pct_1 >49 |
| Young-coniferous | <ol style="list-style-type: none"> 1. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-coniferous and age <41 and elevation <1600 m 2. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = sparse and elevation <1600 m and species_cd_1 = spruce or spruce hybrid or white spruce or Engelmann spruce or Sitka spruce or black spruce or fir or subalpine fir or douglas fir or lodgepole pine or western hemlock and age >40 and species_pct_1 >49 3. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = open and species_cd_1 = spruce or spruce hybrid or white spruce or Engelmann spruce or sitka spruce or black spruce or fir or subalpine fir or douglas fir or lodgepole pine or western hemlock and age >40 and species_pct_1 >49 4. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = dense and species_cd_1 = spruce or spruce hybrid or white spruce or Engelmann spruce or Sitka spruce or black spruce or fir or subalpine fir or douglas fir or lodgepole pine or western hemlock and age >40 and species_pct_1 >49 |

Appendix B. Continued.

| Vegetation Type | Conditions |
|---------------------|---|
| Deciduous/ shrub | <ol style="list-style-type: none"> <li data-bbox="495 375 1860 440">1. bclcs_level_1 = vegetated and bclcs_level_2 = non-treed and bclcs_level_4 = shrub low or shrub high and elevation <1600 m <li data-bbox="495 456 1860 521">2. bclcs_level_1=vegetated and bclcs_level_2=treed and bclcs_level_4=treed-broadleaf and bclcs_level_5=sparse and elevation <1600 m <li data-bbox="495 537 1860 602">3. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-broadleaf and bclcs_level_5 = open <li data-bbox="495 618 1860 683">4. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-broadleaf and bclcs_level_5 = dense <li data-bbox="495 699 1860 805">5. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = sparse and elevation <1600 m and species_cd_1 = black cottonwood or cottonwood or trembling aspen or paper birch or birch <li data-bbox="495 821 1860 927">6. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = open and species_cd_1 = black cottonwood or cottonwood or trembling aspen or paper birch or birch <li data-bbox="495 943 1860 1049">7. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = dense and species_cd_1 = black cottonwood or cottonwood or trembling aspen or paper birch or birch <li data-bbox="495 1065 1860 1203">8. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = sparse and elevation <1600 m and species_cd_1 = spruce or spruce hybrid or white spruce or Engelmann spruce or Sitka spruce or black spruce or fir or subalpine fir or douglas fir or lodgepole pine or western hemlock and species_pct_1 <50 <li data-bbox="495 1219 1860 1365">9. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = open and species_cd_1 = spruce or spruce hybrid or white spruce or Engelmann spruce or Sitka spruce or black spruce or fir or subalpine fir or douglas fir or lodgepole pine or western hemlock and species_pct_1 <50 |

Appendix B. Continued.

| Vegetation Type | Conditions |
|------------------------------------|--|
| Deciduous/ shrub (continued) | 10. bclcs_level_1 = vegetated and bclcs_level_2 = treed and bclcs_level_4 = treed-mixed and bclcs_level_5 = dense and species_cd_1 = spruce or spruce hybrid or white spruce or Engelmann spruce or Sitka spruce or black spruce or fir or subalpine fir or douglas fir or lodgepole pine or western hemlock and species_pct_1 <50 |
| Open- nonvegetated | 1. bclcs_level_1 = non-vegetated and elevation <1600 m |
| Open- vegetated | 1. bclcs_level_1 = vegetated and bclcs_level_2 = non-treed and bclcs_level_4 = herb or herb-forb or herb-graminoid or bryoid or bryoid-moss or bryoid-lichen and elevation <1600 m |

Appendix C. Selection coefficients (β_i) \pm SEs for covariates of the final selection models derived from the top model or averaged competing models (Table 2.3), by herd and season for woodland caribou in central British Columbia.

Table C.1. Selection coefficients (β_i) \pm SEs for covariates of the final selection models, by herd during spring, for woodland caribou in central British Columbia. ^a indicates that the 95% confidence intervals (CIs) were different from zero and so were considered significant.

| Covariates | Spring | | | |
|------------------------|---------------------------------|-----------------------------------|---------------------------------|----------------------------------|
| | Kennedy | Moberly | Quintette | Parsnip |
| Elevation | 11.795 \pm 11.409 | 140.521 ^a \pm 30.177 | 7.022 ^a \pm 0.787 | 66.754 ^a \pm 19.367 |
| Elevation ² | -1.782 \pm 3.695 | -36.305 ^a \pm 8.708 | | -20.366 ^a \pm 6.443 |
| Slope | -0.055 ^a \pm 0.011 | -0.135 ^a \pm 0.015 | -0.060 ^a \pm 0.012 | -0.103 ^a \pm 0.011 |
| North | -1.094 ^a \pm 0.297 | -0.163 \pm 0.199 | -0.754 ^a \pm 0.216 | -0.169 \pm 0.175 |
| East | -0.137 \pm 0.207 | -0.434 ^a \pm 0.204 | -0.528 ^a \pm 0.223 | -0.119 \pm 0.160 |
| South | 0.721 ^a \pm 0.180 | 0.388 ^a \pm 0.194 | 0.482 ^a \pm 0.170 | 0.236 \pm 0.160 |
| West | 0.510 ^a \pm 0.177 | 0.210 \pm 0.180 | 0.799 ^a \pm 0.204 | 0.053 \pm 0.145 |
| No Aspect | | | | |
| Alpine | | | | |
| Parkland | | | | |
| Fir | | | | |
| Fir-leading | | | | |
| Spruce-leading | | | | |
| Pine-leading | | | | |
| Coniferous-unknown | | | | |
| Young-coniferous | | | | |
| Deciduous/shrub | | | | |
| Open-nonvegetated | | | | |
| Open-vegetated | | | | |
| Distance to Road | | | | |

Table C.2. Selection coefficients (β_i) \pm SEs for covariates of final selection models, by herd during calving, for woodland caribou in central British Columbia. ^a indicates that the 95% confidence intervals (CIs) were different from zero and so were considered significant. Coefficients and SEs were calculated by averaging competing models (Table 2.3) for each herd.

| Covariates | Calving | | | |
|------------------------|----------------------------------|---------------------------------|---------------------------------|----------------------------------|
| | Kennedy | Moberly | Quintette | Parsnip |
| Elevation | 37.752 ^a \pm 13.215 | 20.429 \pm 11.419 | 4.469 ^a \pm 1.186 | 94.636 ^a \pm 21.449 |
| Elevation ² | -7.956 \pm 4.199 | -5.675 \pm 4.058 | | -32.111 ^a \pm 7.674 |
| Slope | | 0.002 \pm 0.002 | | |
| North | | 0.081 \pm 0.272 | -0.861 ^a \pm 0.373 | -0.382 \pm 0.255 |
| East | | -1.215 ^a \pm 0.360 | -0.719 ^a \pm 0.326 | -0.208 \pm 0.239 |
| South | | 0.597 ^a \pm 0.243 | 0.543 \pm 0.297 | 0.592 ^a \pm 0.197 |
| West | | 0.525 ^a \pm 0.232 | 1.036 ^a \pm 0.248 | 0.046 \pm 0.212 |
| No Aspect | | | | |
| Alpine | -2.397 ^a \pm 0.556 | 0.093 \pm 0.273 | -0.221 \pm 0.185 | |
| Parkland | | 0.596 ^a \pm 0.243 | | |
| Fir | -0.035 \pm 0.383 | | | -0.269 \pm 0.173 |
| Fir-leading | 0.322 \pm 0.412 | -0.492 \pm 0.263 | 0.188 \pm 0.152 | 0.046 \pm 0.099 |
| Spruce-leading | 2.110 ^a \pm 0.482 | -0.196 \pm 0.291 | 0.033 \pm 0.121 | 0.223 \pm 0.179 |
| Pine-leading | | | | |
| Coniferous-unknown | | | | |
| Young-coniferous | | | | |
| Deciduous/shrub | | | | |
| Open-nonvegetated | | | | |
| Open-vegetated | | | | |
| Distance to Road | 0.026 \pm 0.026 | | 0.112 \pm 0.064 | 0.002 \pm 0.005 |

Table C.3. Selection coefficients (β_i) \pm SEs for covariates of final selection models, by herd during summer/fall, for woodland caribou in central British Columbia. ^a indicates that the 95% confidence intervals (CIs) were different from zero and so were considered significant. Selection coefficients and SEs were calculated by averaging competing models (Table 2.3) for both the Kennedy and Parsnip herds.

| Covariates | Summer/Fall | | | |
|------------------------|---------------------------------|---------------------------------|---------------------------------|----------------------------------|
| | Kennedy | Moberly | Quintette | Parsnip |
| Elevation | 28.113 ^a \pm 8.932 | 9.055 ^a \pm 4.335 | 22.163 ^a \pm 4.459 | 90.535 ^a \pm 16.782 |
| Elevation ² | -6.998 ^a \pm 3.227 | -1.219 \pm 1.442 | -5.953 ^a \pm 1.399 | -31.106 ^a \pm 5.975 |
| Slope | | -0.062 ^a \pm 0.007 | -0.054 ^a \pm 0.009 | -0.006 \pm 0.006 |
| North | 0.430 ^a \pm 0.183 | 0.164 \pm 0.109 | 0.133 \pm 0.133 | 0.017 \pm 0.019 |
| East | -0.210 \pm 0.186 | -0.373 ^a \pm 0.113 | -0.620 ^a \pm 0.176 | -0.008 \pm 0.013 |
| South | -0.339 \pm 0.197 | -0.141 \pm 0.129 | 0.110 \pm 0.148 | 0.000 \pm 0.010 |
| West | -0.099 \pm 0.180 | 0.350 ^a \pm 0.103 | 0.377 ^a \pm 0.127 | -0.009 \pm 0.012 |
| No Aspect | 0.219 \pm 0.522 | | | |
| Alpine | -2.421 ^a \pm 0.328 | | | -0.604 \pm 0.387 |
| Parkland | -1.761 ^a \pm 0.373 | | | |
| Fir | -0.559 ^a \pm 0.274 | | | -0.284 \pm 0.170 |
| Fir-leading | -0.244 \pm 0.275 | | | 0.684 ^a \pm 0.161 |
| Spruce-leading | 0.221 \pm 0.283 | | | -0.005 \pm 0.247 |
| Pine-leading | 8.213 ^a \pm 1.244 | | | |
| Coniferous-unknown | | | | 1.421 ^a \pm 0.426 |
| Young-coniferous | | | | |
| Deciduous/shrub | -2.230 ^a \pm 0.406 | | | -1.212 ^a \pm 0.423 |
| Open-nonvegetated | | | | |
| Open-vegetated | -1.219 \pm 0.653 | | | |
| Distance to Road | | | | 0.065 ^a \pm 0.020 |

Table C.4. Selection coefficients (β_i) \pm SEs for covariates of final selection models, by herd during early winter, for woodland caribou in central British Columbia. ^a indicates that the 95% confidence intervals (CIs) were different from zero and so were considered significant.

| Covariates | Early Winter | | | |
|------------------------|----------------------------------|----------------------------------|----------------------------------|-----------------------------------|
| | Kennedy | Moberly | Quintette | Parsnip |
| Elevation | -33.624 ^a \pm 8.686 | -16.583 ^a \pm 6.209 | 69.289 ^a \pm 19.057 | 82.332 ^a \pm 30.126 |
| Elevation ² | 16.884 ^a \pm 4.020 | 8.340 ^a \pm 1.976 | -18.430 ^a \pm 5.319 | -28.450 ^a \pm 10.786 |
| Slope | -0.198 ^a \pm 0.046 | -0.068 ^a \pm 0.008 | -0.071 ^a \pm 0.009 | -0.054 ^a \pm 0.011 |
| North | 0.103 \pm 0.156 | 0.018 \pm 0.109 | -0.395 ^a \pm 0.149 | -0.175 \pm 0.139 |
| East | -0.287 \pm 0.179 | -0.570 ^a \pm 0.114 | -0.511 ^a \pm 0.168 | 0.013 \pm 0.138 |
| South | 0.004 \pm 0.181 | 0.118 \pm 0.106 | 0.138 \pm 0.156 | 0.089 \pm 0.134 |
| West | 0.171 \pm 0.150 | 0.435 ^a \pm 0.100 | 0.768 ^a \pm 0.141 | 0.073 \pm 0.124 |
| No Aspect | 0.009 \pm 0.185 | | | |
| Alpine | | | | |
| Parkland | | | | |
| Fir | | | | |
| Fir-leading | | | | |
| Spruce-leading | | | | |
| Pine-leading | | | | |
| Coniferous-unknown | | | | |
| Young-coniferous | | | | |
| Deciduous/shrub | | | | |
| Open-nonvegetated | | | | |
| Open-vegetated | | | | |
| Distance to Road | | | | |

Table C.5. Selection coefficients (β_i) \pm SEs for covariates of final selection models, by caribou herd during late winter, for woodland caribou in central British Columbia. ^a indicates that the 95% confidence intervals (CIs) were different from zero and so were considered significant. Selection coefficients and SEs were calculated by averaging competing models (Table 2.3) for the Kennedy herd.

| Covariates | Late Winter | | | |
|------------------------|---------------------------------|----------------------------------|---------------------------------|-----------------------------------|
| | Kennedy | Moberly | Quintette | Parsnip |
| Elevation | -1.272 \pm 3.964 | 52.905 ^a \pm 11.458 | -8.134 \pm 4.702 | 166.895 ^a \pm 18.959 |
| Elevation ² | 2.500 \pm 1.478 | -13.627 ^a \pm 3.466 | 4.267 ^a \pm 1.401 | -57.123 ^a \pm 6.600 |
| Slope | | -0.062 ^a \pm 0.005 | -0.066 ^a \pm 0.006 | -0.044 ^a \pm 0.007 |
| North | -0.033 \pm 0.110 | -0.270 ^a \pm 0.087 | -0.547 ^a \pm 0.108 | -0.049 \pm 0.108 |
| East | -0.312 ^a \pm 0.124 | -0.274 ^a \pm 0.086 | -0.418 ^a \pm 0.099 | -0.340 ^a \pm 0.117 |
| South | -0.137 \pm 0.109 | 0.222 ^a \pm 0.086 | 0.432 ^a \pm 0.088 | 0.027 \pm 0.110 |
| West | -0.076 \pm 0.101 | 0.323 ^a \pm 0.079 | 0.534 ^a \pm 0.098 | 0.361 ^a \pm 0.095 |
| No Aspect | 0.558 ^a \pm 0.240 | | | |
| Alpine | -1.312 ^a \pm 0.271 | | | |
| Parkland | -0.819 ^a \pm 0.243 | | | |
| Fir | 0.082 \pm 0.218 | | | |
| Fir-leading | -0.368 \pm 0.203 | | | |
| Spruce-leading | -0.849 ^a \pm 0.295 | | | |
| Pine-leading | 2.825 ^a \pm 0.482 | | | |
| Coniferous-unknown | | | | |
| Young-coniferous | 2.126 ^a \pm 0.492 | | | |
| Deciduous/shrub | -0.786 ^a \pm 0.318 | | | |
| Open-nonvegetated | | | | |
| Open-vegetated | -0.899 ^a \pm 0.430 | | | |
| Distance to Road | 0.000 \pm 0.001 | | | |

Appendix D. Selection coefficients (β_i) \pm SEs for vegetation-cover type using the Vegetation Type selection model by herd and season for caribou in central British Columbia. ^a indicates that vegetation type was significant (e.g., CIs did not encompass zero).

| Vegetation Type | Kennedy | Moberly | Quintette | Parsnip |
|--------------------|---------------------------------|---------------------------------|---------------------------------|---------------------------------|
| Spring | | | | |
| Alpine | 0.585 ^a \pm 0.181 | 0.314 \pm 0.285 | 0.867 ^a \pm 0.216 | 0.709 ^a \pm 0.223 |
| Parkland | 0.160 \pm 0.235 | | | |
| Fir | 0.036 \pm 0.198 | | 0.712 ^a \pm 0.316 | 0.803 ^a \pm 0.151 |
| Fir-leading | -1.373 ^a \pm 0.270 | | -1.579 ^a \pm 0.335 | 0.171 \pm 0.159 |
| Spruce-leading | | | | -1.643 ^a \pm 0.297 |
| Pine-leading | | | | |
| Coniferous-unknown | | | | -0.019 \pm 0.314 |
| Young-coniferous | | | | |
| Deciduous/shrub | -0.456 \pm 0.256 | | | -0.020 \pm 0.260 |
| Open-nonvegetated | | | | |
| Open-vegetated | 1.048 ^a \pm 0.379 | -0.314 \pm 0.285 | | |
| Calving | | | | |
| Alpine | 0.783 ^a \pm 0.241 | 0.771 ^a \pm 0.209 | 0.507 ^a \pm 0.216 | |
| Parkland | | 1.110 ^a \pm 0.229 | | |
| Fir | 0.812 ^a \pm 0.252 | | | 0.465 ^a \pm 0.163 |
| Fir-leading | -0.988 ^a \pm 0.341 | -0.813 ^a \pm 0.287 | 0.350 \pm 0.217 | 0.387 ^a \pm 0.156 |
| Spruce-leading | -0.607 ^a \pm 0.256 | -1.068 ^a \pm 0.298 | -0.857 ^a \pm 0.285 | -0.853 ^a \pm 0.204 |
| Pine-leading | | | | |
| Coniferous-unknown | | | | |
| Young-coniferous | | | | |
| Deciduous/shrub | | | | |
| Open-nonvegetated | | | | |
| Open-vegetated | | | | |

Appendix D. Continued.

| Vegetation Type | Kennedy | Moberly | Quintette | Parsnip |
|---------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| Summer/Fall | | | | |
| Alpine | -0.059 ± 0.238 | 0.953 ^a ± 0.131 | 0.572 ^a ± 0.167 | -0.936 ^a ± 0.370 |
| Parkland | -0.115 ± 0.293 | 0.484 ^a ± 0.167 | 0.487 ± 0.439 | |
| Fir | 0.663 ^a ± 0.161 | -1.030 ^a ± 0.434 | 0.040 ± 0.249 | 0.382 ^a ± 0.178 |
| Fir-leading | -0.031 ± 0.160 | -0.366 ^a ± 0.158 | 0.108 ± 0.183 | 1.166 ^a ± 0.157 |
| Spruce-leading | -0.730 ^a ± 0.204 | -0.738 ^a ± 0.197 | -1.351 ^a ± 0.328 | -1.012 ^a ± 0.259 |
| Pine-leading | 0.784 ^a ± 0.252 | | 0.143 ± 0.426 | |
| Coniferous-unknown | | | | 1.033 ^a ± 0.409 |
| Young-coniferous | | | | |
| Deciduous/shrub | -1.003 ^a ± 0.336 | | | -0.633 ± 0.444 |
| Open-nonvegetated | 0.491 ± 0.512 | 0.697 ^a ± 0.267 | | |
| Open-vegetated | | | | |
| Early Winter | | | | |
| Alpine | 0.960 ^a ± 0.478 | 1.944 ^a ± 0.148 | 0.652 ^a ± 0.182 | |
| Parkland | | -0.465 ± 0.246 | | |
| Fir | 0.016 ± 0.384 | 0.085 ± 0.350 | -0.652 ^a ± 0.182 | 0.635 ^a ± 0.142 |
| Fir-leading | -1.062 ^a ± 0.322 | -0.461 ^a ± 0.213 | | 0.575 ^a ± 0.126 |
| Spruce-leading | | -1.788 ^a ± 0.434 | | -1.410 ^a ± 0.233 |
| Pine-leading | 0.151 ± 0.182 | | | |
| Coniferous-unknown | | | | 0.200 ± 0.199 |
| Young-coniferous | -0.065 ± 0.230 | | | |
| Deciduous/shrub | | | | |
| Open-nonvegetated | | | | |
| Open-vegetated | | 0.685 ± 0.384 | | |

Appendix D. Continued.

| Vegetation Type | Kennedy | Moberly | Quintette | Parsnip |
|--------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|
| Late Winter | | | | |
| Alpine | 0.756 ^a ± 0.146 | 1.479 ^a ± 0.144 | 0.949 ^a ± 0.107 | -0.526 ± 0.323 |
| Parkland | 0.241 ± 0.177 | 0.161 ± 0.198 | | |
| Fir | 0.690 ^a ± 0.155 | 1.316 ^a ± 0.219 | 0.114 ± 0.159 | 0.932 ^a ± 0.129 |
| Fir-leading | -0.167 ± 0.146 | -2.223 ^a ± 0.446 | -1.063 ^a ± 0.162 | 0.735 ^a ± 0.130 |
| Spruce-leading | -1.515 ^a ± 0.284 | -1.979 ^a ± 0.447 | | -1.169 ^a ± 0.263 |
| Pine-leading | 0.796 ^a ± 0.162 | | | |
| Coniferous-unknown | | | | |
| Young-coniferous | 0.199 ± 0.335 | | | |
| Deciduous/shrub | -0.925 ^a ± 0.288 | -0.092 ± 0.415 | | 0.028 ± 0.201 |
| Open-nonvegetated | | | | |
| Open-vegetated | -0.075 ± 0.370 | 1.338 ^a ± 0.335 | | |