Extension Note

BC Journal of Ecosystems and Management

Movements, foraging habits, and habitat use strategies of northern woodland caribou during winter: Implications for forest practices in British Columbia

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Abstract

Land managers face increasing challenges as they try to balance timber harvesting with the habitat requirements of wildlife, including those of woodland caribou in north-central British Columbia. With the aim of conserving caribou by improving forest practices, we employed a hierarchical, scale-explicit approach to study the processes governing movement and distribution of the northern woodland caribou ecotype.

Investigations of foraging sites north of Prince George, British Columbia revealed that caribou in forested and alpine areas cratered at locations with relatively low snow depths and relatively large amounts of terrestrial lichens. When snow depth, snow hardness, and snow density increased, caribou fed more frequently at trees supporting abundant arboreal lichens. Feeding activities of caribou in forested foraging patches were positively related to the biomass of several terrestrial lichen species and to decreasing snow depth; the number of arboreal feeding sites increased as snow depth and hardness increased. We identified three scales of habitat selection based on movement rates of caribou fitted with GPS collars. For all scales, caribou selected pine-lichen woodland and windswept rocky slopes. Predation risk was greatest for caribou travelling between habitat patches, was lowest for caribou in alpine habitats, and had no apparent influence on intra-patch movements.

Land use plans should address the needs of northern woodland caribou by ensuring that large patches of widely distributed pine-lichen woodland are maintained on the landscape, recognize the limiting effects of deep snow (i.e., > 50–80 cm), and encourage silvicultural strategies that minimize the creation of early seral-stage forests adjacent to caribou movement routes.

KEYWORDS: *northern woodland caribou, habitat, habitat selection, foraging, arboreal lichens, terrestrial lichens, predation risk, conservation, forest practices, British Columbia.*

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Johnson, C.J., K.L. Parker, D.C. Heard, and D.R. Seip. 2004. Movements, foraging habits, and habitat use strategies of northern woodland caribou during winter: Implications for forest practices in British Columbia. *BC Journal of Ecosystems and Management* 5(1):22–35. URL: *www.forrex.org/jem/2004/vol5/no1/art4.pdf*

Introduction

Woodland caribou (*Rangifer tarandus caribou*) in British Columbia and across North America have become a priority for conservation (Cumming 1992; Committee on the Status of Endangered Wildlife in Canada 2002). Trends of declining and extirpated herds have necessitated the implementation of management schemes that will maintain existing populations of woodland caribou, stabilize the decline of other caribou populations, and, in extreme cases, enhance the productivity and size of small unviable populations. The increasing demand for timber from British Columbia's forests has the potential to conflict with the habitat needs, health, and recovery of caribou populations found in this province (Stevenson and Hatler 1985).

Three variants of the woodland caribou subspecies are found across British Columbia (i.e., northern, mountain, and boreal caribou); each variant is identified and managed according to its unique habitat requirements and geographical ranges. Until recently, research and management have focused primarily on populations of mountain caribou found in the southeastern portion of the province. This variant is considered endangered or threatened, and is thus found on the provincial Conservation Data Centre's Red list (Mountain Caribou Technical Advisory Team 2002). The more numerous northern caribou has received little attention, although in the central and northern reaches of British Columbia this variant is considered threatened by expanding forestry activities. Of principal concern are: direct loss of habitats; increases in the distribution, abundance, and efficiency of predators; and displacement of caribou from habitats due to human activities.

During winter, northern woodland caribou forage primarily on terrestrial, and to a lesser extent, arboreal lichens. Patches of terrestrial lichens are sparsely distributed and are inaccessible to caribou when the snow is deep. Harvesting activities such as log skidding potentially reduce the amount and availability of terrestrial lichens. Also, deciduous vegetation, which is attractive to moose, is more prevalent at recently disturbed sites such as cutblocks. Increases in the distribution and abundance of moose will in turn support larger, more widely dispersed wolf packs. Wolves are the primary predator of caribou, and are a limiting factor for caribou populations (Bergerud and Elliot 1986, 1998).

To mitigate the negative effects of timber harvesting on caribou, land managers, planners, foresters, and biologists attempt to implement silvicultural strategies that retain the natural distribution and amounts of winter habitat (e.g., by mimicking natural disturbances) (Seip 1998). Our ability to accommodate northern woodland caribou in land use plans would be enhanced by a more complete understanding of the ecotype's habitat requirements, movements, and responses to predators.

The increasing demand for timber from British Columbia's forests has the potential to conflict with the habitat needs, health, and recovery of caribou populations found in this province

Because caribou range over large areas, and because changes in population dynamics are observable only over long time periods, it is difficult to implement experimental research that effectively measures the impacts of forest practices on caribou distribution and persistence (Hargrove and Pickering 1992). Recognizing these limitations, in 1996 we implemented a four-year research project focusing on the environmental and behavioural processes that influence caribou movements and habitat selection during winter (Lima and Zollner 1996).

Objectives

The principal objectives of the study were:

1. Describe the fine-scale feeding behaviour of northern woodland caribou relative to forage availability and snow conditions.
2. Model and define discontinuities in the spatial and temporal patterns of caribou movements.
3. Use GIS databases to identify important environmental attributes that influence habitat selection and movements of caribou at scales of behaviour larger than those observable with field-based methods.

In this paper we outline the major findings of our research and discuss the potential application of the findings to initiatives for conserving northern woodland caribou in British Columbia. We focus our discussion on the limiting factors that are most closely related to timber harvesting: reduced availability of forage and increased distribution and abundance of predators. The recommendations and findings presented here are a synthesis of other work that is available in the peer-reviewed literature. We encourage the reader to seek out those sources (see References section) for a more complete description of methods and results.

Study Area

We studied female caribou from the Wolverine herd. These animals range throughout a 5100-km^2 area located approximately 250 km northwest of Prince George, B.C. (Heard and Vagt 1998). Terrain across the study area varies from valley bottoms at approximately 900 m elevation to alpine summits at approximately 2050 m elevation. The terrain is characterized by numerous vegetation associations occurring in the BWBSdk1, SBSmk1, SBSmk2, SBSwk2, ESSFmv3, ESSFmvp3, and ATn variants of the biogeoclimatic ecosystem classification.[1] Forest types below 1100 m elevation are dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), hybrid white spruce (*P. glauca* x *engelmannii*), and subalpine fir (*Abies lasiocarpa*). Between 1100 and 1600 m elevation, a moist cold climate prevails with forest types consisting primarily of Engelmann spruce (*P. engelmannii*) and subalpine fir. Areas at elevations greater than 1600 m are alpine tundra and are distinguished by gentle to steep windswept slopes vegetated with shrubs, herbs, bryophytes, lichens, and occasional krummholz trees (Meidinger and Pojar 1991).

Methods

Research Components

We stratified the research into two components according to our ability to observe the behaviours of caribou at successively coarser spatial and temporal scales. First, over areas larger than the 25 × 25-m grain size of the GIS, we used movement paths of caribou to define discrete spatial scales at which animals interact with the environment. Each scale served as a constraint in defining breaks in behavioural decisions. Using this as a framework, we measured the importance of the following to the caribou's movements and positioning across the landscape: vegetation, predation risk, landscape structure, and the energetic costs of movement.

Second, at a resolution finer than that of the GIS, collared animals were trailed and feeding sites were investigated. At each feeding site, we measured plant and lichen abundance as well as snow conditions. We used a number of statistical approaches to quantify the behaviour of caribou and the trade-offs they made when selecting feeding sites. In addition to revealing habitat selection by caribou at fine scales, this component of the research explained and highlighted possible mechanisms for patterns of movement and selection at coarser spatial scales.

Data Collection

We used a hierarchical sampling design to study some of the mechanisms that influence caribou. At the scale of foraging behaviour, we assessed environmental factors that influenced selection of feeding sites and vegetative patches. During our investigations of feeding sites, we located excavations (i.e., feeding craters) in the snow where caribou had fed on terrestrial lichens and we located trees where caribou had fed on arboreal lichens. We matched feeding sites (craters and trees) with randomly selected locations and compared the amount of lichen and moss, snow depth, snow density, and snow hardness. Over two winters we examined caribou feeding sites along eighty-five 100-m forest transects and twenty-three 50 × 50-m alpine quadrats (Johnson *et al.* 2000, 2001). For this scale of investigation, we considered the *foraging patch* to be the average percent cover and abundance of lichens and snow conditions across a transect or quadrat.

At broader spatial scales, we used GPS collars to record the movements of caribou (see inset) (Johnson *et al.* 2002a). Over four winters (March 1996 to June 1999), we collected 7218 locations from 16 collared caribou (Johnson *et al.* 2002b) (Figure 1). We used those locations and a statistical model to identify the successively larger scales of movements that occurred within habitat patches (intra-patch), between habitat patches (inter-patch), and across collections of habitat patches (Johnson *et al.* 2002c) (Figure 2). We considered a *habitat patch* to be all levels of heterogeneity larger than a feeding site or a foraging patch, but not extending beyond the most dominant and observable ecotone. Habitat patches were identified using *Landsat* Thematic Mapper satellite imagery and were classified

[1] As per Meidinger and Pojar (1991), these ecosystem classifications are:

BWBSdk1	Stikine variant of the Dry Cool subzone of the Boreal White and Black Spruce zone
SBSmk1	Mossvale variant of the Moist Cool subzone of the Sub-Boreal Spruce zone
SBSmk2	Williston variant of the Moist Cool subzone of the Sub-Boreal Spruce zone
SBSwk2	Finlay-Peace variant of the Wet Cool subzone of the Sub-Boreal Spruce zone
ESSFmv3	Omenica variant of the Moist Very Cold subzone of the Engelmann Spruce–Subalpine Fir zone
ESSFmvp3	Omenica variant of the Moist Very Cold Parkland subzone of the Engelmann Spruce–Subalpine Fir zone
ATn	Alpine Tundra subzone

WHY USE GPS COLLARS?

Global positioning system (GPS) collars are a relatively new tool for the wildlife scientist. The collars are similar to the hand-held GPS units used for recreation or surveying, but they are smaller and have added weather- and shockproofing. These devices take advantage of a network of satellites that continuously broadcast signals containing the transmission time and the location of the satellite in space. A GPS collar receives the signal and can calculate a distance to each satellite by measuring the difference in time between transmission and reception and multiplying that time difference by the speed of light. When a collar receives three or more signals it can triangulate the animal's location.

These collars offer a number of advantages over conventional radio-telemetry techniques, including: frequent automated collection of animal locations (up to one location per second); collection of locations during night and through weather conditions that may limit conventional telemetry; and greater accuracy of animal locations (within 3–8 m versus approximately 100 m). However, compared to conventional radio-telemetry devices, GPS collars are more expensive, less reliable, and function for a shorter period of time (Johnson *et al.* 2002a).

In our study of northern woodland caribou, we programmed GPS collars to record one location every three or four hours. We then converted distances between locations to movement rates (i.e., speed) and used a statistical model to identify discontinuities in the frequency of those rates (Johnson *et al.* 2002c). The hypothesis underlying those analyses was that caribou would make many slow small-scale movements when foraging, and would make a small number of relatively fast large-scale movements when travelling between habitat patches. This approach allowed us to identify behaviourally meaningful scales of movement and resource selection.

according to a set of 13 cover types of unique vegetative and topographic association (Johnson *et al.* 2003).

During short-distance intra-patch movements we assessed the importance of vegetation cover types and predation risk (as modelled from locations of radio-collared wolves; Johnson *et al.* 2003). During inter-patch movements, we measured the influences of cover types, relative predation risk, and the energetic costs of movement. At the widest spatial scale of resource use, we assessed selection by caribou for configuration and composition of cover types and for variation in predation risk across areas of forested and alpine landscapes consisting of collections of habitat patches. All analyses of GPS-collar locations were constrained to a GIS grain size of a 25 × 25-m pixel.

Results and Discussion

Selection of Landscapes

At the scale of forested and alpine landscapes, caribou demonstrated one of three broad strategies of habitat occupancy: (1) wintering exclusively within forested habitats, (2) wintering exclusively within alpine landscapes, or (3) wintering in both forested and alpine landscapes. Data were sparse relative to repeat winters; only one animal spent all four winters in the same landscape (alpine), whereas other animals demonstrated variability in choice over successive winters. We recorded distinct differences in snow conditions, lichen biomass, and predation risk for caribou occupying forested versus alpine landscapes. Relative to caribou ranging across the alpine, caribou in forested landscapes used feeding sites and foraging patches with thicker, more widely distributed patches of lichens and patches with deeper snow but less variable depths (Table 1). Caribou that selected alpine habitats incurred less risk of encountering wolves; thus, they may have traded off forage abundance in favour of forage accessibility and lower predation risk (Figure 3).

Selection of Collections of Habitat Patches

Caribou locations collected with GPS collars revealed repeated small-scale movements—likely associated with foraging—across collections of habitat patches

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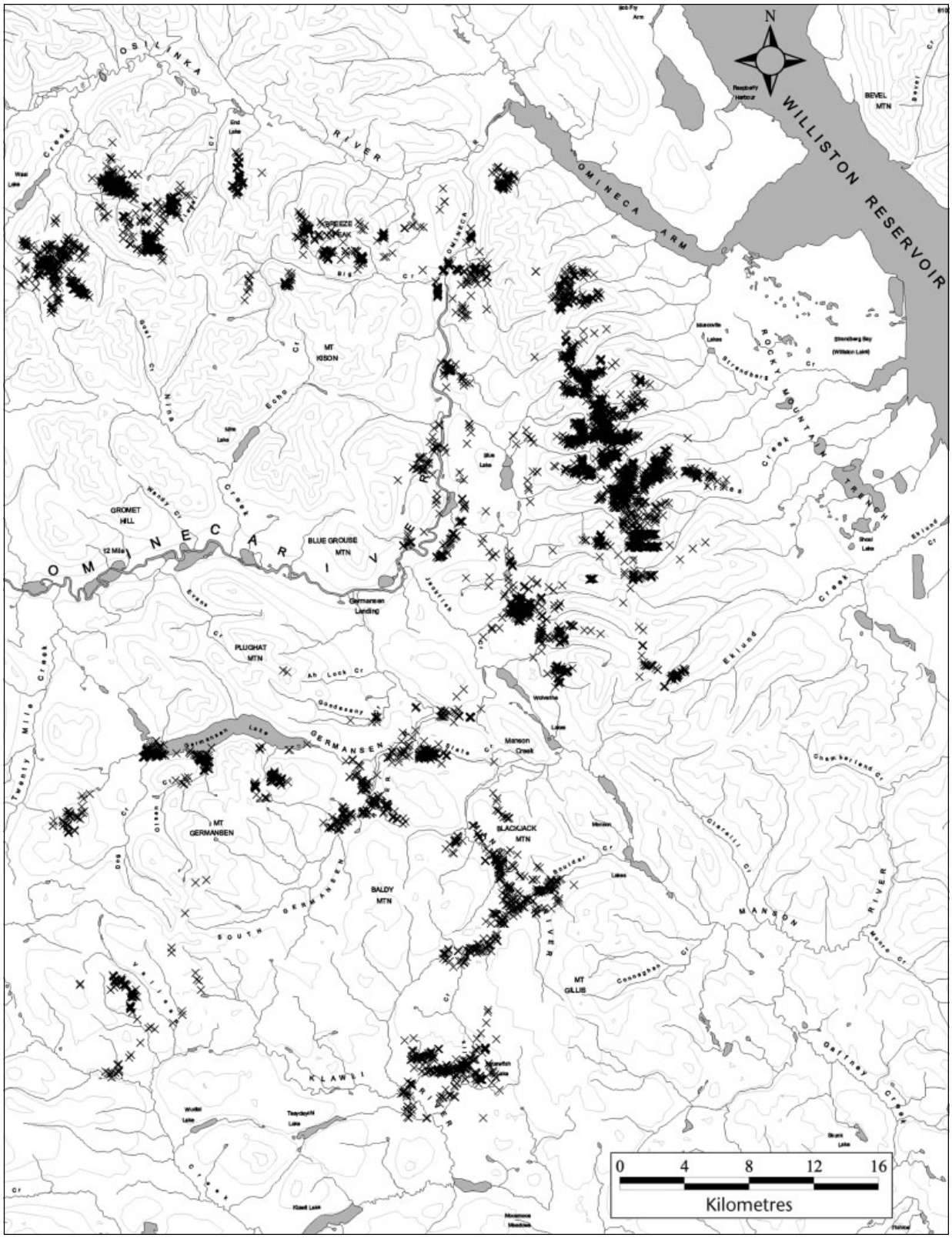

FIGURE 1. Locations of GPS-collared caribou of the Wolverine herd in north-central British Columbia for the winters of late 1995/96, 1996/97, 1997/98, and 1998/99.

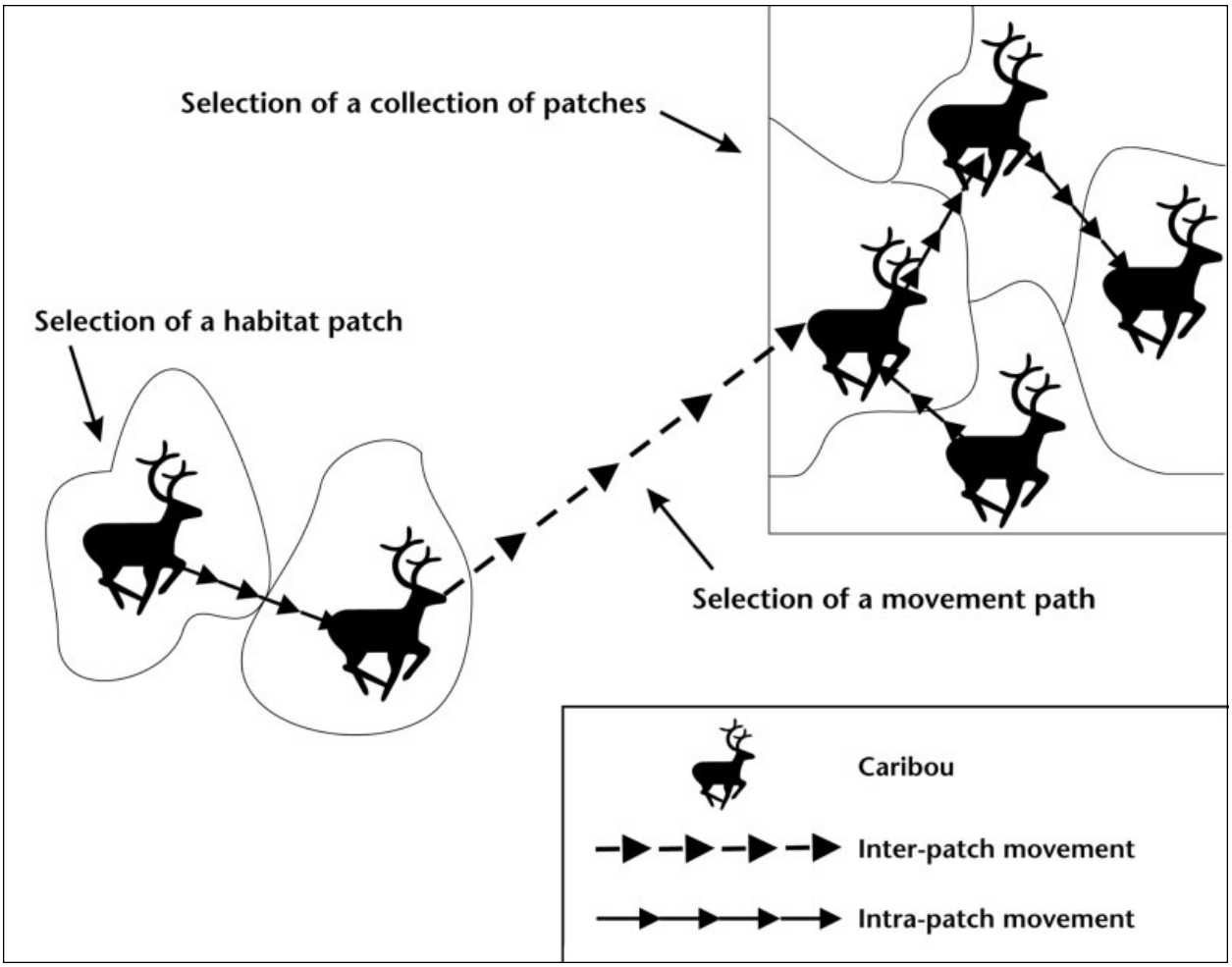

FIGURE 2. Schematic representation of three scales of movement and habitat selection identified using locations collected with GPS collars placed on caribou of the Wolverine herd in north-central British Columbia.

TABLE 1. Lichen and snow conditions at forested and alpine feeding sites and foraging patches used by caribou of the Wolverine herd in north-central British Columbia

	Lichen		Snow depth		Snow hardness	
Habitat type	Mean (g/m^2)	Coefficient of variation	Mean (cm)	Coefficient of variation	Mean (g/m^2)	Coefficient of variation
Forested area						
Feeding site	345.9	0.48	55.1	0.32	0.7	0.52
Patch	270.0	0.48	57.8	0.31	0.6	0.44
Alpine area						
Feeding site	173.3	0.67	15.5	0.50	3.3	1.71
Patch	34.7	0.85	19.6	0.36	3.4	0.90

FIGURE 3. Variation in predation risk, as determined from wolf locations, across a portion of the Wolverine caribou herd's winter range. Predation risk decreases as distance from high-risk patch types (i.e., pine, spruce, and wetlands; and lakes and rivers) increases.

(Figure 2). At that scale, caribou were relatively selective. Animals in the forest chose pine-lichen woodland with understories of abundant *Cladina* and *Cladonia* lichens, whereas caribou in the alpine selected rocky ridges and slopes with sparsely distributed lichens, and windswept ridges with more productive, deeper soils dominated by grass communities (Johnson *et al*. 2002b) (Figures 4 and 5). However, not all caribou selected those cover types in isolation of surrounding habitat patches. Landscape adjacency matrices indicated that pine-lichen woodland used by caribou were often adjacent to wetlands and black spruce patches, or mixed stands of black spruce and pine (Mladenoff and DeZonia 1999). For alpine cover types, adjacency matrices indicated that caribou selected rocky ridges and slopes that were distant from forested habitat patches. Contagion, a landscape metric that reports the dominance of a cover type, did not reveal consistent selection by caribou for large versus small patches of pine-lichen woodland or windswept alpine ridges (Figure 6). At the scale of multiple habitat patches, forage appeared to be a more important consideration for caribou than predation risk.

Selection of Movement Paths

Caribou selected a wider range of cover types when travelling between habitat patches: pine-lichen woodland, rocky alpine ridges and slopes, lakes and rivers, grassy alpine ridges, and hybrid white spruce stands (Johnson *et al*. 2002b). Caribou also chose flat areas with little elevation change in order to achieve a relatively low energetic cost of movement. Overall, the findings suggest that caribou select valley bottoms as movement routes. Radio-collared wolves also selected patches of spruce, pine, wetlands, lakes, and rivers; these areas may offer caribou an energetic gain, but they also present a relatively higher level of predation risk (Johnson *et al.* 2002b; Figure 3).

Selection of Habitat Patches

When engaged in intra-patch movements, caribou demonstrated strong selection for pine-lichen woodland and for rocky alpine ridges and slopes, followed by patches of black spruce or mixed stands of black spruce and pine (Johnson *et al*. 2002b) (Figure 7). Predation risk was unimportant at this scale. In forested foraging patches, the number of feeding sites was positively related to the biomass of *Cladina mitis*, *Cladonia* spp., and decreasing snow depth, whereas the number of arboreal feeding sites increased as snow depth and hardness increased (Johnson *et al*. 2001).

At the scale of multiple habitat patches, forage appeared to be a more important consideration for caribou than predation risk.

In the alpine, no relationship was discernible between patch type selection and terrestrial lichen abundance and snow conditions.

Most of our site investigations were conducted in pine-lichen woodland (66%) and in more productive, wetter pine stands with lesser amounts of terrestrial lichens (15%). In the alpine, we trailed caribou across rocky (80%) and grass-dominated (15%) ridges and slopes.

Selection of Feeding Sites and Forage Species

Over two winters of trailing caribou, we observed animals consistently selecting several lichen species (Johnson *et al*. 2000, 2001). Caribou in the forest cratered at sites with abundant *Cladina mitis* and *Cladonia* spp. and avoided those sites dominated by mosses (Figure 4). Caribou in the alpine selected a wider variety of lichens including *Cladina rangiferina*, *Cetraria cucullata*, *Cetraria nivalis*, *Cladina mitis*, *Thamnolia* spp., and *Stereocaulon alpinum* (Figure 5). Across both forested and alpine areas, caribou foraged more frequently at sites where the snow was less deep, typically at sites with snow depths less than 60 cm (Figure 8). When snow depth, snow density, and snow hardness limited access to terrestrial lichens in the forest, caribou foraged more frequently on arboreal lichens (*Bryoria* spp.). Caribou selected trees with a higher biomass of lichen than was randomly available along the movement paths we studied.

Lessons Learned: Implications for Forest Management

Identification of multiple scales of caribou movement and habitat selection allowed us to investigate process-specific responses of caribou to the environment. The outcomes of these investigations will assist land managers, planners, foresters, and biologists assess and mitigate the effects of timber harvesting on caribou habitat when they prepare land use plans and conduct operational forestry activities. We summarize our findings as they relate to the two primary limiting factors for northern woodland caribou: the availability of lichens and the distribution of wolves.

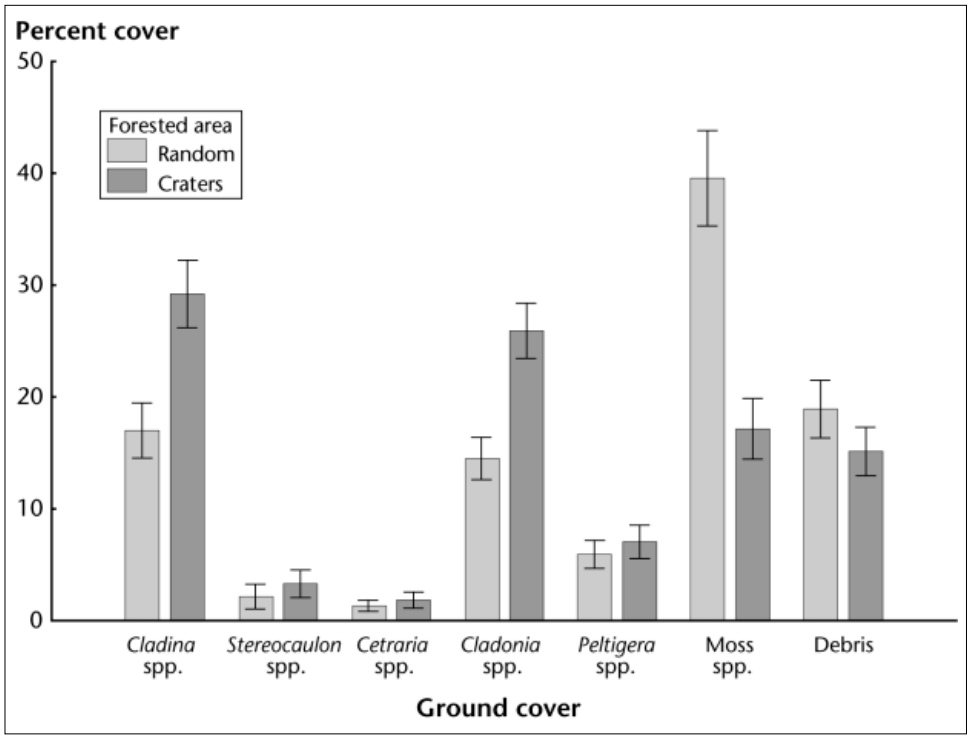

FIGURE 4. Average percent ground cover of vegetation at randomly selected sites and at sites cratered by caribou in forested areas across the winter range of the Wolverine herd of north-central British Columbia. Error bars represent 95% confidence intervals.

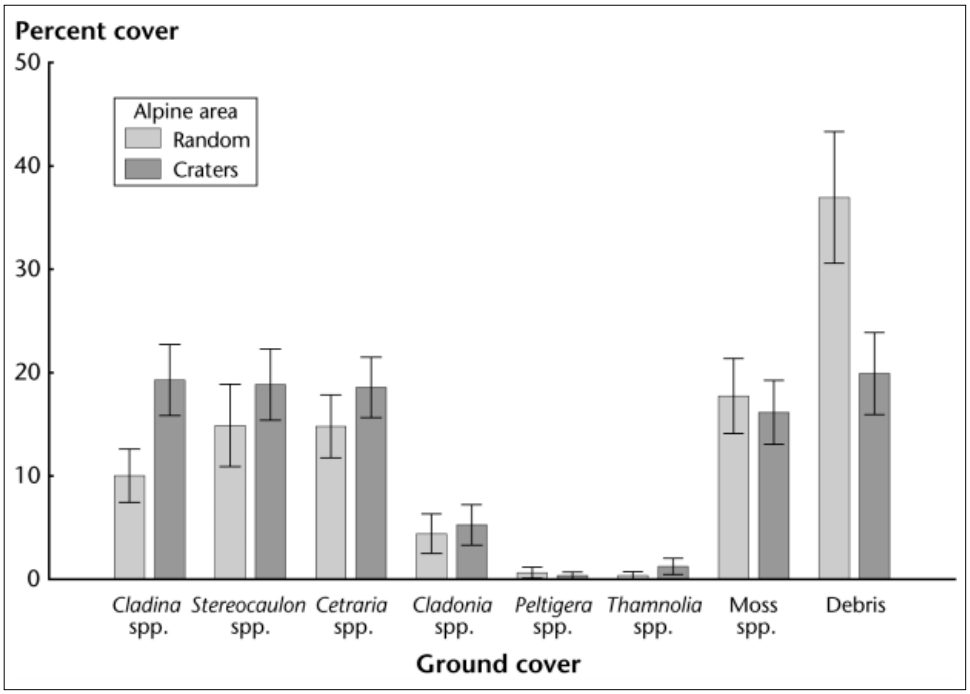

FIGURE 5. Average percent ground cover of vegetation at randomly selected sites and at sites cratered by caribou in alpine areas across the winter range of the Wolverine herd of north-central British Columbia. Error bars represent 95% confidence intervals.

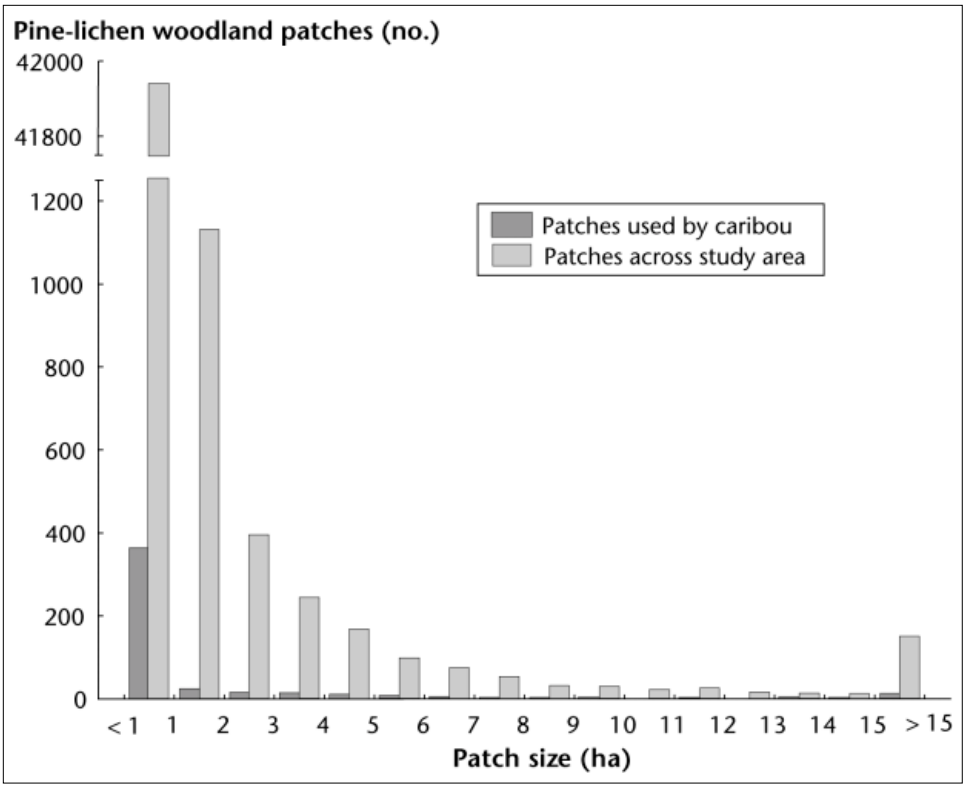

FIGURE 6. Frequency distribution of patch sizes of pine-lichen woodland used by caribou of the Wolverine herd of north-central British Columbia during winter. Woodland areas were identified through supervised classification of a *Landsat* Thematic Mapper image (Johnson *et al.* 2003).

Forage Distribution and Availability

1. Caribou that occupied forested habitats during winter demonstrated strong selection for pine-lichen woodland. This type of habitat patch was important at all scales of analysis and should be maintained across areas that are managed for northern woodland caribou winter range. Caribou did not actively select for large patches of pine-lichen woodland. We observed caribou using patches that ranged from 0.063 ha (resolution of the GIS data) to 359 ha. Given the wide-ranging movements and distribution of caribou during winter, these data suggest that even small habitat patches are of value.

   Pine-lichen woodland supports thick mats of terrestrial lichens and is often characterized by the poor productivity and well-drained soils associated with glacio-fluvial landforms. Across our study area, stands rich in terrestrial lichens typically corresponded with site series 02 of the SBSmk2, SBSwk2, BWBSdk1, and ESSFmv3 (MacKinnon *et al.* 1990). Foresters should attempt to differentiate pine-lichen woodland from pine stands occurring on wetter, more productive soils, because the latter typically support fewer lichens. Satellite imagery is an effective tool for making such distinctions at coarse spatial scales (Johnson *et al.* 2003). Pine-lichen woodland is dynamic and older stands will often succeed to a moss-dominated understorey (Coxson and Marsh 2001). Natural or artificial disturbance may be necessary to ensure the long-term productivity of terrestrial lichens across most patches of pine-lichen woodland (Sulyma and Coxson 2001).

2. Researchers have observed associations between caribou and mosaics of pine-lichen woodland, wetlands, and patches of black spruce (Terry and Wood 1999). Our work suggests that caribou not only occupy, but actively select such patch mosaics. Wetlands and black spruce stands support sedges, which caribou may eat to balance a winter diet otherwise dominated by high-energy, low-protein

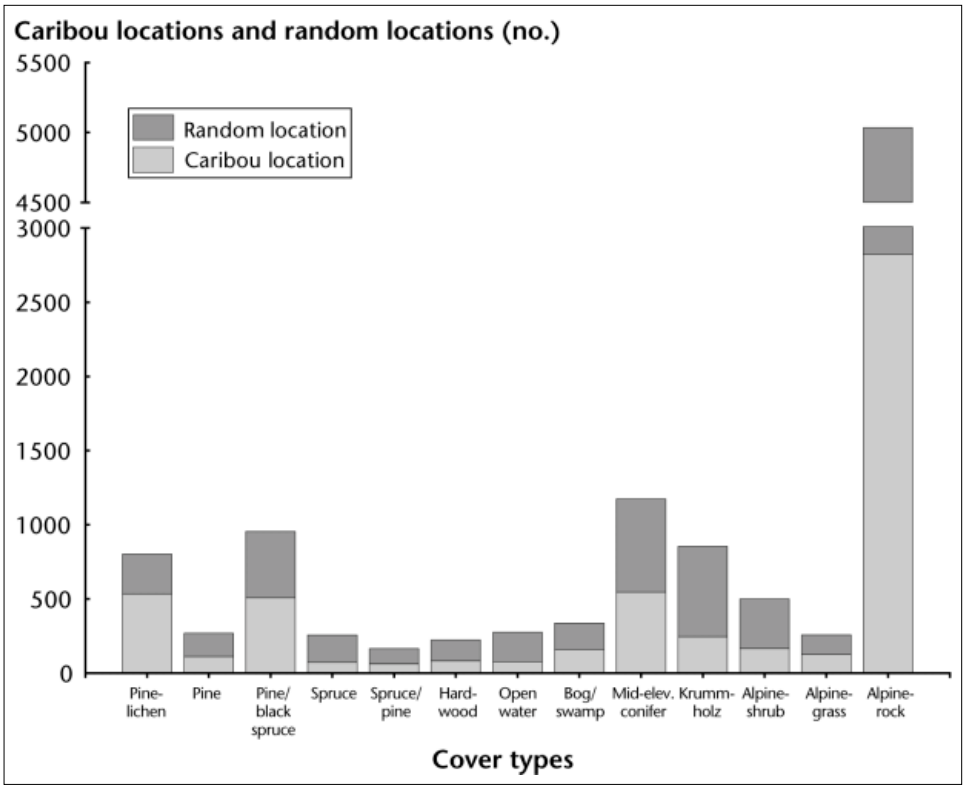

FIGURE 7. Number of caribou locations and paired random locations recorded across cover types during small-scale movements. Location data were collected from 1996 to 1999 during the winter for 16 caribou of the Wolverine herd in north-central British Columbia.

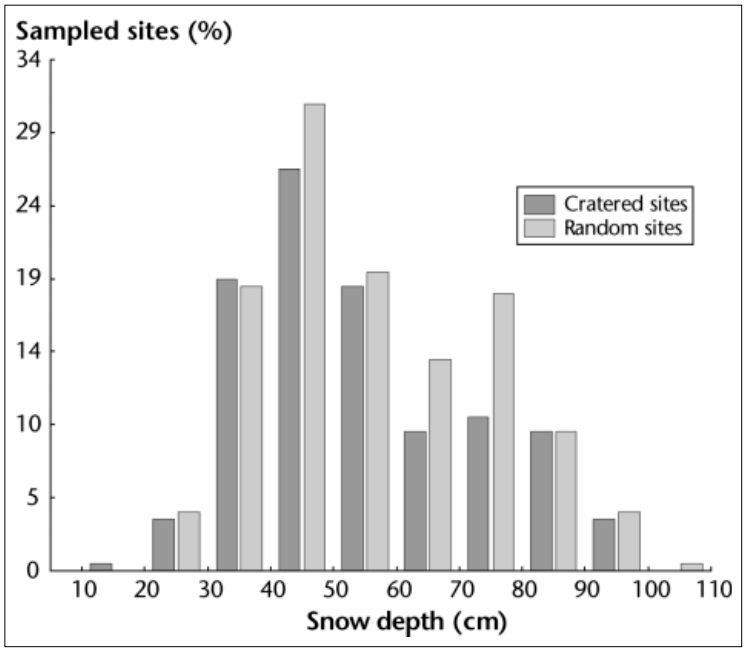

FIGURE 8. Frequency distribution of snow depths measured at sites cratered by caribou and at randomly selected sites in forested areas across the winter range of the Wolverine herd of north-central British Columbia.

Harvesting that maintains terrestrial lichens, but fails to retain arboreal lichens, may not meet the full range of habitat requirements for caribou.

terrestrial lichens (Storeheier *et al*. 2002a). Mosaics of pine-lichen woodland, wetlands, and black spruce should be maintained across areas managed for caribou habitat.

3. Areas of pine-lichen woodland vary in size. They can occur as small patches that may not be represented on habitat maps. In those instances, the percent cover of *Cladina mitis* and *Cladonia* spp. may serve as useful indicators of the potential of a patch to provide forage for caribou. We found that *Cladina rangiferina* and *Stereocaulon* spp. are important species for alpine-dwelling caribou. Caribou are adaptable and may forage on a wide variety of lichens (Bergerud and Nolan 1970). If the successional progression of lichen communities across forested winter range includes *Cladina rangiferina* or *Stereocaulon* spp., those lichens should also be recognized and maintained during habitat assessments and forestry operations (Coxson and Marsh 2001). Our data do not provide explicit guidance regarding the size of a patch of pine-lichen woodland that foresters should consider during habitat inventories, nor regarding the amount of lichen necessary for caribou to forage at a feeding site. We observed use of habitat patches that met the grain of our GIS data (0.063 ha) and feeding at sites with as little as 19% cover of lichen. However, caribou do not select lichens in isolation of other limiting factors. The availability and type of forage, snow conditions, distribution of predators, and other unstudied factors interact to influence the behaviour and distribution of caribou at a number of spatial and temporal scales.
4. Caribou forage on arboreal lichens when they range across pine-dominated forested areas with deep, dense, and (or) hard snow. To date, habitat research and silvicultural prescriptions concerning northern woodland caribou have favoured the maintenance or regrowth of terrestrial lichens. Harvesting that maintains terrestrial lichens, but fails to retain arboreal lichens, may not meet the full range of habitat requirements for caribou. This suggests that a variable retention or small-block harvesting strategy should be used; however, such approaches may not be economically feasible.
5. Snow is widely recognized as limiting to the movements and foraging efficiency of woodland caribou. Individuals of the Wolverine herd also demonstrated marked responses to snow conditions. Caribou selected feeding sites where snow depth, snow density, and (or) snow hardness were least; during late winter, the caribou may have abandoned southern portions of their range because the snow was too deep, dense, and (or) hard. When evaluating winter range, foresters and biologists should consider the distribution of pine-lichen woodland relative to the limiting effects of snow. Other researchers have reported the threshold depth for cratering by caribou and reindeer to be 50–80 cm (Stardom 1975; Helle and Saastamoien 1979; Darby and Pruitt 1984). Likewise, we found that the majority of feeding craters occurred in snow depths less than 90 cm (Figure 9), although we measured craters as deep as 97 cm, and Brown and Theberge (1990) recorded craters 123 cm deep. We suggest that managers and planners consider areas of deep snow to be low-value caribou habitat. Silvicultural practices could create closed canopy conditions, which in turn would lead to greater snow interception; however, other research suggests that such forest conditions impede the growth of terrestrial lichens (Sulyma and Coxson 2001).

Predation

1. With the exception of mineral development and backcountry recreation, human activities do not directly affect caribou in alpine habitats. However, the indirect effects of forest practices need to be considered across the entire range of a caribou population. Forest practices that encourage the types of early seral stages of vegetation favoured by moose have implications for caribou in both forested and alpine landscapes. An increased moose population leads to an increased wolf population; greater levels of predation could eliminate forested areas as viable habitat and reduce some of the survival strategies available to caribou. Caribou that are restricted to islands of alpine habitat would have little opportunity for range expansion or for gene exchange with adjacent populations (Poole *et al*. 2000). Maintaining the distribution of caribou

Where possible, harvesting should be minimized across known caribou movement routes.

across both forested and alpine landscapes would help ensure population connectivity.

2. Caribou had the highest exposure to risk when making inter-patch movements (Figure 3). At that scale, animals often moved across valley bottoms within relatively high-risk cover types (i.e., wetlands, lakes, rivers, pine, and spruce). Where possible, harvesting should be minimized across known caribou movement routes, or silvicultural strategies should be employed to reduce the availability of moose forage and, consequently, the number of wolves (Rea 2003). Increased predation across movement routes may lead to population sinks or to a reduction in winter range connectivity.
3. Northern woodland caribou rarely selected mid-elevation coniferous or high-elevation krummholz forests. This is in contrast to the mountain caribou ecotype, which typically winters in older coniferous stands while foraging on arboreal lichens (Terry *et al.* 2000). Mid- or high-elevation cuts, however, would be accompanied by road development that may allow wolves easier access to alpine-dwelling caribou. Vegetative regrowth in those cuts may also favour moose populations and thereby increase the likelihood of caribou-wolf interactions. Land use plans should include provisions to minimize the spatial and temporal adjacency of moose and wolves to high-elevation caribou refugia.

Acknowledgements

We thank Mike Wolowicz, Glen Keddie, Glen Watts, Greg Altoft, Larry Frey, Eric Stier, and a large number of volunteers for their assistance in trailing caribou and with animal capture and relocation. C. Wainwright, S. McNay, and one anonymous reviewer provided insightful comments on an earlier version of this manuscript. This work would not have been possible without the financial support of Forest Renewal BC; the University of Northern British Columbia; the Natural Sciences and Engineering Research Council; the British Columbia Ministry of Environment, Lands and Parks; and the Boone and Crockett Club.

References

Bergerud, A.T. and J.P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. Canadian Journal of Zoology 64:1515–1519.

_____ . 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. Canadian Journal of Zoology 76:1551–1569.

Bergerud, A.T. and M.J. Nolan. 1970. Food habits of hand-reared caribou *Rangifer tarandus* L. in Newfoundland. Oikos 21:348–350.

Brown, W.K. and J.B. Theberge. 1990. The effect of extreme snowcover on feeding-site selection by woodland caribou. Journal of Wildlife Management 54:161–168.

Committee on the Status of Endangered Wildlife in Canada. 2002. Canadian species at risk. Canadian Wildlife Service, Environment Canada, Ottawa, Ont.

Coxson, D.S. and J. Marsh. 2001. Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. Canadian Journal of Botany 79:1449–1464.

Cumming, H.G. 1992. Woodland caribou: Facts for forest managers. Forestry Chronicle 68:481–491.

Darby, W.R. and W.O. Pruitt, Jr. 1984. Habitat use, movements and grouping behaviour of woodland caribou, *Rangifer tarandus caribou*, in southeastern Manitoba. Canadian Field Naturalist 98:184–190.

Hargrove, W.W. and J. Pickering. 1992. Pseudoreplication: A *sine qua non* for regional ecology. Landscape Ecology 6:251–258.

Heard, D.C. and K.L. Vagt. 1998. Caribou in British Columbia: A 1996 status report. Rangifer (Special Issue) 10:117–123.

Helle, T. and O. Saastamoinen. 1979. The winter use of food resources of semi-domestic reindeer in northern Finland. Communicationes Instituti Forestalis Fenniae 95:1–27.

Johnson, C.J., N.D Alexander, R.D. Wheate, and K.L. Parker. 2003. Characterising woodland caribou habitat in sub-boreal and boreal forests. Forest Ecology and Management 180:241–280.

Johnson, C.J., D.C. Heard, and K.L. Parker. 2002a. Expectations and realities of GPS animal location collars: Results of three years in the field. Wildlife Biology 8:153–159.

Johnson, C.J., K.L. Parker, and D.C. Heard. 2000. Feeding site selection by woodland caribou in north-central British Columbia. Rangifer (Special Issue) 12:159–172.

_____ . 2001. Foraging across a variable landscape: Behavioural decisions made by woodland caribou at multiple spatial scales. Oecologia 127:590–602.

Johnson, C.J., K.L. Parker, D.C. Heard, and M.P. Gillingham. 2002b. A multi-scale behavioral approach to understanding the movements of woodland caribou. Ecological Applications 12:1840–1860.

_____ . 2002c. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology 71:225–235.

Lima, S.L. and P.A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11:131–135.

MacKinnon, A., C. DeLong, and D. Meidinger. 1990. A field guide for identification and interpretation of ecosystems of the northwest portion of the Prince George Forest Region. Research Branch, B.C. Ministry of Forests, Victoria, B.C. Land Management Handbook No. 21.

Meidinger, D. and J. Pojar. 1991. Ecosystems of British Columbia. Research Branch, B.C. Ministry of Forests, Victoria, B.C. Special Report Series No. 6.

Mladenoff, D.J. and B. DeZonia. 1999. APACK 2.11 analysis software. Forest Ecology Lab, Department of Forestry, University of Wisconsin–Madison, Wis.

Mountain Caribou Technical Advisory Team. 2002. A strategy for the recovery of mountain caribou in British Columbia. B.C. Ministry of Water, Land, and Air Protection, Victoria, B.C. Version 1.0. URL: *http://wlapwww.gov.bc.ca/wld/documentsmtcaribou_rcvrystrat02.pdf*

Poole, K.G., D.C. Heard, and G. Mowat. 2000. Habitat use by woodland caribou near Takla Lake in central British Columbia. Canadian Journal of Zoology 78:1552–1561.

Rea, R.V. 2003. Modifying roadside vegetation management practices to reduce vehicular collisions with moose *Alces alces*. Wildlife Biology 9:81–91.

Seip, D.R. 1998. Ecosystem management and the conservation of caribou habitat in British Columbia. Rangifer (Special Issue) 10:203–212.

Stardom, R.R.P. 1975. Woodland caribou and snow conditions in southeast Manitoba. *In* Proceedings of First International Reindeer and Caribou Symposium, Fairbanks, Alaska. J.R. Luick, P.C. Lent, D.R. Klein, R.G. White (editors). University of Alaska, Fairbanks, Alaska. Biological Papers of the University of Alaska, Special Report No. 1. pp. 420–422.

Stevenson, S.K. and D.F. Hatler. 1985. Woodland caribou and their habitat in southern and central British Columbia. Forest Science Program, B.C. Ministry of Forests, Victoria, B.C. Land Management Report No. 23. Volumes 1 and 2.

Storeheier P.V., S.D. Mathiesen, N.J.C. Tyler, I. Schjelderup, and M.A. Olsen. 2002. Utilization of nitrogen- and mineral-rich vascular forage plants by reindeer in winter. Journal of Agricultural Science 139:151–160.

Sulyma, R. and D.S. Coxson. 2001. Microsite displacement of terrestrial lichens by feather moss mats in late seral pine-lichen woodlands of north-central British Columbia. Bryologist 104:505–516.

Terry, E.L., B.T. McLellan, and G.S. Watts. 2000. Winter habitat ecology of mountain caribou in relation to forest management. Journal of Applied Ecology 37:589–602.

Terry, E.L. and M.D. Wood. 1999. Seasonal movements and habitat selection by woodland caribou in the Wolverine Herd, north-central British Columbia Phase 2: 1994–1997. Peace/Williston Fish and Wildlife Compensation Program, Prince George, B.C. Report No. 204.