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A MULTI-SCALE BEHAVIOURAL APPROACH TO UNDERSTANDING THE MOVEMENTS OF WOODLAND CARIBOU

by

Chris J. Johnson

B.Sc. (Hon.), University of Victoria, 1994

THESIS SUBMITTED IN PARTIAL FULFILMENT OF

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DOCTOR OF PHILOSOPHY

in

NATURAL RESOURCES AND ENVIRONMENTAL STUDIES

^oChris J. Johnson, 2000

THE UNIVERSITY OF NORTHERN BRITISH COLUMBIA

August 2000

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ABSTRACT

In British Columbia, an increased demand for merchantable timber has led to a heightened awareness of the conflict between human encroachment and the requirements of woodland caribou (*Rangifer tarandus caribou*) (Stevenson and Hatler 1985). To meet the needs of both industry and caribou, resource managers, planners, and biologists must understand the processes governing movements and distribution of those animals (Stevenson and Hatler 1985). I employed a hierarchical scale-explicit approach to understand some of the mechanisms influencing caribou behaviour. Over two winters (December 1996 – April 1998), I trailed caribou in forested and alpine habitats and recorded attributes of feeding sites and patches. At larger scales (larger geographic area), I used Global Positioning System (GPS) collars to record the movements of caribou (March 1996 – June 1999).

At the scale of the feeding site, caribou in the forest and alpine cratered at locations with lower snow depths and greater amounts of terrestrial lichens. In the forest, they selected *Cladina mitis* and *Cladonia* spp. and avoided mosses; in the alpine, they selected *Cladina rangiferina*, *Cetraria cucullata*, *C. mitis*, *Thamnolia* spp., and *Stereocaulon alpinum* and avoided sites with debris. Across both forested and alpine areas, caribou selected the most abundant, but not the most nutritious lichen species. Following increases in snow depth, hardness, and density, caribou in the forest fed more frequently at trees with abundant arboreal lichens (*Bryoria* spp.). Foraging effort at patches (defined as collections of feeding sites) was positively related to the biomass of *Cladina mitis*, *Cladonia* spp., and decreasing snow depth; number of arboreal feeding sites increased as snow depth and hardness increased. In the alpine, no relationship existed between patch selection by caribou and abundance of terrestrial lichens or snow conditions. The incongruity between variables important at the scale of the feeding site and those important at the patch indicated that foraging decisions of woodland caribou were affected by spatial scale.

Reliability of GPS collars to record movements of 23 female caribou was highly variable. Collars attempted 41,822 locations and collected 15,247 3-D and 10,411 2-D locations, which affects the accuracy of the location. I converted the intervals between GPS locations to movement rates, and used a two-process model to identify the break point between large-scale, inter-patch and small-scale, intra-patch movements. Caribou experienced a greater energetic cost of movement and were exposed to greater predation risk at large scales, had more highly correlated movements at small scales, and selected unique land-cover types at each scale of movement. I was unable to differentiate between large-scale inter-patch movements and migratory movements using a nonlinear modelling approach.

I tested the influence of correlated movements, cover type and predation risk on intrapatch movements; cover type, predation risk, and the energetic costs of movement on interpatch movements; and cover type, land-cover configuration (patch contagion and adjacency), and predation risk on the selection of general habitats (forest, alpine, forest-alpine). Pinelichen woodlands and wind-swept rocky slopes were the most important cover types selected by caribou at all scales in the forest and alpine, respectively. A relatively lower energetic cost of movement, and selection for lakes and rivers, suggested that during inter-patch movements, caribou often chose routes along valley bottoms. Selection of general habitats was more strongly related to composition than configuration of cover types. Caribou in the forest did, however, demonstrate a weak affinity for pine-lichen woodlands within a matrix of wetlands, and pine-black spruce or black spruce stands. Animals in the alpine selected rocky ridges and slopes that were not adjacent to forest types. Predation risk had no effect at the scale of intrapatch movements, was the greatest for caribou making inter-patch movements, and was lowest for caribou in alpine habitats. To conserve populations of woodland caribou, forest managers should maintain large patches of widely distributed pine-lichen woodlands, recognise the limiting effects of deep snow, and employ silvicultural strategies that minimise early seral-stage forests adjacent to caribou movement routes.

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FOREWORD

Throughout the thesis I use the first person plural to recognise the contributions of members of the supervisory committee and the assistance of field technicians and volunteers. Of special note, Dr. Kathy Parker, Mr. Doug Heard, and Dr. Mike Gillingham were involved from thesis conception to defence, aiding with the development and refinement of research questions, collecting and sorting data, and editing or reviewing thesis chapters. Their contributions are recognised through co-authorship of subsequent publications. As lead author, I developed the study design, organised and conducted field studies, chose appropriate statistical techniques, analysed and interpreted all data, and was responsible for producing draft manuscripts suitable for peer review.

CHAPTER 1 - THESIS INTRODUCTION

CONTEXT

Woodland caribou (*Rangifer tarandus caribou*) in British Columbia and across North America have become a high priority species for management (Cumming 1992). Historical trends of declining populations or extirpated herds have necessitated management schemes that will not only conserve and stabilise existing populations, but possibly enhance others (Edmonds 1988). In British Columbia, Canada, an increased demand for merchantable timber has led to a heightened awareness of the conflict between human encroachment and the habitat needs of caribou (Stevenson and Hatler 1985, Stevenson *et al.* 1994). To meet the requirements of both caribou and industry, information on the habitat needs and population dynamics of caribou is essential (Stevenson and Hatler 1985).

In British Columbia, much of the habitat research has focused on the southeastern populations of mountain caribou (Terry *et al.* 2000). The relatively stable northern-caribou ecotype has received little attention, but is now thought to be increasingly threatened by expanding forestry practices in the central and northern reaches of the province. Managers are planning for or mitigating effects of forest practices on forage availability for caribou, and on the distribution and abundance of predators (Seip 1998). Forage choices of northern woodland caribou are limited to terrestrial lichens during winter. Those lichens are patchily distributed according to the availability of suitable growing sites, and accessibility may vary depending on snow conditions. Relative to predators, caribou tend to separate themselves spatially from both predators such as wolves (*Canis lupus*) and other prey species such as moose (*Alces alces*) (Seip 1992). Forest harvesting increases the distribution of early seral stages of forests. Although not important as foraging habitats for caribou, those areas may lead to an increase in the productivity of moose populations and consequently wolf populations (Seip 1998).

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Additionally, a reduction in the availability or spatial extent of lichens may force caribou to occupy smaller or more predictable areas, thereby increasing efficiency of predation or the chance of caribou, moose, and wolves interacting.

Caribou appear to respond to environments at several spatial and temporal scales. Previous studies can be placed into one of three broad scales that serve as a framework to summarise our knowledge of woodland caribou habits and habitat use: 1) microhabitat or feeding sites, 2) patch or vegetative stands, and 3) landscape.

Feeding-Site Selection

Skogland (1985a, 1986) documented the density-dependent effects of food limitation during winter on recruitment rate and adult female body size of wild reindeer (*Rangifer tarandus tarandus*), and pregnancy rates have been found to increase progressively with increasing marrow and kidney fat reserves in female Peary caribou (*R. t. pearyi*) (Thomas 1982). In contrast, Reimers (1983) stated that differences in growth rates and body size were mainly attributed to availability of summer forage, with the quality of winter forage having only a minor effect.

During the winter, caribou forage primarily on terrestrial and arboreal lichens; the proportion of each species selected varies with herd location (Bergerud 1972, Cichowski 1993, Danell *et al.* 1994, Wood 1996). Reindeer select lichen species with the highest total nonstructural carbohydrates and nitrogen content, and the lowest fibre content, although they will broaden their feeding niche as the availability of preferred forage decreases (Skogland 1984). Selection of specific feeding sites and movements between feeding sites are influenced by snow depth, hardness, and the formation of ice layers. Relative to other ungulates, including moose, elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*) and bison (*Bison bison*), caribou are the best adapted behaviourally and morphologically to exist within deep-snow environments (Telfer and Kelsall 1984). Despite these adaptations, deep snow still hampers caribou movements (Helle 1984), and increases energy expenditures associated with locomotion (Fancy and White 1987). Cratering facilitates feeding by caribou during winter. Fancy and White (1985) noted that the energy costs of cratering depended on snow conditions, and that increased snow hardness and density in combination with a thick crust influenced mean energy expenditures and the ability of caribou to smell lichens. Skogland (1978), Helle and Tarvainen (1984), and Brown and Theberge (1990) reported similar relationships between decreased cratering efficiency or occurrence and increased snow hardness, density, and depth. Snow cover thresholds for cratering generally range from 50 – 80 cm (Bergerud 1974*a*, Stardom 1975, LaPerriere and Lent 1977, Darby and Pruitt 1984), although a maximum depth of feeding craters of 123 cm was reported for caribou in central Labrador (Brown and Theberge 1990).

Researchers have described individual variables that may influence habitat selection by caribou in different geographic locations. Few studies, however, were conducted to explain the conflicting influences of multiple variables. Effects of snow conditions and abundance of terrestrial and arboreal lichens have been quantified, but the interaction of those variables, and their influence on selection decisions and feeding behaviour have not been investigated.

Patch Selection

Relatively little is known about patch selection by northern woodland caribou, but patch use of vegetative communities is likely specific to individual herds (Bergerud and Nolan 1970). Depending on year and time of winter, caribou from the Wolverine herd in northcentral British Columbia selected lodgepole pine (*Pinus contorta*), fen-wetland areas, and alpine-subalpine areas (Terry and Wood 1999). Caribou south of the Wolverine herd selected spruce-fir (*Picea engelmannii – Abies lasiocarpa*) forests and alpine habitats during the winter

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(Poole *et al.* in press). Cichowski (1993) noted similar trends in habitat selection for two herds of caribou located in westcentral British Columbia. Those animals used a combination of immature and mature lodgepole pine stands, mature pine-spruce stands, meadow and alpine areas; proportion of use differed between season and herds. Caribou within the Spatsizi Wilderness Area of northern British Columbia occupied pine-dominated forests, open muskegs and meadows and moved to wind-blown alpine habitats following snow accumulation (Boonstra and Sinclair 1984, Hatler 1986). The previously cited studies considered patches at one or several arbitrarily defined scales and without regard to their spatial positioning across the landscape. Patches were considered only in the context of vegetation (excluding predation risk and snow), and the ecological meaningfulness of those patches to caribou behaviour was inferred from forest inventory data (e.g., pine stands >80 years = a component of caribou habitat). With the exception of work done by Cichowski (1993), patch selection also was not related to behaviours occurring at smaller scales.

Landscape Movements

At the multi-patch or landscape level, large-scale movements by caribou indicate that habitat selection occurs at the scale of landscapes. Woodland caribou may require large tracts of continuous suitable habitat to disperse widely and minimise predator encounters (Seip 1992, Bergerud *et al.* 1984). Wolves are the principal predator of caribou in winter, and predation is cited frequently as the limiting factor to population growth (Gasaway *et al.* 1983, Bergerud and Elliot 1986, Edmunds 1988, Seip 1992). Caribou reduce the risk of predation by taking refuge at less-accessible locations, such as high alpine areas or islands (Bergerud *et al.* 1984, Bergerud 1985, Bergerud and Page 1987, Cumming and Beange 1987, Seip 1992, James 1999). Specific movement corridors across the landscape also have been recognised (Hatler 1986, Lance and Mills 1996). Steventon (1996) reported that caribou of the TweedsmuirEntiako herd in westcentral British Columbia were associated with old forest on sites of poor productivity and with wetland mosaics while transiting between winter and summer ranges. The combined influences of predators, patch configuration, and corridors on the large-scale movements of northern woodland caribou have not been quantified.

STUDY OBJECTIVES

I began thesis design and research in autumn 1995. My primary objective was to provide forest-resource planners and managers with a greater understanding of the processes governing the movements and distribution of northern woodland caribou relative to several potentially limiting factors including forage, predators, the energetic costs of movement (i.e., movement routes), and snow characteristics. I initially adopted an arbitrary spatial framework to assess habitat use at the microhabitat, patch, and landscape scales. There were, however, several philosophical and practical limitations to most conventional and widely adopted use versus availability approaches (e.g., Bradshaw et al. 1995) that could be applied to the latter two scales. First, habitat usually is considered to be vegetation; other biotic or abiotic variables are seldom included (Hall et al. 1997). Second, there is no behavioural justification for the definitions of patch or landscape relative to the investigation of resource selection. Third, there have been few attempts to understand how animals respond to patchy environments across different spatial scales. And, fourth, used and available habitats have been poorly defined or based on criteria not directly related to the study animal (e.g., study area boundaries).

Because of the large scales over which caribou range, experimental work to define the effects of disturbance and forest practices on animal distribution and population dynamics is particularly difficult (Hargrove and Pickering 1992, Johnson *et al.* 1992). One strategy is to study the processes that influence animal movement and habitat selection. An increased

understanding of mechanistic responses would allow managers to predict the effects of harvesting more easily and extrapolate results of this study to other caribou herds (Hobbs and Hanley 1990). By adopting this strategy, I changed from simply viewing patterns of points on vegetation maps to developing a means of inquiry by which I could postulate and link mechanisms at a variety of spatial and temporal scales. Lima and Zollner (1996) discussed the advantages of studies designed to integrate techniques and knowledge of the behaviourist working at small scales and the landscape ecologist. Those authors asserted that the development of a "behavioural ecology of ecological landscapes" would further our ability to meet conservation objectives for far-ranging species. This thesis was designed to explore such ideals and apply them towards understanding the mechanisms that govern the winter movements and distribution of female northern woodland caribou. Specific objectives were:

1) to identify the temporal and spatial scales to which caribou respond;

- to implement a flexible modelling approach, not constrained by the limitations of conventional use versus availability techniques, that would allow me to test and compare resource selection at several temporal and spatial scales; and
- to measure the importance of forage, snow, predation risk, the energetic costs of movement and patch configuration on the movements and distribution of caribou at each of the identified scales, and contribute to defining the processes that govern caribou-habitat relationships.

THESIS ORGANISATION

I wrote this thesis as a series of independent, but related chapters to be submitted for journal publication. In Chapter 2, I present the lichen species and snow conditions that characterise feeding sites selected by caribou foraging across both forested and alpine habitats in northcentral British Columbia. The primary objective of this chapter is to provide managers, foresters, and biologists with an understanding of attributes that can be used to identify components of caribou foraging habitats during winter. In Chapter 3, I describe the foraging behaviour of caribou at three spatial scales. Specifically, I assess whether caribou were confronted with trade-offs and whether foraging decisions occurred as a linear multiscale process (i.e., as scale increased, similar decision criteria were used at each scale). In Chapter 4, I introduce how global positioning system (GPS) technology was used to monitor movements of caribou, and then discuss the advantages and disadvantages of using GPS collars for wildlife research. In Chapter 5, I use frequent animal relocations and a nonlinear curve-fitting model to identify scales of movement for individual caribou. I provide evidence that the model identifies intra- and inter-patch movements. In Chapter 6, I use the nonlinear model to identify three nonarbitrary spatiotemporal scales at which caribou respond to the environment. Selection of cover types, areas of low predation risk, and movement terrain was analysed relative to small-scale movements that likely occurred within patches and large-scale movements that occurred when animals moved between patches. The selection of collections of patches where animals concentrated small-scale movements was assessed relative to composition and configuration of cover types and predation risk. The final chapter of the thesis is a synthesis of findings. I discuss results and present recommendations with direct application to the conservation of woodland caribou.

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CHAPTER 2 - FEEDING SITE SELECTION BY WOODLAND CARIBOU IN NORTHCENTRAL BRITISH COLUMBIA¹

SUMMARY

The increased demand for merchantable timber in British Columbia has led to a heightened awareness of the conflict between resource extraction and the requirements of woodland caribou. Relatively few studies have been conducted on the northern caribou ecotype, and these have not addressed fine-scale habitat attributes. We examined the foraging habits of the northern woodland caribou ecotype at the scale of the individual feeding site. Field data were collected in northcentral British Columbia over two winters (December 1996 -April 1998). We trailed caribou and measured vegetation characteristics (species composition and percent cover), snow conditions (depth, density, and hardness), and canopy closure at terrestrial and arboreal feeding sites, and at random sites where feeding had not occurred. Logistic regression was used to determine the attributes of feeding sites that were important to predicting fine-scale habitat selection in forested and alpine areas. In the forest, caribou selected feeding sites that had a greater percent cover of *Cladina mitis* and *Cladonia* spp, lower snow depths, and a lower percentage of debris and moss. Biomass of Bryoria spp. at the 1- to 2-m stratum above the snow significantly contributed to predicting what trees caribou chose as arboreal feeding sites. In the alpine, caribou selected feeding sites with a greater percent cover of Cladina mitis, Cladina rangiferina, Cetraria cucullata, Cetraria nivalis, Thamnolia spp., and Stereocaulon alpinum as well as lower snow depths. The above lichen species and snow conditions should be considered when evaluating winter ranges of northern woodland caribou.

¹ Chapter has been accepted for publication as: C.J Johnson, K.L. Parker, and D.C. Heard (in press).

INTRODUCTION

The habitat requirements of the northern woodland caribou ecotype of British Columbia are largely unknown (Harrison and Surgenor 1996). This ecotype has been the subject of few studies, but is known to inhabit areas of low to moderate snow depths in lowelevation forests, and to forage primarily on terrestrial lichens during winter (Hatler 1986, Cichowski 1993, Lance and Mills 1996, Wood 1996). Most caribou research in British Columbia has focused on the mountain-caribou ecotype, which spends little time in lowelevation areas during the winter, but forages instead on arboreal lichens at high elevations (Servheen and Lyon 1989, Terry *et al.* 2000).

Further understanding of the life-history strategies of the northern woodland caribou ecotype is important in view of increasing demands for timber in the province. Wintering populations of this ecotype use low-elevation forests that are valued for commercial wood products (Cichowski 1993, Wood 1996). Consequently, they are likely to be negatively affected by habitat alteration, fragmentation, and increased road access.

As part of a larger research project to define the processes that affect the movements and distribution of northern woodland caribou across the landscape, we investigated the influence of forage species, abundance, and accessibility on the selection of individual feeding sites during winter. Specifically, we examined:

- the influence of snow depth, density, and hardness as well as vegetation composition and abundance on the selection of terrestrial feeding sites at small spatial scales in forested and alpine habitats; and
- 2) the influence of lichen biomass on the selection of arboreal feeding sites.

STUDY AREA

The group of caribou chosen for this study is known as the Wolverine herd (Heard and Vagt 1998), and ranges throughout a 5,100-km² area, approximately 250 km northwest of Prince George, British Columbia (Fig. 2.1). Terrain varies, from valley bottoms at approximately 900 m to alpine summits at 2,050 m, and is characterised by numerous vegetation associations resulting from diverse topography, soils, and succession (see Appendix A for more detailed description). Forest types below 1,100 m have been influenced extensively by wildfires and are dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), hybrid white spruce (*P. glauca x P. engelmannii*) and subalpine fir (*Abies lasiocarpa*). Between 1,100 and 1,600 m, a moist cold climate prevails with forest types consisting primarily of Engelmann spruce (*P. engelmannii*) and subalpine fir. Elevations greater than 1,600 m are alpine tundra and are distinguished by gentle to steep wind-swept slopes vegetated by shrubs, herbs, bryophytes, and lichens with occasional trees in krummholz form (MacKinnon *et al.* 1990, DeLong *et al.* 1993).

METHODS

Field investigations occurred at two- to three-week intervals between December and April 1996 – 1997 and 1997 – 1998. After locating recent tracks in the snow of radio-collared or non-collared caribou in the forest, we assessed the immediate area for signs of foraging behaviour: meandering tracks, craters and/or sniffing holes at terrestrial feeding sites, and trampling at the base of trees, broken twigs, and arboreal litter at arboreal feeding sites. If some sign of foraging behaviour was present, we selected a starting point in the snow along the caribou tracks using a random number table of distances, defined our transect by placing a 100-m tape along the track, and counted all terrestrial (craters) and arboreal feeding sites (Fig.



Figure 2.1. Winter range of the Wolverine caribou herd in northcentral British Columbia showing locations of forest transects and alpine quadrats measured in this study (December 1996 - April 1998)



Figure 2.2. Schematic representation of the sampling design used along a 100-m segment of recent caribou tracks in the snow.

2.2). A maximum of 12 sites were randomly selected for measurement along the 100-m transect: three sites where there had not been terrestrial feeding, three trees where there were no signs of arboreal feeding, and, if present, three cratering sites and three arboreal feeding sites.

In alpine areas, we used a 50 x 50-m quadrat as our sampling unit rather than a 100-m length of track because of the aggregated distribution of the feeding sites and safety concerns in precipitous terrain. All craters in the quadrat were counted, and we randomly selected three to six craters for measurements. The corresponding non-feeding sites were located at a random compass bearing and random number of paces (one to 20 paces) from the sampled craters.

One difficulty in repeatedly sampling animal behaviour and performing conventional statistical analyses is that of meeting the biological and statistical assumption of data independence (Hurlbert 1984). To minimise the risk of pseudoreplicating our sample unit, the feeding site, we limited the number of samples to not exceed the observed or, where animals were not sighted, the average number of caribou typically occurring within a group during the winter (n = 9) (Wood 1996, C.J. Johnson, unpubl. data). Furthermore, because we wanted to sample all collared animals and visit as many geographically separate locations as possible, we restricted the maximum number of transects sampled at one location to three, for a maximum of nine terrestrial and nine arboreal feeding sites. To further reduce the effects of spatial autocorrelation and allow an opportunity for changes in behaviour across space, and presumably time, successive transects were separated by a distance of 100 m. At alpine locations only one quadrat per group of animals was sampled, within which three to six craters and corresponding random sites were measured.

At each terrestrial feeding and random site, we measured snow depth to the nearest 0.5 cm, and the penetrability (i.e., hardness) of the upper snow layer with an instrument of our own design which was similar to the Rammsonde penetrometer (Mellor 1964, Skogland 1978). A British Columbia Ministry of Environment. Lands, and Parks (1981) Snow Survey Sampling Kit was used to measure snow density by inserting a cylinder of known volume vertically into the snow, recording the depth minus the soil plug, and weighing the contents. Because the scale used to measure the mass of the cored snow is insensitive at low snow depths, density could not be reliably calculated for alpine sites. For cratered sites, undisturbed edges were used for sampling. We also measured overstory cover using a moosehom (Moosehom Coverscopes, Medford, Oregon, USA) at all terrestrial and random sites.

Following the measurements of snow depth, density, and hardness, the snow was cleared and the percent cover of lichens, moss, and debris was assessed with a 16 pin, 0.5 x 0.5-m point frame (Bookhout 1994). Lichen and moss were identified to species, genus or morphological group depending on ease and reliability of field classification (hereafter referred to as distinct or composite classes).

At each arboreal feeding and random site, a lichen clump (*Bryoria* spp.) with a predetermined oven-dried weight was used as a standard lichen unit to visually estimate arboreal lichen biomass (g) (Antifeau 1987, Stevenson and Enns 1993). We counted the number of units that occurred within the reach of a typical caribou (1- to 2-m above the snow) and multiplied those units by the mass of the standard lichen unit to obtain total biomass within the 1- to 2-m stratum. Tree species and diameter at breast height were also recorded.

We used multiple logistic regression analyses to estimate the influence of percent cover of vegetation, snow conditions, and canopy closure on the selection of terrestrial feeding sites by caribou in forested and alpine areas. To assess the selection of arboreal feeding sites, we
tested a simple logistic regression model, consisting of foraged versus random trees as the dependent variable and grams of arboreal lichens in the 1- to 2-m stratum as the independent variable.

For the multiple logistic regression models (terrestrial forest and alpine), the Wald backward-elimination procedure (SPSS Version 8.0) was used to identify the most parsimonious model for describing site selection of cratering locations (Menard 1995). As recommended by Bendel and Afifi (1977), the α of 0.05 was relaxed to 0.15 during the backward-elimination procedures to reduce the likelihood of excluding important variables. We used Pearson correlation values and tolerance scores with a collinearity threshold of 0.20 (Menard 1995) to diagnose the presence of collinearity amongst the independent variables. Collinearity is an indication of redundancy within the statistical model and can lead to inflated error terms and in extreme cases render matrix inversion unstable (Tabachnick and Fidell 1996). Although logistic regression is robust to most multivariate assumptions, data and model screening procedures (leverage statistics, Pearson standardised residuals) were employed as recommended by Menard (1995) and Tabachnick and Fidell (1996); procedures were reported only if model validity was threatened.

For both terrestrial and arboreal feeding sites, we used the proportional reduction in the χ^2 statistic (R^2_L) to indicate how much the inclusion of each significant explanatory variable improved model fit; the higher the value, the better the measured variables explain the differences between selected and random sites (i.e., analogous to the linear regression r^2) (Hosmer and Lemeshow 1989). Odds ratios were used to interpret the effect of each explanatory variable on the response variable and are more intuitive than the regression coefficient when discussing the relative strength of each explanatory variable (Hosmer and Lemeshow 1989). Univariate logistic function plots were used to graphically present the

relationships between statistically significant vegetation, debris, and snow variables and the predicted probability of a caribou selecting a feeding site (Tabachnick and Fidell 1996).

To provide a relative measure of the availability of forage species, we used Bonferronicorrected 95% confidence intervals to test differences in mean percent cover of lichens, mosses, grass, and debris between feeding and random sites, and among species (Neter *et al.* 1990). The relationship between tree diameter at breast height (130 cm) and amount of arboreal lichens was investigated with a simple linear regression equation. An α of 0.05 was used for all tests of statistical significance.

RESULTS

Over the two winters we examined caribou feeding sites along 85 forest transects and 23 alpine quadrats (Fig. 2.1). We sampled 461 terrestrial (206 feeding, 255 random) and 356 arboreal (102 feeding, 251 random) sites in the forest and 136 sites (70 feeding, 66 random) in the alpine. Nine distinct species of *Cladina*, *Cladonia*, *Cetraria*, and *Peltigera* lichens and eight composite groupings of lichen and moss types were regularly observed at alpine and forested terrestrial feeding sites (Table 2.1). *Cladina stellaris*, *Nephroma arcticum*, *Solorina crocea*, and *Dactylina arctica* were also noted, but because they occurred at <10 feeding sites and could not be easily grouped with another lichen species, they were excluded from the analysis. *Bryoria* spp. were the dominant arboreal lichens.

Feeding Sites in Forest Locations

Average snow depths at cratered sites ranged from 23 - 97 cm and at random sites from 27 - 102 cm. Average snow hardness at cratered and random sites ranged from 0.27 - 3.19 g/cm² and 0.25 - 4.2 g/cm² and snow density from 5.0 - 46.97 g/cm³ and 6.25 - 40.0 g/cm³, respectively. Table 2.1. Lichen and moss species and groups identified at terrestrial feeding sites used by caribou and random sites; classification is based on ease and reliability of field identification, and frequency of occurrence in northcentral British Columbia (December 1996 – April 1998).

Ground Cover	Description	Location
Cladina mitis	Distinct lichen class.	Forest-Alpine
Cladina rangiferina	Distinct lichen class.	Forest-Alpine
Cetraria islandica	Distinct lichen class.	Alpine
Cetraria ericetorum	Distinct lichen class.	Forest
Cetraria nivalis	Distinct lichen class.	Alpine
Cetraria cucullata	Distinct lichen class.	Alpine
Peltigera aphthosa	Distinct lichen class.	Forest
Peltigera malacea	Distinct lichen class.	Forest
Cladonia uncialis	Distinct lichen class.	Forest
Cladonia spp.	Composite class consisting of rarely found and unidentified Cladonia species; composite of C. uncialis, C. ecmocyna, C. gracilis, C. cenotea, C. chlorophaea, C. cornuta, C. crispata, C. deformis, C. fimbriata, C. multiformis, C.	Forest-Alpine
	pyxidata, and C. sulphurina.	
Cladonia ecmocyna	Composite class consisting of <i>C. ecmocyna</i> with a lesser component of <i>Cladonia gracilis</i> (J. Marsh, pers. Comm.).	Forest
Stereocaulon alpinum	Composite class consisting primarily of S. alpinum with a small component of S. glareosum, S. tomentosum, and S. paschale (J. Marsh pers Comm.)	Forest-Alpine
Thamnolia spp.	Composite class consisting of T. vermicularis and T. subuliformis.	Alpine
Lichen spp.	Composite class consisting of unidentified lichens.	Alpine
Peltigera spp.	Composite class consisting of <i>P. aphthosa</i> and <i>P. malacea</i> .	Alpine
Cladina stellaris	Rare and ornitted from analysis.	Forest
Nephroma arcticum	Rare and omitted from analysis.	Forest
Solorina crocea	Rare and omitted from analysis.	Forest
Dactylina arctica	Rare and omitted from analysis.	Alpine
Pleurozium schreberi	Composite class consisting primarily of P. schreberi with a lesser component of Hylocomium splendens and Ptilium crista- castrensis.	Forest
Moss spp.	Composite class consisting of unidentifiable or rare moss species and liverworts.	Forest-Alpine
Debris	Rock, litter, and composting vegetative matter.	Forest-Alpine

Percent cover of all of the lichen species was greater at cratered sites, but nonoverlapping confidence intervals revealed differences only for *Cladina mitis* and *Cladonia* spp. (Fig. 2.3). At cratered sites *C. mitis* and *Cladonia* spp. averaged 24.7% (\pm 1.40 SE) and 14.0 \pm 0.90%, respectively, relative to 12.9 \pm 1.04% and 7.1 \pm 0.60% at random sites. In contrast, random sites had a greater percent cover of mosses and debris than crater sites. *Pleurozium schreberi* was the only non-lichen variable to differ significantly, having an average percent cover of 10.6 \pm 1.25% and 26.2 \pm 2.19% for cratered and random sites, respectively. Canopy closure ranged from an average of 27.1 \pm 1.85% at cratered sites to 28.8 \pm 1.61% at random sites.

The multiple logistic regression model used to describe site selection of terrestrial feeding sites in the forest correctly classified 71.2% of the cases as cratered or random sites and explained 20.2% ($R^2_L = 0.202$) of the between-feeding-site variation (Table 2.2). Snow depth, percent cover of debris, *C. mitis, Cladonia* spp., and the two moss classes significantly contributed to the statistical differentiation of cratered and random sites (Fig. 2.4). *Cladonia* spp. had the highest odds ratio at + 4.3% and the greatest influence on the selection of cratering sites by caribou (Table 2.2, Fig. 2.4). Snow depth had the least influence on selection of a feeding site; in this case, the odds ratio implies that a 1-cm increase in snow depth will reduce the likelihood that a caribou will crater by 2% (Table 2.2, Fig. 2.4).

Feeding site selection may not be linked specifically to the presence or absence of moss or individual lichen species. The tolerance scores for each variable in the model were greater than 0.20, but several of the variables were significantly bivariate correlated. *Cladina mitis* was negatively correlated with debris (r = -0.227), *P. schreberi* (r = -0.403), and moss spp. (r = -0.155), and *Cladonia* spp. was correlated with *P. schreberi* (r = -0.370).



Figure 2.3. Percent ground cover of lichens at random sites (n = 255) and sites cratered by caribou (n = 206) in forested locations of northcentral British Columbia (December 1996 – April 1998). Error bars represent Bonferroni-corrected 95% confidence intervals and asterisks designate statistically significant differences between corresponding sites.

TERRESTRIAL FEEDING SITES (<i>n</i> = 460; model χ^2 = 128.58, <i>df</i> = 6, <i>P</i> < 0.001)							
Variables Retained in Model	В	SE	Р	Odds Ratio			
Moss spp.	-0.030	0.011	0.007	-3.0%			
Debris	-0.026	0.008	0.002	-2.5%			
Pleurozium schreberi	-0.023	0.006	<0.001	-2.3%			
Snow Depth	-0.021	0.007	0.002	-2.0%			
Cladina mitis	0.024	0.008	0.003	+2.4%			
Cladonia spp.	0.042	0.011	<0.001	+4.3%			
Constant	1.173	0.565	0.040				
Variables Excluded From Model							
Canopy Closure			0.289				
Snow Hardness			0.174				
Snow Density			0.325				
Cladina rangiferina			0.165				
Cladonia ecmocyna			0.155				
Cladonia uncialis			0.961				
Cetraria ericetorum			0.996				
Stereocaulon alpinum			0.862				
Peltigera aphthosa			0.456				
Peltigera malacea			0.642				

Table 2.2. Summary of multiple logistic regression model derived using the Wald backwardelimination procedure for terrestrial and arboreal feeding sites used by caribou in forested locations in northcentral British Columbia (December 1996 – April 1998).

ARBOREAL FEEDING SITES ($n = 356$; model $\chi^2 = 17.01$, $df = 1$, $P < 0.001$)						
Variable	B	SE	P	Odds Ratio		
Bryoria spp. (g/1 – 2 m)	0.095	0.026	<0.001	+9.9%		
Constant	-1.183	0.145	<0.001			

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Figure 2.4. Predicted probability of caribou of the Wolverine herd of northcentral British Columbia (December 1996 – April 1998) foraging at terrestrial or arboreal forest sites relative to the percent cover of vegetation or debris (measured in units of 6.25% cover), biomass of arboreal lichens (g), and snow depth (cm).

When choosing to browse arboreal lichens, caribou selected those trees with a greater biomass of *Bryoria* spp. than found in randomly available trees. On average, selected trees had 4.9 g (\pm 0.74 SE) in the 1- to 2-m stratum versus 2.3 \pm 0.24 g for random trees. *Pinus contorta* was the dominant tree species at both selected (81%) and random sites (90%). *Bryoria* spp. was a meaningful predictor of what trees caribou chose to browse (Table 2.2, Fig. 2.4). The logistic regression model accounted for only a small amount of the variation between feeding and random sites ($R^2_L = 0.039$); however, 72.2% of the cases were correctly classified as feeding or random sites. The odds ratio indicated that a 1-g increase in the amount of *Bryoria* spp. would increase the likelihood of a caribou foraging by 9.9%. There was a significant, but weak linear relationship between tree diameter and arboreal lichen abundance (F = 17.495, df = 250, P < 0.001, $r^2 = 0.066$).

Feeding Sites in Alpine Locations

Average snow depth per quadrat ranged from 3 - 37 and 0 - 69 cm, and snow hardness between 0.54 - 28.89 and 0 - 30.38 g/cm² for cratered and random sites, respectively. Percent cover of lichen classes tended to be greater at cratered sites, but not significantly so, with *C*. *mitis, Stereocaulon alpinum*, and *Cladina rangiferina* demonstrating the largest differences (Fig. 2.5). Debris was the only variable to illustrate a significant difference in mean percent cover, being more prominent at random ($\overline{x} = 37.3\% \pm 3.30$ SE) than cratered sites (20.0 ± 1.99%).

The multiple logistic regression model used to describe site selection of terrestrial feeding sites in the alpine accounted for 31% ($R^2_L = 0.31$) of the between-site variation, and correctly classified 76.5% of the cratered and random sites (Table 2.3). Statistically significant variables were snow depth, percent cover of C. mitis, C. rangiferina, Cetraria cucullata, Cetraria nivalis, Thamnolia spp., and S. alpinum (Fig. 2.6). Thamnolia spp. had the



Figure 2.5. Percent ground cover of lichens at random sites (n = 66) and sites cratered by caribou (n = 70) in alpine locations of northcentral British Columbia (December 1996 – April 1998). Error bars represent Bonferroni-corrected 95% confidence intervals and asterisks designate statistically significant differences between corresponding sites.

TERRESTRIAL FEEDING SITES (n = 136; model $\chi^2 = 58.75$, df = 9, P < 0.001) Variables Retained in Model B SE Ρ **Odds Ratio** Cetraria islandica -0.106 0.062 0.085 -10.1% -0.071 0.023 0.002 -6.8% Snow Depth Stereocaulon alpinum 0.036 0.015 0.014 +3.7% Cetraria nivalis 0.060 0.026 0.022 +6.2% Snow Hardness 0.064 0.040 +6.6% 0.112 0.087 0.023 Cladina mitis <0.001 +9.1% Cetraria cucullata 0.095 0.033 0.004 +10.0% Cladina rangiferina 0.159 0.052 0.002 +17.2% 0.240 0.119 0.044 Thamnolia spp. +27.1% Constant -1.888 0.699 0.007 Variables Excluded From Model Debris 0.626 Cladonia spp. 0.146 Peltigera spp. 0.900 Lichen spp. 0.464 0.700 Moss spp. 0.216 Poaceae

Table 2.3. Summary of multiple logistic regression model derived using the Wald backwardelimination procedure for terrestrial feeding sites used by caribou in alpine locations in northcentral British Columbia (December 1996 – April 1998).



Figure 2.6. Predicted probability of caribou of the Wolverine herd of northcentral British Columbia (December 1996 – April 1998) cratering at alpine sites relative to the percent cover of vegetation or debris (measured in units of 6.25% cover) and snow depth (cm).

highest odds ratio at + 27.1% and the greatest influence on the selection of feeding sites followed by C. rangiferina, and C. cucullata at + 17.2 and + 10%, respectively (Table 2.3, Fig. 2.6). Cladina mitis and C. rangiferina (r = 0.171) and C. rangiferina and C. nivalis (r = -0.239) were the only significant bivariate correlations for variables identified as important by the logistic regression model. Most cover types were highly correlated with debris with the highest correlation occurring with S. alpinum (r = -0.453).

DISCUSSION

Past studies have found that most continental populations of caribou and reindeer forage primarily on fruticose lichens throughout the winter (Pegau 1968, Helle and Saastamoinen 1979, White and Trudell 1980, Klein 1982, Boertje 1984, Skogland 1984, Cichowski 1993, Terry *et al.* 2000), and that snow conditions may restrict access to that food source (Laperriere and Lent 1977, Skogland 1978, Duquette 1988, Brown and Theberge 1990). With few exceptions (e.g., Bergerud 1974*a*, Thing 1984, Frid 1998), however, most investigators failed to classify forage beyond food type or genus or to consider the interaction between snow conditions and forage selection. Furthermore, the lack of comparative control sites has frequently resulted in the analysis of forage use as opposed to selection by the animals. We attempted to improve upon those studies by investigating the influence of lichen species in combination with the limiting effects of snow on the fine-scale selection of feeding sites in forested and alpine areas.

Selection of Feeding Sites by Caribou

Using data collected over two years across a broad geographic area, we developed statistically significant models to predict the selection by woodland caribou of terrestrial and arboreal feeding sites in forested locations, and terrestrial feeding sites in alpine areas. All

three of the models had relatively low explanatory power (R^2_L) indicating that the independent variables (i.e., ground cover and snow condition) captured only a small proportion of the differences between selected and random sites. We believe that this is a consequence of four sources of error in our sampling design and analysis. First, it is likely that we did not recognise, measure, or include all of the variables that are important to the cognitive processes that caribou use when choosing where to feed. For instance, we allowed the backwardelimination procedure to determine the most parsimonious model. This excluded certain variables that contributed relatively little new statistical information, but which may have been of some importance to explaining overall differences between the selected and random sites. It is also possible that model aptness was affected by aggregate variables, such as *Cladonia* spp., which may have masked or confounded individual lichen species that were highly selected or avoided by caribou. Frid (1998) identified a similar limitation in his study of crater site selection by woodland caribou.

Second, although we are confident in our ability to identify feeding sites, it is possible that some sites were incorrectly classified. Caribou may have cratered but not fed at certain terrestrial sites, or trees may have been incorrectly classified as browsed when they were not. Sampling error also may have been introduced by classifying our random sites as non-selected sites when in actuality caribou did not make a choice, but passed by that location for reasons not directly related to a foraging decision (e.g., satiation, minor disturbance). Furthermore, because caribou remain in an area for some period, our random samples may contain a proportion of sites that would have been cratered at a later date. To reduce this source of error, we should have chosen random sites where it could be confirmed that a caribou had made a decision not to crater, such as unexcavated sniffing holes (e.g., Helle 1984). Because snow conditions often made the identification of sniffing sites difficult, this approach was abandoned in favour of sampling random locations along the tracks.

Third, we assumed that the lichens remaining at a sampled feeding site were representative of the pre-cratering lichen cover, although the foraging and digging actions of caribou may have resulted in our underestimating the percent cover of lichens at feeding sites. To minimise this bias, we chose percent cover, as opposed to biomass, as our measure of relative lichen availability. Caribou rarely cropped the entire lichen thalus, thus using a point frame with 6.25% increments we were able to measure accurately and precisely percent cover by species at feeding sites.

Fourth, selection strategies of the caribou may have changed during or between winters, confounding the importance of individual variables. For example, nutritional requirements may vary over time or abundance of lichen species may vary spatially, resulting in temporally variable selection patterns. This, and the sources of error listed above did not invalidate our results, but rather forced us to test a more conservative model, which may have decreased the likelihood of obtaining significant differences and lowered the R^2_L values.

Influence of Vegetation on Feeding Site Selection

Numerous conclusions, in some cases contradictory, have been reported by researchers using field studies or cafeteria-type experiments to investigate preference and selection of lichen species by caribou and reindeer (see DesMeules and Heyland 1969). Bergerud and Nolan (1970) concluded that comparing food lists between areas or populations is of little value because caribou are adapted to eat most species of plants and, therefore, localised studies reflect only what is available rather than universal selection criteria by *Rangifer*. We also recognise that there may be inter-population variability, but feel that our results placed in the context of other works add to the understanding of the similarities and plasticity in foraging habits of these animals.

Our data indicate that northern woodland caribou select cratering sites based on the percent cover of several lichen species. In most cases our results agree with other studies. For example, C. mitis is commonly reported as being preferred or selected by caribou and reindeer (Helle and Saastamoinen 1979, Helle 1984, Lance and Mills 1996). Cafeteria-style experiments have concluded that woodland caribou (R. t. caribou) preferred a mixture of C. stellaris, C. mitis, and Cladonia uncialis, followed by C. rangiferina, Cetraria islandica, and Stereocaulon spp. (DesMeules and Heyland 1969); and that reindeer exhibited a preference for C. stellaris, C. rangiferina, Stereocaulon paschale, Cetraria richardsonii, and Peltigera aphthosa, in that order (Holleman and Luick 1977). Analysis of faecal samples from the Porcupine Caribou Herd (R. t. granti) indicated that their winter diet consisted predominantly of Cladonia and Cladina spp., followed by Stereocaulon, Cetraria and Peltigera spp.; the proportions of these species, however, may have been more related to availability than to selection (Russell et al. 1993). Dannell and others (1994) assigned high preference rankings to Cladina arbuscula, which is morphologically indistinguishable from C. mitis, C. rangiferina, and S. paschale and a low ranking to P. schreberi. Research by Frid (1998) in the southern Yukon is the most comparable to ours in method and species designation. He reported that the probability of a woodland caribou digging a crater increased as the percent cover of Cladonia spp., C. mitis, C. cucullata, and C. islandica increased, but the amount of C. rangiferina, C. nivalis, Peltigera spp., and Stereocaulon spp. had no effect. With a few exceptions, mostly being the lichens selected in the alpine, those results are in accordance with the findings of our study.

Through our conclusions we do not infer causal relationships between feeding site selection and the importance of individual lichen and moss species. We emphasise this *caveat* because of the high correlations between several of the significant lichen and moss species. For example, where the model shows a strong effect for lichens and mosses at forested sites, caribou may be selecting for lichens or may be avoiding mosses; the statistical importance of one may be the product of the presence or absence of the other. *Pleurozium schreberi* may be an important discriminating variable only because it occurs where *C. mitis* and *Cladonia* spp. are not found, not because caribou avoid sites where it is found. High negative correlations likely occur because these species of mosses and lichens have distinct light and moisture requirements and, therefore, grow in different locations (Robinson *et al.* 1989, Ahti and Oksanen 1990).

Interpretation of our results is complicated by the inconsistencies in selected lichen species across forested and alpine sites. Most notably, *C. rangiferina* and *S. alpinum*, which were important discriminating variables at alpine sites, were not selected, even though available, by caribou at forested sites. Our results from the forested sites agree with most of the above cited studies that have shown that these species, especially *Stereocaulon* spp., are relatively less palatable. This discrepancy suggests that depending on location, forest or alpine, animals may have different foraging strategies.

We observed that the majority of the lichens found in forested areas appeared more vigorous and occurred in greater abundance than those in the alpine (Figs. 2.3 and 2.5; C.J. Johnson, unpubl. data). Furthermore, at alpine sites clumps of lichen were more unevenly distributed, being separated by bare areas of rock or debris, as reflected by the high negative correlation between debris and *S. alpinum*. Caribou in the less productive alpine areas may be less selective, taking advantage of those sites with the greatest amount of lichen regardless of

palatability. The use of a larger number of species and less palatable yet more prevalent lichens, such as *S. alpinum*, may be an adaptation to a less productive environment where foraging decisions are based largely on availability. This is consistent with the hypothesis of Bergerud and Nolan (1970) that caribou are adaptive and flexible in the forage species they select.

In our study area, woodland caribou in the forest fed on both terrestrial and arboreal lichens; although, based on feeding site frequency, it appeared that cratering is the predominant activity (C.J. Johnson, unpubl. data). Comparable findings were reported for our study animals by Wood (1996) and for other woodland caribou populations (Cichowski 1993). Selection of arboreal lichens may increase following some threshold in accessibility or abundance of terrestrial lichens (Bergerud 1974*a*, Sulkava and Helle 1975, Helle and Saastamoinen 1979, Helle 1984, Vandal and Barrette 1985).

Our study animals selected trees, principally *P. contorta*, that supported the greatest biomass of arboreal lichens. Across the transects we sampled, which occurred mainly in *P. contorta* or mixed *P. contorta* – *P. glauca* x *P. engelmannii* stands, the predominant epiphyte was *Bryoria* spp. with only trace amounts of *Alectoria sarmentosa*. *Bryoria* spp. has been reported as a highly palatable food type (Dannell *et al.* 1994) and studies of the mountaincaribou ecotype have revealed preference for this lichen group over other alectorioid species (Rominger and Robbins 1996). The lack of a strong linear relationship between amount of lichens within the 1- to 2-m stratum and tree diameter suggests that lichen growth and the selection of arboreal feeding sites are related to factors other than tree size.

Influence of Snow Conditions and Canopy Closure on Site Selection

Although caribou are well adapted to deep snow environments (Telfer and Kelsall 1984), snow can hinder both the accessibility and detection of forage. Previous studies

reported the threshold depth for cratering by caribou and reindeer as 50 to 80 cm (Formozov 1946, Pruitt 1959, Stardom 1975, LaPerriere and Lent 1977, Helle and Saastamoinen 1979, Darby and Pruitt 1984), although craters as deep as 123 cm have been reported (Brown and Theberge 1990). The ability to crater is also influenced by other snow conditions including hardness and ice layers (Formozov 1946, Skogland 1978, Helle and Tarvainen 1984, Adamczewski *et al.* 1988, Brown and Theberge 1990). Bergerud and Nolan (1970) concluded that Newfoundland caribou could not smell terrestrial lichens under snow exceeding 25 cm in depth, but Helle (1984) reported that reindeer in Finland detected lichens through a snow thickness of 91 cm. Over our two-year study period, the maximum crater depths we observed were 97 and 50 cm for forested and alpine sites, respectively.

Canopy closure increases snow interception and correspondingly reduces snow depth and the effort necessary to expose lichens (Schaefer 1996). Across the range of the Wolverine herd, canopy closure did not affect the selection of cratering sites. In contrast, Cichowski (1993) and Lance and Mills (1996) found that cratering occurred most often in forested areas with more open canopies. In both cases, however, there was an interaction with the presence of terrestrial lichens suggesting that open canopy stands were more productive. Our analysis used a moosehorn coverscope as opposed to a visual estimate of canopy closure (Cichowski 1993, Lance and Mills 1996). The latter estimates closure of a much larger portion of the canopy (i.e., scale of the stand) than the coverscope (i.e., scale of the feeding site). This likely accounts for the differences between our results and other studies.

If caribou attempted to minimise the energetic costs of cratering, then selection of sites with shallower, softer, and less dense snow would be expected as long as the additional search time did not exceed the cost of finding more accessible lichens (Fancy and White 1985). In agreement with this premise, LaPerriere and Lent (1977) found snow depths and hardness to be less in feeding areas relative to adjacent uncratered areas. At the individual feeding sites we surveyed, caribou appeared to partially meet these criteria by selecting locations to crater where snow depths were shallower than random sites. The greatest effect, as indicated by the odds ratio and univariate logistic plots (Fig. 2.4, 2.6), was in the alpine where, because of uneven topography and drifting snow, we observed snow depths to be much more variable. Neither snow hardness nor density appeared to influence crater site selection. In other studies, Frid (1998) found no effect of snow depth or penetrability on crater site selection, but attributed this to the relatively low snow depths of his study area ($\bar{x} = 31.5$ cm ± 5.8 SD). Cichowski (1993) found that crater sites had greater snow depths, but reduced penetrability when compared to random sites. Duquette (1988) studying the Porcupine herd, reported that snow depths were deeper along migration trails than within adjacent feeding areas, and snow hardness did not differ between the two areas.

MANAGEMENT IMPLICATIONS

Our research suggests that particular scale-specific habitat characteristics may be important to manage for, or consider during an assessment of the winter range of northern woodland caribou. Forested areas should be managed to contain terrestrial lichen mats with a high percent cover of *C. mitis*, *Cladonia* spp., and a high biomass of arboreal lichens (*Bryoria* spp.). *Cladina mitis*, *C. rangiferina*, *C. cucullata*, *C. nivalis*, *S. alpinum*, and *Thamnolia* spp. are important species that should be considered when assessing and managing alpine areas. Because snow may limit access to forage and restrict use to specific areas of the range, snow depths should be considered in conjunction with the abundance of lichens when assessing the suitability and availability of caribou winter range. Our results describe selection of foraging sites by caribou at one explicitly defined scale, the individual feeding site. The relationship between an organism and its environment, however, is often complicated by multi-scale influences. Factors from both finer and broader scales may act in unison to elicit responses that may not be detected by measurements designed to record responses at one particular scale. To accommodate the recording and understanding of these interactions, a multi-scale hierarchical approach should be pursued (Senft *et al.* 1987, Kotliar and Wiens 1990, Wiens *et al.* 1993*a*). This study was designed to measure just one of many scales that may be relevant to how caribou perceive and respond to their environment (Johnson 1980). The results and conclusions must, therefore, be viewed within the context of other scale-sensitive influences on movement and distribution across the landscape (e.g., large-scale distribution of snow, habitat patch configuration, predation risk), which are necessary considerations when managing winter range of woodland caribou (Cumming 1992).

CHAPTER 3 - FORAGING ACROSS A VARIABLE LANDSCAPE: BEHAVIOURAL DECISIONS MADE BY WOODLAND CARIBOU AT MULTIPLE SPATIAL SCALES¹

SUMMARY

Foraging behaviour can vary across both time and space, possibly obscuring animalhabitat relationships that are based on observations insensitive to that variability. Yet few studies have focussed on how factors that influence foraging behaviour differ between scales or how to integrate behaviour across scales. We examined the foraging behaviour of woodland caribou relative to the spatial and temporal heterogeneity of their environment. We assessed (1) whether caribou altered their behaviour over time while making trade-offs between forage abundance and accessibility; and (2) whether foraging decisions were consistent across spatial scales (i.e., as scale increased, similar decision criteria were used at each scale). We discuss whether caribou adjusted their behaviour to take advantage of changing forage availability through time and space. At the scale of the feeding site (as revealed by discriminant function analyses), caribou in both forested and alpine (above treeline) environments selected sites where the biomass of particular lichen species was greatest and snow the least deep. Caribou did not select those species with the highest nutritional value (i.e., digestible protein and energy) in either area. Where snow depth, density, and hardness limited access to terrestrial lichens in the forest, caribou foraged instead at those trees with the greatest amount of arboreal lichens. Selection of lichen species and the influence of snow differed across time, indicating that in this system the abundance or accessibility of forage temporally influenced foraging behaviour. A path analysis of forest data and multiple regression analysis of alpine data were used to test the hypothesis that variables important at

¹ Chapter has been submitted for publication with the following authorship: C.J Johnson, K.L. Parker, and D.C. Heard.

the scale of the feeding site explained foraging effort at the scale of the patch. For forest patches, our hypothesised model reliably explained foraging effort, but not all variables that were statistically important at the scale of the feeding site were significant predictors at the scale of the patch. For alpine patches, our hypothesised model did not explain a statistically significant portion of the variation in the number of feeding sites within the patch, and none of the individual variables from the feeding site remained statistically significant at the patch scale. The incongruity between those variables important at the scale of the feeding site and those important at the patch revealed that spatial scale affects the foraging decisions of woodland caribou. At the scale of the landscape, a trade-off existed between forage abundance and accessibility. Relative to the alpine, caribou in the forest foraged at feeding sites and patches with greater amounts of less variably distributed lichens, but deeper less variable snow depths. Considering the behavioural plasticity of woodland caribou, there may be no distinct advantage to foraging in one landscape over the other.

INTRODUCTION

Foraging behaviour by animals is a series of consecutive decisions arising from choices such as what to eat, when to eat, and where to eat. Although simple from a reductionist perspective, those choices and resulting decisions are a complex function of interactions involving changes in the environment, and changes in the past, present, and future internal states of animals (Cheverton *et al.* 1985, Mangel and Clark 1986, Ludwig and Rowe 1990, Sinclair and Arcese 1995, Bowyer *et al.* 1998). Most mammalian herbivores demonstrate complex behavioural patterns in response to multidimensional internal and external stimuli. For example, relative to foraging behaviour, animals must fulfil a range of requirements and also assess risks such as locating and moving amongst patches of forage (e.g., Vivås and Sæther 1987, Gillingham and Bunnell 1989, Langvatn and Hanley 1993, Forchhammer 1995, Gross *et al.* 1995), satisfying intake and nutritional requirements (Trudell and White 1981, Owen-Smith and Novellie 1982, McNaughton 1988, Gillingham *et al.* 1997), minimising the probability of encountering or being captured by a predator (Lima and Dill 1990, Nelson and Mech 1991, Seip 1992, Hughes and Ward 1993, Bowyer *et al.* 1999, Kie 1999), and weighing the costs and benefits of inter- and intra-specific competition (Risenhoover and Bailey 1985, Hughes *et al.* 1994, Movlar and Bowyer 1994, Roberts 1996). Optimal foraging theory assumes that animals will make the appropriate choices from this complex and often conflicting range of requirements and risks in accordance with maximising nutrient and energetic rewards while minimising costs (MacArthur and Pianka 1966, Charnov 1976, Engen and Stenseth 1984). The decision-making process for free-ranging animals faced with variable and stochastic environments is not, however, as simple as optimal foraging hypotheses developed for controlled experiments would suggest (Schluter 1981, Mangel and Clark 1986).

Predictions of optimality are difficult to test when observed behaviour is the product of complex decisions made by animals responding to multiple variables. Those decisions, hereafter referred to as trade-offs, characterise naturally functioning systems. Evidence of this real-world complexity spans taxonomic lineages and has been demonstrated by researchers studying predation risk (e.g., Lima 1985, Lima *et al.* 1985, Gilliam and Fraser 1987, Sih *et al.* 1990, Walters and Juanes 1993, Kotler and Blaustein 1995, Cowlishaw 1997), thermal cover (Schmitz 1991), and trade-offs between forage selection and nutritional and allometric benefits (Spalinger *et al.* 1988, Vivås *et al.* 1991, Palo *et al.* 1992, Shipley and Spalinger 1992). Solutions have been presented to model and test behaviour in complex environments where trade-offs occur (Mangel and Clark 1986, Grünbuam 1998, Mysterud and Ims 1998).

Describing the behavioural choices available to an animal is further complicated by the identification of the appropriate spatial and temporal scales. Turner and others (1989) defined scale as the spatial or temporal dimensions of an object or process, characterised by both grain and extent. The study of animal behaviour is founded on the observations that each species responds to its surroundings from its own unique suite of spatial and temporal scales, and that explanations for observed behaviour differ depending on the scale of measurement (Morris 1987, 1992; Wiens 1989, Levin 1992, Bowyer *et al.* 1996). Allen and Hoekstra (1992) argue that it is necessary to consider several scales simultaneously: the one in question, one below for mechanisms, and one above for context.

There is a rudimentary appreciation of scale inherent within optimal foraging theory (Danell et al. 1991). The ideal-free distribution was one of the first theoretical recognitions of foraging as a spatial process (Fretwell and Lucas 1970). Mathematical models of prey and patch choice were later developed, and tested empirically. Although interactions and linkages between different scales were not quantified, those early studies served as a foundation by which hierarchy theory (Allen and Star 1982) could be applied to the study of foraging behaviour (Senft et al. 1987). In recent years, a multi-scale hierarchical approach has been suggested as a means by which to model and investigate foraging behaviour while recognising the importance of perception of scale by animals (Legrende and Demers 1984, Addicott et al. 1987, Blondel 1987, Senft et al. 1987, Kotliar and Wiens 1990, Lavorel et al. 1993, Wiens et al. 1993a, Lima and Zollner 1996). This is an improvement over investigations founded on an arbitrarily defined single spatial scale (Wiens 1989). There has been little quantitative theory or empirical work, however, describing how changes in scale may affect ecological processes (Milne et al. 1989, Turner et al. 1989). Care must be taken to identify the scale at which research findings are applied to avoid erroneous extrapolations of relationships at one

particular scale to smaller or larger scales (Urban *et al.* 1987, Wiens *et al.* 1993*a*, Collins and Glenn 1997, Gustafson 1998). Working at the wrong scale can be as misleading as asserting the incorrect relationships (Allen and Hoekstra 1992).

During winter (December – April), northern woodland caribou occurring in the boreal and sub-boreal forests of central and northern British Columbia, Canada, make foraging decisions that are likely complicated by trade-offs between abundance and accessibility of forage that occur at multiple spatial and temporal scales. Those decisions are dependent on locations on the landscape, daily nutritional state, seasonal energy and protein budgets, and scale-dependent spatial and temporal variation in the environment. Because woodland caribou can be tracked in the snow and their feeding sites identified reliably, these herbivores are an excellent model for investigating complex multi-scale foraging strategies that have evolved within heterogeneous, stochastic landscapes.

We recognise that behavioural decisions are hierarchical, but are unsure of the responses by caribou to the order of that hierarchy (i.e., whether they prioritise decisions first by the small scale (feeding site) or first by the landscape scale). We have, however, organised our model of foraging strategies to progress from small- to large-scales. This allowed us to use all available data (which are numerous for small-scale observations) to investigate decisions at each successively higher level of the hierarchy. At a small spatial scale, caribou select a particular forage species to consume. Although the winter forage consists almost exclusively of lichens, caribou may choose from species differing in morphological structure, growing location, patch size, nutritional content, and abundance (e.g., Ahti 1964, Moser *et al.* 1979, Carroll and Bliss 1982, Robinson *et al.* 1989, Ahti and Oksanen 1990). At a somewhat larger scale, animals choose sites at which to forage. For woodland caribou during winter, this can be either a terrestrial site where the snow must be cratered (excavated) to access lichens

growing on the ground, or an arboreal site where lichens growing on lower tree branches can be browsed directly (Bergerud 1974*a*, Sulkava and Helle 1975, Helle and Saastamoinen 1979, Helle 1984, Vandal and Barrette 1985). Selection for feeding sites has been linked to availability of forage as dictated by accessibility of forage, which is influenced by snow conditions and amount and type of both terrestrial and arboreal lichens (Formozov 1946, Skogland 1978, Helle and Saastamoinen 1979, Helle 1984, Helle and Tarvainen 1984, Adamczewski *et al.* 1988, Brown and Theberge 1990, Cichowski 1993, Frid 1998, Chapter 2).

At the next level, caribou choose patches to concentrate their feeding sites. From a foraging perspective, this could be related to mean abundance of terrestrial or arboreal lichens by species, mean snow conditions relative to other patches, or a trade-off between abundance and accessibility. At an even greater spatial scale, caribou in northcentral British Columbia choose between patches across forested or alpine landscapes. Those locations differ in plant composition and snow conditions, but are closely juxtapositioned, allowing for choice with relatively little additional energetic cost of moving between the two landscapes. Few studies have been conducted at those latter two scales and none have focussed on the integration of foraging behaviour across all four scales.

The objectives of this study were to assess (1) whether caribou exhibited trade-off decisions in response to the temporal or spatial variability of forage and snow conditions; and (2) whether foraging decisions were consistent across scale (i.e., as spatial scale increases, similar decision criteria are used at each scale). We discuss the results of those two objectives in the context of whether caribou adjusted their decisions to maximise nutritional gain and minimise foraging costs through time and space.

Because we have incomplete knowledge of the processes that govern caribou actions, we organised our description of foraging behaviour around the simple rules that we believe an animal should follow when maximising nutritional gain and minimising foraging costs across multiple spatial and temporal scales. This predictive framework has been employed in previous investigations of animal behaviour and provides an *a priori* means by which to organise observations and test foraging strategies (e.g., Ward and Saltz 1994, Gross *et al.* 1995). In defence of the ecological and evolutionary validity of this decision-making strategy, these simple rules are the mechanisms by which animals respond to complex environments and that in some instances these rules approximate the optimal solution to a problem (Janetos and Cole 1981, Green 1984, Bergelson 1985, Bouskila and Blumstein 1992).

The rules that should be adopted by a forager that maximises benefits and minimises costs were developed according to our knowledge of the foraging behaviour of caribou and organised within a spatially oriented, hierarchical decision-making framework based on selection of (1) foraging species, (2) feeding sites, (3) patches within which to feed, and (4) locations across the landscape (i.e., forest or alpine) within which to select patches. We defined a *feeding site* as a discrete terrestrial (50 x 50 cm) or arboreal (1- to 2-m stratum) foraging location; a *patch* as a collection of feeding sites representing the composition and availability of lichens and snow conditions across a 100-m linear distance (forest) or 50 x 50-m (alpine) quadrat; and a *landscape* as a collection of patches with unique ecological factors (e.g., vegetation and animal communities, climate, topography).

Predictions

Relative to the *forage* and *feeding site*, caribou should: (1) select terrestrial lichen species highest in digestible protein and energy; (2) choose feeding sites with less deep, less dense, and less hard snow; (3) choose sites with greater amounts of terrestrial lichens as snow depth, density, and hardness increase: and in the forest (4) begin foraging on arboreal lichens at some threshold in accessibility (snow conditions), choosing those trees with the greatest biomass of lichens.

Relative to the *patch*, caribou should: (5) forage in patches in proportion to the abundance of the lichen species that were selected at the scale of the feeding site; (6) forage on terrestrial lichens to a greater extent in more accessible patches with mean snow conditions that are relatively less deep, dense, and hard; and (7) browse on arboreal lichens in forested patches with unfavourable snow conditions for cratering or low biomass of terrestrial lichens. And, relative to two *landscapes* that differ in lichen abundance and snow conditions, caribou should: (8) choose to forage across the landscape that affords the greatest overall energetic and nutritional benefit.

FIELD METHODS AND DESIGN

Field investigations were as reported in Chapter 2. Briefly, we relocated GPS-collared and uncollared caribou at two- to three-week intervals in both forested and alpine habitats. After identifying an area as containing foraging sites, we measured the percent cover of lichens, mosses, and vascular plants at feeding craters and random locations, the biomass of arboreal lichens (*Bryoria* spp.) at selected and random trees, and snow depth, density, and hardness at each terrestrial site. We used a 16-pin (each pin was marked vertically at 1-cm intervals), 0.5 x 0.5-m point frame to assess the standing height of lichens (Bookhout 1994). We estimated the volume of lichens within each frame by multiplying the area covered by each identified lichen species by its corresponding mean height (Fleischman 1990).

Biomass Estimation

Because caribou remove lichens during foraging, there is the potential to consistently underestimate lichen volume at foraged craters and arboreal feeding sites (Chapter 2). At arboreal feeding sites, caribou removed only small amounts of lichens from one or two branches (i.e., differences in the amounts of arboreal lichens between selected and random trees were difficult to distinguish visually). Assuming that caribou select trees with a greater biomass of lichens, this bias would lessen differences between random and foraged trees, but because it was our impression that only small amounts were removed, removal was unlikely to invalidate our results. At forested terrestrial sites, however, we observed that the lichens were often cropped close to the ground. To provide an estimate of pre-foraged volume, a correction factor was calculated for each lichen species that consistently had a large proportion of its volume removed. We regressed the volume against the corresponding area covered by each species for random and then for cratered sites; confidence intervals were used to test for differences between slopes and intercepts (Lewis-Beck 1980). Where significant, the difference between the slopes of the two equations was multiplied by the area of that particular lichen species for each crater. When added to the measured volume remaining at each crater, this provided an estimate of the volume of lichens that was present before a caribou fed at that site. Volume of terrestrial lichens was converted to biomass (g dry weight/m²) with ratio estimates (Cochran 1977) calculated by Fleischman (1990) for percent cover to biomass for Peltigera spp. and volume (dm^3/m^2) to biomass for all other fruticose lichens.

Forage and Feeding Site Selection

Relative to the selection of forage and feeding sites, we used a discriminant function analysis (DFA) to describe the foraging decisions of caribou (Tabachnik and Fidell 1996). At forested sites, DFA was designed to statistically separate four potential foraging sites: (1) terrestrial lichen feeding or cratering; (2) random terrestrial sites; (3) arboreal feeding; and (4) random arboreal sites. Because trees were not present at alpine locations, that analysis involved only a comparison of two sites: (1) terrestrial lichen feeding; and (2) random

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terrestrial sites. We tested three models for both forested and alpine locations. The first model described feeding sites based on the biomass of lichen species (Table 2.1), area of moss and debris, snow depth, density, and hardness. The second and third models were similar except that lichen biomass within each model was replaced by an interaction term ([lichen biomass x week, calculated from the sampling date] or [lichen biomass x Northing x Easting, UTM geographic locations]) to test whether the foraging behaviour of caribou differed over time or space.

At arboreal feeding and random sites, only the biomass of arboreal lichens was estimated; there was no measurements made specifically beneath the trees for terrestrial lichens or snow conditions. Therefore, those sites could not be compared directly to terrestrial feeding or random sites because different variables were measured. To allow a comparison of terrestrial versus arboreal feeding choices, lichen biomass and snow conditions at all terrestrial sites associated within the 100-m transect were averaged and those values were applied during our analysis to the arboreal feeding and random sites. Similarly, the average biomass of arboreal lichens was applied to the craters and terrestrial random sites on the same transect. In effect, this recombination of measured variables allowed us to compare those sites chosen by caribou to random sites of the same behaviour (terrestrial or arboreal) as well as to the alternative feeding behaviour.

We used a χ^2 statistic to test the significance of the successive discriminant functions (canonical roots) generated by the four-group model. Model reliability was further assessed using the explained between-group variance, and non cross-validated classification results (Williams 1983, Williams *et al.* 1990, Tabachnik and Fidell 1996). Within each function, differences between feeding and random sites were interpreted from a visual examination of group centroid plots (Tabachnik and Fidell 1996). The importance of the individual variables (vegetation, snow) in differentiating the feeding and random sites was assessed with parallel discriminant ratio coefficients (DRC, Thomas and Zumbo 1996). Variables of importance were ranked in ascending order; a variable was considered unimportant if its discriminant ratio coefficient was below 1/(2p), where p represents the number of variables in the model (Thomas and Zumbo 1996). To assess whether a relationship existed between the potential energetic cost of digging a crater and the biomass of excavated lichens, each statistically important snow measure was regressed against each important lichen species.

Patch Selection

We examined two relationships at the scale of the patch. First, we investigated the importance of vegetation and snow on the foraging efforts and patch use by caribou. Second, we tested whether foraging relationships and selection strategies used by caribou at the scale of the feeding site were related to foraging strategies at the scale of the patch. For both questions we assumed a priori that a linear relationship existed between the importance of each variable at the scale of the feeding site and foraging effort, as determined by the number of feeding sites per transect or quadrat in the patch. Importance reflects the relative influence of each independent variable on the discrimination of groups (i.e., feeding locations) within the DFA. For example, if the lichen Cladina mitis was important at the feeding site, then as biomass of C. mitis increased, there should have been a correspondingly greater foraging effort (i.e., more craters) in patches with more C. mitis. We used a path analysis to determine if a linear multi-scale relationship existed between feeding sites (terrestrial and arboreal) and patches in the forest, and to measure the importance of individual variables on patch selection (Mitchell 1992, Shipley 1997). Only one dependent variable (number of craters) was measured at alpine patches, and therefore, we used a multiple regression analysis to address previous objectives. The results of the discriminant function analyses were used to select

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important vegetation or snow variables and specify relationships within the path analysis and multiple regression models. Because the number of animals at a particular location also may explain differences in feeding intensity, the number of animals at each patch during the time of sampling also was included as an independent variable. Where animals were not sighted, the average number of caribou typically occurring within a group during winter was used (Wood 1996, C.J. Johnson, unpubl. data). To accommodate the constraint of time on foraging behaviour and recognise that an animal can not feed at two places simultaneously, the number of craters was used as an explanatory determinant of the number of arboreal feeding sites.

For the path analysis of scale-sensitive selection, population parameters were estimated with the generalised least squares method (Ullman 1996). Model fit was evaluated using a χ^2 statistic with the desired outcome being a nonsignificant difference between the sample correlation matrix and the estimated population correlation matrix. Because this statistic is sensitive to sample size (Ullman 1996), the Joreskog Adjusted Goodness of Fit Index, McDonald's Index of Noncentrality, the Steiger-Lind RMSEA Index, and the root mean square standardised residual also was used to assess model fit. Good fit is indicated by values >0.95 for the former two indices, and by values <0.05 for the latter two indices (StatSoft, Inc. 1997). The standardised path coefficient (analogous to the Beta coefficient of multiple regression) represented the contribution to the model of each independent variable and was tested with the asymptotic normal statistic (*T*, StatSoft, Inc. 1997).

Landscape Selection

At the largest spatial scale, selection by caribou for feeding sites and patches was assessed between two distinct landscapes: alpine and forest. We tested whether animals that spent the winter in one of those two areas chose an environment with greater or less biomass and variability of important lichen species, and more or less extreme and variable snow conditions. Results of investigations performed at scales of the feeding site and patch were used to select the lichen species and snow conditions that were included in the landscape analyses. From the scale of the feeding site, differences were tested for all terrestrial feeding sites between landscapes. From the scale of the patch, average lichen and snow conditions of both feeding and random sites across all transects or quadrats were compared between landscapes. Independent *t*-tests calculated with separate group variances were used to test for differences in mean biomass of important lichen species (as defined by analyses at the scale of the forage species) and snow conditions between landscapes. The coefficient of variation (CV) served as a measure of lichen and snow variability across the two landscapes.

All statistical tests were performed with STATISTICA (Release 5.1, StatSoft, Inc. 1997) and were considered significant at an α of 0.05. Where appropriate, effect sizes are reported as a measure of practical significance (Cohen 1992, Kirk 1996). Effect-size statistics eliminate the confounding effects of sample size when illustrating group differences or the strength of relationships between variables. Cohen (1992) defined a medium effect size as one that is visible to the naked eye of a careful observer, a small effect size as one that is noticeably smaller than medium but not so small as to be trivial and a large effect size as the same distance above medium as small was below. We used the effect size index r (product moment correlation) for the DFA and f^2 (multiple partial correlation) for the regression analyses, where 0.10, 0.30, and 0.50 and 0.02, 0.15, and 0.35 represent small, medium, and large effect sizes, respectively. Variables were transformed as necessary to improve normality and reduce the influence of outliers. Variables used in the path analysis, regression analyses, and confidence intervals were tested for independence with the Durbin-Watson d statistic, a residual correlation (p) threshold of 0.30, and through inspection of residuals (Savin and White 1977, Ostrom 1990). Where unacceptable levels of autocorrelation were detected, the

Cochrane-Orcutt procedure was used to transform the offending dependent and independent variables (Neter *et al.* 1990).

RESULTS

Over two winters, we examined caribou feeding sites along 85 forest transects and 23 alpine quadrats (Fig. 2.1). We sampled 461 terrestrial (206 feeding, 255 random) and 356 arboreal (102 feeding, 251 random) sites in the forest and 136 sites (70 feeding, 66 random) in the alpine. On forested transects, the lichen volumes measured for four lichen species were consistently (all P < 0.05) lower at crater sites than at random terrestrial sites. Regression coefficients (*B*) for the relationships between volume (cm³) and cover (cm²) varied for *C. mitis* (crater: (*B*) = 1.45 ± 0.064; random: *B* = 1.57 ± 0.046), *C. rangiferina* (crater: *B* = 1.52 ± 0.042; random: *B* = 1.65 ± 0.044), *C. ericetorum* (crater: *B* = 1.32 ± 0.036; random: *B* = 1.40 ± 0.039), and *P. malacea* (crater: *B* = 1.15 ± 0.043; random: *B* = 1.247 ± 0.034). Preforaging volumes for those species were corrected accordingly. At alpine locations, the volume of lichens removed did not consistently differ (all P > 0.05) between foraged and random sites for any species. There were no significant differences (all P > 0.05) in the regression intercepts for forested or alpine lichens.

Forage and Feeding Site Selection

Forested Sites. – In forested locations, vegetation, debris, and snow variables discriminated between feeding sites. The first discriminant function differentiating terrestrial and arboreal sites (Fig. 3.1) accounted for 75% of the between-site variation ($\chi^2 = 722.86$, df = 48, P < 0.001; r = 0.687). Eleven variables were statistically important in discriminating those sites with the most important being *P. schreberi*, moss spp., and debris (Table 3.1). There were greater amounts of moss and debris, and deeper snow at the arboreal sites and more



Figure 3.1. Mean discriminant function scores (centroids \pm SE) for feeding sites used by caribou and random sites at forested locations in northcentral British Columbia (December 1996 – April 1998). Separation of terrestrial from random sites is illustrated at the first function, terrestrial feeding (n = 202) from random terrestrial sites (n = 252) at the second function, and arboreal feeding (n = 99) from random arboreal sites (n = 254) at the third function. Important variables are listed below each function with the direction of influence indicated by arrows.

Table 3.1. Variables identified by discriminant function (DF) analysis as important (threshold = 0.031) in defining each successive discriminant function and separating terrestrial feeding sites used by caribou, random terrestrial sites, arboreal feeding sites used by caribou, and random arboreal sites at forested locations in northcentral British Columbia (December 1996 – April 1998). Variables are ranked according to their importance using the parallel discriminant ratio coefficient (DRC, Thomas and Zumbo 1996). Mean measures of lichens (g dry weight/m²) and mosses/debris (cm²) are calculated by site type.

Discriminant Function	Variable	Parallel DRC Score	Terrestrial Feeding Site		Random Terrestrial Site		Arboreal Feeding Site		Random Arboreal Site	
			Ī	SD		SD	Ī	SD	Ī	SD
1 st DF	P. schreberi	0.223	264.60	440.59	721.11	909.25	549.90	566.63	512.85	536.40
	Moss spp.	0.218	162.53	219.20	277.16	450.46	328.92	494.94	250.48	331.49
	Debris	0.102	380.03	382.87	470.61	512.56	384.57	248.04	431.98	254.72
	C. rangiferina	0.065	22.91	42.06	23.72	56.90	15.97	18.74	24.41	32.61
	S. alpinum	0.063	28.05	71.29	16.53	59.61	24.51	53.49	24.45	47.55
	P. aphthosa	0.054	28.74	54.79	28.91	55.24	27.03	24.52	28.64	28.04
	C. uncialis	0.047	9.76	28.47	5.96	20.30	5.69	14.00	8.03	16.88
	C. mitis	0.041	121.68	112.61	65.10	93.06	93.16	65.85	87.05	68.05
	С. естосупа	0.040	76.71	106.40	50.71	86.11	58.33	57.05	61.41	55.57
	C. ericetorum	0.039	4.24	10.86	2.92	7.86	3.28	4.91	3.58	4.81
	Snow Depth (cm)	0.032	55.59	17.61	57.67	18.65	69.05	17.78	57.56	17.64
2 nd DF	Cladonia spp.	0.357	76.71	78.62	41.73	62.08	46.98	36.37	54.15	40.04
	C. mitis	0.346	121.68	112.61	65.10	93.06	93.16	65.85	87.05	68.05
	P. schreberi	0.132	264.60	440.59	721.11	909.25	549.90	566.63	512.85	536.40
	Snow depth (cm)	0.053	55.59	17.61	57.67	18.65	69.05	17.78	57.56	17.64
	Moss spp.	0.034	162.53	219.20	277.16	450.46	328.92	494.94	250.48	331.49
3 rd DF	Bryoria spp.	0.560	2.82	2.95	2.88	3.46	4.76	6.20	2.26	3.66
	Snow depth (cm)	0.158	55.59	17.61	57.67	18.65	69.05	17.78	57.56	17.64
	Snow density (g/cm ³)	0.138	22.25	5.02	21.93	5.47	24.78	4.24	22.51	4.56
	C. mitis	0.071	121.68	112.61	65.10	93.06	93.16	65.85	87.05	68.05
	Snow hardness (g/cm ²)	0.047	0.639	0.100	0.634	0.343	0.681	0.162	0.643	0.001
biomass of lichens at the sampled crater sites (Table 3.1). In interpreting this function, it is important to consider that differences in group centroids result largely from our averaging those variables at terrestrial feeding and random sites and applying those means to arboreal sites on the same transect. Thus, if the two terrestrial site types had different values, their average, applied to their corresponding arboreal foraged and random sites, would show correspondingly large differences in group centroids.

Craters and random terrestrial sites were differentiated by a second discriminant function (Fig. 3.1), accounting for 17.6% of the between-site variation ($\chi^2 = 217.77$, df = 30, P < 0.001; r = 0.416). On average, cratered sites had a greater biomass of lichens (*Cladonia* spp., *C. mitis*), less moss and lower snow depths than sites where caribou did not feed (Table 3.1).

Arboreal feeding and random arboreal sites were differentiated by a third discriminant function (Fig. 3.1), accounting for 7.5% of the between-site variation ($\chi^2 = 67.47$, df = 14, P < 0.001; r = 0.286). Mean differences in the amount of *Bryoria* spp. and *C. mitis*, and snow characteristics indicated that caribou fed on arboreal lichens at trees where there was more *Bryoria* spp., and when the surrounding area had more *C. mitis* and deeper, denser, and harder snow, relative to transects where caribou did not arboreal feed (Table 3.1).

The discriminant function model correctly classified 62.2% of the samples into their appropriate sites compared to a classification accuracy of 27.5% based on chance alone. The highest misclassification (81.7%) occurred for the arboreal feeding sites, which often were misclassed as random arboreal sites.

The statistical and interpretative outcome of the biomass x location model was similar to that reported for the previous noninteraction lichen biomass model. The biomass x time model differed in that the third discriminant function was responsible for explaining a larger proportion of the overall between-site variation relative to the former two models (Table 3.2). Some minor reordering occurred in the ranking of variables for the two interaction models, and several variables were included or excluded as important when describing their respective discriminant functions. For the biomass x time model, *Bryoria* spp. (Parallel DRC = 0.051) and *C. ecmocyna* (Parallel DRC = 0.043) were included as important and moss spp. was unimportant when explaining the second discriminant function, whereas snow hardness (Parallel DRC = 0.005) became unimportant relative to the third discriminant function. When compared to the noninteraction model, neither variable inclusion nor order of importance differed for the second and third discriminant functions of the biomass x location model.

The biomass of important lichen species measured at feeding sites showed a weak, but significant linear relationship with snow depth (C. mitis: F = 16.71, df = 1, 169, P < 0.001, $r^2 = 0.090$, $f^2 = 0.100$; Cladonia spp.: F = 15.49, df = 1, 164, P < 0.001, $r^2 = 0.086$, $f^2 = 0.094$).

Alpine Sites. – At alpine sites, craters measured in the alpine were distinguished from random sites with a classification accuracy of 78.7% relative to a 50.1% classification accuracy based on chance alone ($\chi^2 = 59.18$, df = 12, P < 0.001; r = 0.608) (Fig. 3.2). Caribou fed at sites with more lichens (*C. rangiferina*, *C. cucullata*, *C. mitis*, *Thamnolia* spp., *S. alpinum*), less deep snow, and less debris than random sites (Table 3.3). With the exception of small differences in the χ^2 statistic, the interaction models of biomass x time and biomass x location in the alpine did not differ from the noninteraction model (Table 3.2). Biomass of C. *rangiferina* measured at feeding sites was linearly related to snow depth (F = 10.30, df = 1, 21, P = 0.004, $r^2 = 0.329$, $f^2 = 0.490$). Regression equations for the other important lichens (*C. cucullata*, *C. mitis*, *Thamnolia* spp., and *S. alpinum*) were not significant (all P > 0.05). Table 3.2. Chi-square values, explained variability, and effect sizes (L = large, M = medium, S = small, Cohen 1992) presented by discriminant function for comparison of the Biomass, Biomass x Time, and Biomass x Location interaction models for feeding sites used by caribou and random sites at forested and alpine locations in northcentral British Columbia (December 1996 – April 1998). All discriminant functions were statistically significant (P < 0.001).

Model	Discriminant	χ^2 Statistic	Explained	Effect Size (r)
Forest Biomass	1	722.86	74.97	0.687 (L)
	2	217.77	17.56	0.416 (M-L)
	3	67.47	7.47	0.286 (M)
Forest Biomass x Time	1	628.31	71.57	0.644 (L)
	2	206.70	17.28	0.382 (M-L)
	3	82.41	11.15	0.315 (M)
Forest Biomass x Location	1	718.02	73.88	0.682 (L)
	2	223.42	18.56	0.423 (M-L)
	3	67.31	7.56	0.286 (M)
Alpine Biomass	1	59.18	100	0.608 (L)
Alpine Biomass x Time	1	57.00	100	0.600 (L)
Alpine Biomass x Location	1	54.66	100	0.590 (L)



Figure 3.2. Mean discriminant function scores (centroids \pm SE) for alpine locations in northcentral British Columbia (December 1996 – April 1998) illustrating the separation of terrestrial feeding sites used by caribou (n = 70) from random terrestrial sites (n = 68). Variables are listed below each function with the direction of influence indicated by arrows.

Table 3.3. Variables identified by discriminant function analysis as important (threshold = 0.042) in differentiating terrestrial feeding sites used by caribou from random terrestrial sites at alpine locations in northcentral British Columbia (December 1996 – April 1998). Variables are ranked according to their importance with the parallel discriminant ratio coefficient (DRC) (Thomas and Zumbo 1996). Mean measures of lichens (g dry weight/m²) are presented by site type.

	Parallel DRC	Terrestrial		Random	
Variable		$\overline{\vec{x}}$	SD	<u> </u>	SD
Snow depth (cm)	0.169	15.52	7.72	22.50	14.94
C. rangiferina	0.162	13.60	27.65	2.12	7.33
C. cucullata	0.160	9.34	10.89	4.91	6.94
C. mitis	0.158	32.00	29.39	20.19	35.42
Thamnolia spp.	0.114	4.68	15.92	0.51	2.50
S. alpinum	0.109	113.67	105.74	105.74	91.20
Debris (cm ²)	0.053	497.77	416.63	937.50	662.91

Patch Selection

Forested Patches. – In the forest, there were approximately 4 times more craters (\overline{X} = 8.5 \pm 0.94 SE) than arboreal feeding sites ($\bar{x} = 2.1 \pm 0.39$) per patch (n = 85). The path model used to describe patch use (Fig. 3.3) included lichens, snow, and moss and was identified by the 2nd and 3rd discriminant functions (Table 3.1) of the noninteraction discriminant function analysis, as well as the estimated number of animals using the patch. Our model did not statistically differ from empirical data ($\chi^2 = 12.01$, df = 6, P = 0.062), with the indices of fit also suggesting a good fit between hypothesised and empirical models (Steiger-Lind RMSEA index = 0.109; McDonald noncentrality index = 0.965; RMS standardised residual = 0.049). Snow depth (T = -5.24, P < 0.000), C. mitis (T = 4.27, P < 0.0000), C. mitis (T = 4.270.001), and Cladonia spp. (T = 4.42, P < 0.001) contributed to explaining the number of terrestrial feeding sites within the patch, while snow depth (T = 5.28, P < 0.001) and snow hardness (T = 2.45, P = 0.014) were significant predictors of the number of arboreal feeding sites in the patch (Fig. 3.3). Number of craters did not significantly contribute to the explanation of the number of arboreal feeding sites and the number of animals in a patch did not affect the number of arboreal or terrestrial feeding sites.

Alpine Patches. – In the alpine, number of craters averaged 31.8 ± 5.2 per patch (n = 23). Five species of lichen, debris, and snow depth – each identified as important in influencing foraging decisions at the feeding site – and the number of animals sighted at each patch were included in our model predicting the use of alpine patches by caribou (Fig. 3.4). The regression model was not significant (F = 1.178, df = 8, 13, P < 0.381, $R^2 = 0.420$; $f^2 = 0.725$).



Figure 3.3. Path diagram illustrating a hypothesised linear scalar relationship between the variables identified as important to the selection of feeding sites at forested locations and the selection of feeding patches by woodland caribou in northcentral British Columbia (December 1996 – April 1998). Numerals near each path indicate standardised path coefficients; asterisks indicate values significantly different from 0.



Figure 3.4. Path diagram illustrating a hypothesised linear scalar relationship between the variables identified as important to the selection of feeding sites at alpine locations and the selection of feeding patches by woodland caribou in northcentral British Columbia (December 1996 – April 1998). Numerals near each path indicate standardised regression coefficients; all variables were non-significant.

Lichen biomass was summed for *C. rangiferina*, *S. alpinum*, *C. uncialis*, *P. aphthosa*, *C. ericetorum*, *C. mitis*, *Cladonia* spp., and *C. ecmocyna* at forested terrestrial feeding sites and for *C. mitis*, *C. rangiferina*, *Thamnolia* spp., *C. cucullata*, and *S. alpinum* at alpine sites. Caribou foraging at forested sites ($\bar{x} = 345.9 \pm 11.65$ SE g/m²) had access to twice as much biomass of important lichen species relative to animals foraging at alpine sites ($\bar{x} = 173.3 \pm 13.88 \text{ g/m}^2$) (t = 8.80, df = 127.26, P < 0.001). Lichen biomass also was less variable at forested sites (CV = 0.48) relative to alpine feeding sites (CV = 0.67). Snow depth was deeper and less variable at feeding sites in the forest ($\bar{x} = 55.1 \text{ cm}$, CV = 0.32) when compared with those sampled in the alpine ($\bar{x} = 15.5 \text{ cm}$, CV = 0.50) (t = 18.34, df = 83.11, P < 0.001). Snow hardness was greater and more variable in the alpine ($\bar{x} = 3.3 \text{ g/cm}^2$, CV = 1.71) than in the forest ($\bar{x} = 0.7 \text{ g/cm}^2$, CV = 0.52) (t = 12.62, df = 96.23, P < 0.001).

Relative to patches on the landscape, biomass of the previously listed lichens (Table 3.1), with the addition of *Bryoria* spp. for forested patches, was summed across foraged and random sites for each transect. On average, lichen biomass was greater and less variable at forested patches ($\bar{x} = 270.0 \text{ g/m}^2$, CV = 0.48) when compared with alpine patches ($\bar{x} =$ 34.7 g/m², CV = 0.85; t = 15.77, df = 68.25, P < 0.001). Snow depth also differed significantly between the two landscapes, being deeper and less variable at forested patches ($\bar{x} = 57.8 \text{ cm}$, CV = 0.31; $\bar{x} = 19.6 \text{ cm}$, CV = 0.36; t = 14.77, df = 46.04, P < 0.001). Snow at forest patches was less hard and less variable ($\bar{x} = 0.6 \text{ g/cm}^2$, CV = 0.44) than the snow measured at alpine patches ($\bar{x} = 3.4 \text{ g/cm}^2$, CV = 0.90; t = 8.99, df = 25.97, P < 0.001).

DISCUSSION

Effects of Spatial Scale on Foraging Decisions

Ecologists have advocated a multi-scale hierarchical approach for studies of resource selection and animal behaviour to incorporate the breadth of biotic and abiotic stimuli that affect the choices and decisions of individuals and ultimately populations (Delcourt *et al.* 1983, Senft *et al.* 1987, O'Neill *et al.* 1989, Kotliar and Wiens 1990). We addressed two related questions in our study: (1) do woodland caribou exhibit trade-off decisions between forage abundance and accessibility and (2) does spatial scale affect the foraging behaviour of caribou? Our analyses of the foraging decisions by woodland caribou at four spatial scales confirm the importance of using a multi-scale approach and the potential for interactions between both time and space resulting in trade-off decisions.

At the finest scale we measured, caribou selected specific species of terrestrial lichens (*Cladonia* spp., *C. mitis*) (Table 3.1). These herbivores chose sites to feed where selected lichens were the most abundant and snow depths least deep. When snow conditions limited accessibility, animals in the forest began feeding on the more accessible, yet less abundant arboreal lichens (*Bryoria* spp.) (Table 3.1, Fig. 3.1). Thereafter, the choice of feeding site was the consequence of abundance of arboreal lichens, snow depth, density, and hardness, and was likely independent of the smaller-scale use of terrestrial lichen species. *Cladina mitis* was, however, still present at transects where animals had chosen to feed on arboreal lichens. We interpret this result as an interaction between the forage species and the feeding site, where selection of *C. mitis* occurred concurrently with *Bryoria* spp. when snow depths neared the threshold limit for cratering by caribou. Our data also revealed that when choosing arboreal lichens, caribou selected those trees with the greatest abundance of *Bryoria* spp (Table 3.1). We believe, therefore, that caribou in forested areas decide between terrestrial feeding sites,

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which are favoured, and the alternate arboreal feeding sites based on two interacting effects: accessibility as limited by snow depth, density, and hardness, and availability of arboreal lichens on individual trees. We originally predicted that the amount of favoured terrestrial lichens might act as a third interacting variable in the choice of feeding sites. Our regression analyses, however, indicated that the abundance of terrestrial lichens had little affect on the amount of snow that caribou would excavate to access lichens. With the exception of *C*. *rangiferina*, the same held for alpine sites.

At one scale higher, lichen species and variables describing snow characteristics, which were important to caribou choosing discrete feeding sites, did not always explain selection of a patch. Of the eight variables statistically significant at the scale of the feeding site, only two lichen species (C. mitis, Cladonia spp.) and snow depth were important in explaining number of terrestrial feeding sites in a patch, and only snow depth and hardness explained the number of arboreal feeding sites in a patch (Fig. 3.3). The influence of snow on patch use supports the assertions of other researchers that caribou select areas of relatively shallow snow (Pruitt 1959, LaPerriere and Lent 1977, Skogland 1978, Darby and Pruitt 1984). Where snow conditions restricted access to terrestrial lichens, caribou in our study fed on arboreal lichens (Bryoria spp.), regardless of their total availability across the patch (Fig. 3.3). This outcome is contrary to behaviour demonstrated at the scale of the feeding site (Table 3.1). and indicates that an interaction likely occurred between the feeding site and patch. Where caribou do not select patches based on the abundance of arboreal lichens, they may instead select those trees with the greatest biomass of *Bryoria* spp. within currently occupied patches. This likely occurs following some threshold in the accessibility of terrestrial lichens. This result demonstrates that trade-off decisions occur at multiple spatial scales, and that foraging

decisions at the scale of the patch may be dictated by a simpler suite of variables than present at the scale of the feeding site.

At the scale of the patch, the alpine model was not significant. Neither biomass of lichens nor snow influenced patch use in the alpine. This result is counterintuitive when considering the relatively high variability in lichen biomass and snow depths among alpine patches. Other factors, aside from forage biomass and accessibility, probably drive patch selection in the alpine.

At the largest spatial scale we measured, woodland caribou chose between two landscapes that differed in biomass and accessibility of lichens. Relative to the forest, animals in the alpine foraged across an environment with shallower more variable snow and less abundant more variably distributed lichens. Animals in the forest likely encountered higher energetic costs of obtaining food (Fancy and White 1985) with the nutritional advantage of greater forage biomass. We were not, however, able to estimate the energetic costs of cratering in different snow conditions (e.g., Fancy 1986) or the intake rates of foraging animals (e.g., Parker *et al.* 1999).

There are likely factors, other than those related to foraging decisions, that affect the choice of a landscape at which to spend a large portion of winter (Senft *et al.* 1987). For example, caribou may reduce the risk of predation from wolves by distancing themselves from other prey species such as moose or seeking refuge in terrain that is relatively inaccessible to predators (Bergerud *et al.* 1984, Bergerud 1985, Cumming and Beange 1987, Seip 1992). Inhabiting alpine locations would segregate caribou from moose and potentially decrease the probability of encountering wolves (Seip 1992, but see Dale *et al.* 1994). Responding to predation risk at the scale of the landscape also may affect behaviour at smaller scales (Stephens and Krebs 1986, Lima and Dill 1990). Caribou in the alpine may be more risk

adverse, weighing lower forage accessibility and abundance against factors such as escape terrain and visibility that would reduce the risk of being surprised or captured by a predator (Ferguson *et al.* 1988, Bowyer *et al.* 1999). This is one possible explanation for the inferior fit of the hypothesised model of patch use by caribou in the alpine relative to the forest.

Balancing competing biotic and abiotic variables is not unique to woodland caribou. As examples, Ward and Saltz (1994) reported that dorcas gazelles (Gazella dorcas) excavated less sand to expose the bulbs of madonna lilies (Pancratium sickenbergeri) as the sand became more compact; McCorquodale (1993) reported that as snow depth increased, elk (Cervus elaphus) became more sedentary and fed on more accessible forage; and Schaefer and Messier (1995) surmised that muskoxen (Ovibos moschatus) compromised between the abundance and accessibility of their forage as dictated by snow conditions. In many instances, however, behavioural responses to the environment and trade-off decisions in particular, may be scaledependent. For example, Powell (1994) noted that the foraging behaviour of fishers (Martes pennanti) differed across scales and Logerwell et al. (1998) reported that interactions between thick billed murres (Uria lomvia) and their prey were dependent on both spatial and temporal scales. Domestic cows have been reported to select for energy and minerals at the scale of the landscape, but showed weak or no selection at the scale of vegetation units (Wallis de Vries and Schippers 1994). Gutzwiller and Anderson (1987) noted that, depending on the species, patterns of habitat use of cavity-nesting birds may or may not be predictable from those at other scales. Alternatively, multi-scale studies of habitat selection by muskoxen and coyotes (Canis latrans) reported that behavioural decisions largely remained consistent across scale (Gese et al. 1988, Schaefer and Messier 1995). Our comparison of the importance of variables at the feeding site and patch demonstrated that the foraging behaviour of caribou varies across

scales and that conclusions cannot necessarily be extrapolated from one scale to another (Gardner et al. 1989, Turner et al. 1989, Turner 1990).

Trade-off Decisions at Multiple Scales: Implications for Optimal Foraging

Forage abundance and accessibility at the level of the individual animal are necessary to maintain productive populations of caribou. Skogland (1985, 1986) documented the density-dependent effects of food limitation during winter on recruitment rate and adult female body size of wild reindeer in a predator-free environment; pregnancy rates increase with increasing fat and protein reserves in female Peary caribou (*R. t. pearyi*) and barren-ground caribou (*R. t. granti, R. t. groenlandicus*) (Thomas 1982, Allaye-Chan 1991, Ouellet *et al.* 1997). Furthermore, White (1983) reported that selective feeding strategies facilitating even small gains in quality or intake can have significant "multiplier effects" on the weight gain of reindeer. Although the individual roles of energy, protein, and digestibility are often difficult to separate, forage quality has been shown to influence diet selection in both wild and captive ungulates (Kyriazakis and Oldham 1993, Wang and Provenza 1996, Berteaux *et al.* 1998). Therefore, if caribou adopt foraging strategies that maximise nutritional gain, those strategies should be observable at the scale of the individual forage species.

Caribou and other sub-species of *Rangifer* have evolved physiological mechanisms to subsist on a diet low in protein (Klein and Schønheyder 1970, Westerling 1970). Most fruticose lichens, however, are composed of 2 – 5% crude protein, which is less than the 6 – 8% recommended by Van Soest (1982) as necessary for a positive protein balance (Scotter 1965, Russel *et al.* 1993). Considering the relatively high digestible energy content of lichens and the suspected negative over-winter protein budget of caribou, the optimal diet likely would be one rich in digestible protein (DP), although energy also has been reported to be limiting during winter (Cameron 1972, Pulliainen 1971, Huot 1989, Allaye-Chan 1991). From previously published values used to calculate digestible protein and digestible energy (Hanley *et al.* 1992), lichen species highly selected by caribou in this study likely were not the most 'nutritious' of those available. For example, *Bryoria* spp. (~0.9% DP; 14.7 KJ/g), *S. alpinum* (~2.3% DP; 8.8 KJ/g), and *P. aphthosa* (~10.7% DP; 8.4 KJ/g) are higher in digestible protein and energy than *C. mitis* (~-1.6% DP; 8.2 KJ/g) and higher in digestible protein than *Cladonia* spp. (~-0.5% DP; 7.6 KJ/g) (C.J. Johnson, unpubl. data, Solberg 1967, Bergerud 1972, Scotter 1965, 1972, Thing 1984, Thomas *et al.* 1984, Dannell *et al.* 1994). Assuming that caribou had the choice of all lichen species at each foraging location, this result is contrary to an optimal diet model predicting that caribou should select lichen species that rank highest in digestible protein and energy (Stephens and Krebs 1986).

One possible explanation for why caribou did not select the most nutritious species is that caribou do not respond to dietary feedback and the associated affects on fitness at such a fine scale (Galef 1991). Alternatively, caribou may be selecting forage species for reasons other than maximising nutritional gain per unit biomass. As caribou locate lichens through the snow using olfactory cues, selecting the most conspicuous lichens would reduce search time and increase foraging efficiency. Animals would maximise net gain by increasing intake of those species that are the easiest to detect. We have no knowledge of the detection thresholds of individual species, but perhaps those lichens that are selected have a stronger scent. As the snow deepens, however, terrestrial lichens may become more difficult to detect (Bergerud and Nolan 1970, Bergerud 1974*a*) and a switch to an alternate more conspicuous and consequently more dense forage, arboreal lichens, would become the optimal strategy (Dukas and Ellner 1993).

A third factor that may influence the selection of lichen species by caribou is the availability of lichen. Even if caribou are capable of selecting forage based on nutrient content, it may be more advantageous to increase intake and reduce search time by selecting the most abundant species, especially if discrimination errors are large and nutritional differences are small (Yoccoz et al. 1993). Unlike some types of plants, there is a positive relationship between availability of lichens and intake by reindeer (Trudell and White 1981). With some exceptions, our ranking of importance of lichens to site selection in the forest corresponded with abundance of the individual species across feeding and random terrestrial sites (Table 3.1 and Table 3.3). Our interaction models, which were designed to test the prediction that foraging caribou would adjust their behaviour to match temporal and spatial changes in the abundance and accessibility of lichens, further support this explanation. As the winter advanced, Bryoria spp. and C. ecmocyna (~0.03% DP, 7.6 KJ/g) became more important and snow hardness less important in discriminating terrestrial and arboreal feeding sites, respectively. Because both of those lichen species are of lower nutritive value than other lichens, this shift likely resulted from caribou selecting the most accessible or abundant species over time. As snow depths increased, which correlated with time during winter, animals cratered as well as selected trees with greater amounts of arboreal lichens (Bryoria spp.). Cladonia ecmocyna was more abundant at locations frequented by caribou during the later portions of the winter, suggesting an interaction between both time and space. Snow hardness was statistically displaced by other lichen variables that, when combined with time, explained a higher proportion of the variation between feeding and random arboreal sites. In the alpine, the importance of individual lichen species and snow conditions did not deviate across time or space.

At the scale of the patch, caribou foraging intensity (as measured by the number of feeding sites) was explained by abundance of favoured lichens and snow depth. If foraging intensity is considered synonymous with time in a patch, our results agree with the predictions

of several optimal patch use models (Charnov 1976, Parker and Stuart 1976, Iwasa *et al.* 1981). This is despite the complexity of our system, which included the interaction of abundance and accessibility. Optimal foraging within patches was also reported for free ranging dorcas gazelles (Baharav 1982, Baharav and Rosenzweig 1985) and moose used in experimental trials of patch selection relative to browse availability (Vivås and Sæther 1987).

At the scale of the landscape, caribou experienced a trade-off between abundance, accessibility, and variability of lichen biomass and snow conditions. Choosing between forest or alpine landscapes, however, may offer no distinct nutritional advantage with ecological or evolutionary consequences. Rather, the two landscapes exemplify two potential solutions for a species that shows extreme behavioural and physiological plasticity across a wide variety of mid- to high-latitude habitats (Williams and Heard 1986). Caribou are well adapted for dealing with extreme snow conditions (Telfer and Kelsall 1984) and have evolved an energetically efficient technique for travelling over and obtaining terrestrial lichens from beneath the snow (Fancy and White 1985). The threshold depth for cratering by caribou and reindeer ranges from 50 to 80 cm (Formozov 1946, Pruitt 1959, Stardom 1975, LaPerriere and Lent 1977, Helle and Saastamoinen 1979, Darby and Pruitt 1984), although craters as deep as 123 cm have been reported (Brown and Theberge 1990); we observed craters as deep as 97 cm in the forest. Relative to the selection and availability of lichens, field studies commonly report different results (DesMeules and Heyland 1969). This is not to say that caribou are unselective within a chosen landscape, or that they do not choose between landscapes, just that they can forage effectively across a wide range of environmental conditions.

CONCLUSION

The extent to which animals integrate information and make behavioural decisions across scales is unknown (Danell *et al.* 1991). We developed our predictions of foraging caribou assuming that decisions are scale-dependent. At the scale of the forage species and feeding site, caribou chose terrestrial sites with the shallowest snow (Prediction 2) and trees with the greatest amount of arboreal lichens (Prediction 4), but did not select specific lichens based on nutritive value (Prediction 1) or compensate for deep snow conditions by selecting sites with the greatest biomass of favoured lichens (Prediction 3). At the scale of the patch, the biomass of terrestrial lichens (Prediction 5) and snow (Prediction 6) affected the frequency of cratering in the forest, but not the alpine, whereas foraging on arboreal lichens was only influenced by snow depth and hardness rather than biomass of lichens (Prediction 7). At the scale of the landscape, a trade-off may have occurred where reduced accessibility in the forest relative to the alpine could be balanced by increased biomass of terrestrial and arboreal lichens (Prediction 8).

The application of our data to the above predictions contributes to the understanding of foraging behaviour of woodland caribou. Our results support the assertion that animal behaviour is a scale-dependent process (Senft *et al.* 1987). We demonstrated that there was not always a linear relationship between the importance of specific variables across different spatial scales. Furthermore, trade-offs involving the interaction of selection with time and space (lichen abundance and accessibility) illustrate that foraging behaviour by caribou is a dynamic multidimensional process. In total, these observations reveal that there is likely no single 'optimal strategy' that a foraging animal should adopt, but rather a variety of strategies to meet changing needs and circumstances. The challenge, therefore, is to develop, model, and test theory that ascribes the integrated complexity of time and space to real-world foraging

decisions and the range of potentially good solutions from which a forager may choose

(Hanley 1997).

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CHAPTER 4 - EXPECTATIONS AND REALITIES OF GPS ANIMAL LOCATION COLLARS: RESULTS OF THREE YEARS IN THE FIELD¹

SUMMARY

GPS (Global Positioning System) collars have the potential to automatically collect large numbers of relatively accurate animal relocations. Collar costs, levels of accuracy, and satellite signal reception have been reported by other studies, but there has been little discussion of long-term performance under field conditions. Between March 1996 and April 1999, we placed 11 GPS collars on 23 individual caribou for a total of 26 collar deployments. Collars were scheduled to operate for either 249 (n = 3) or 549 (n = 8) days. Reliability was highly variable; some collar deployments operated normally for the expected period, others functioned for less than one-half of their expected lives, and one deployment collected no data. Collars attempted 41,822 locations and collected 15,247 3-D and 10,411 2-D locations, for an average acquisition rate of 59%. We review the workings of the technology and discuss the benefits and costs of several features available with GPS collars. We recommend that researchers carefully consider project objectives, budget constraints, and available options, such as differential correction and remote collar communication, before purchasing GPS collars.

INTRODUCTION

Global Positioning System (GPS) collars are a relatively new tool available to wildlife biologists for monitoring movements and activities of large terrestrial mammals. Collars can be sized for animals as small as wolves and cougars (*Puma concolor*) and offer features such as remote drop-off devices, differential correction of locations, multi-directional activity counters, and mortality and temperature sensors. GPS collars are useful to researchers for

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several reasons. When compared to aerial telemetry, triangulation, LORAN-C, and satellitebased (i.e., Argos) methods, GPS has the fewest biases and provides the most precise locations (Hoskinson 1976, Lee *et al.* 1985, Garrott *et al.* 1986, White and Garrott 1986, Fancy *et al.* 1988, Mills and Knowlton 1989, Findholt *et al.* 1996, Moen *et al.* 1997). Also, GPS collars can relocate an animal frequently (up to once per second) during day or night regardless of weather (Rodgers *et al.* 1996, Edenius 1997). Relative to other techniques, GPS collars have the potential for gathering greater amounts of data at a significant cost savings per location, with greater safety for the researcher, and without the temporal biases associated with weather and daylight (Springer 1979, Beyer and Haufler 1994).

Manufacturers and the published literature (e.g., Rodgers and Anson 1994, Moen *et al.* 1996a, Rodgers *et al.* 1996) have noted the benefits and some of the limitations of GPS collars. Experimental trials have demonstrated that both terrain and canopy coverage can reduce the likelihood of a GPS collar acquiring the satellite signals necessary to calculate a location (Rempel *et al.* 1995, Moen *et al.* 1996a, Edenius 1997, Dussault *et al.* 1999). Researchers have investigated the influence of differential correction software, number and geometry of satellites, animal movement, and collar-antenna orientation on location accuracy and precision (Rempel *et al.* 1995, Edenius 1997, Moen *et al.* 1997, Rempel and Rodgers 1997). GPS collars tend to have a lower cost per location, but the high purchase price may lead to fewer animals being collared over a shorter time period, thus limiting the inferences that can be made at the level of the population (Moen *et al.* 1996a, Rodgers *et al.* 1996).

Although Merrill *et al.* (1998) evaluated the performance of a prototype collar over a relatively short time, there has been no documentation of the ability of commercially available GPS collars to meet the objectives of long-term studies (at least two years) conducted under uncontrolled field conditions. We used GPS collars to assess the movements, distribution, and

habitat selection of woodland caribou in northcentral British Columbia for 3.5 years. We appraised the performance of GPS collars under field conditions and the usefulness of these collars to meet study objectives. We review the practical workings and theoretical limitations of the technology relative to our experience with a collar produced by one manufacturer. We specifically address: 1) collar reliability; 2) data retention, recovery, and catastrophic loss; 3) location acquisition bias and realised accuracy; and 4) animal welfare. We discuss GPS collars in general and provide recommendations that researchers should consider during study design.

BACKGROUND

Global Positioning Systems: A Review of the Principles

GPS collars function similarly to handheld GPS devices used for survey or navigation. There are 24 high-altitude satellites orbiting the earth with four to nine satellites visible above the horizon at any one time from any location. These satellites broadcast radio signals that contain information on their exact position in space and signal transmission time. A clock in the receiver of the collar is synchronised with clocks in the satellites. After receiving a signal from a satellite, the collar measures the time difference between transmission and reception, multiplies the transmission time by the speed of light and calculates a distance. A horizontal location (x, y) is calculated using the distances from three satellites. If the collar acquires signals from at least four satellites, it uses those satellites with the most suitable spatial configuration to calculate a horizontal location (x, y) and an elevation (z). Widely spaced satellites >15° above the horizon provide a more accurate location than spatially contiguous satellites. A variety of unit-less measures describe the geometric configuration, or dilution of precision (DOP), of the satellites used to calculate a location (e.g., vertical DOP, horizontal DOP, positional DOP, northern DOP, eastern DOP). Positional DOP (PDOP) and horizontal DOP (HDOP) are the most commonly reported values and relate to the precision of the horizontal and vertical or just the horizontal component of the location, respectively. Lower DOP values indicate more accurate positioning (British Columbia Ministry of Environment, Lands, and Parks 1995).

In theory, GPS collars are capable of calculating an animal location within a 14-m radius of the true location 95% of the time (Lotek Engineering 1998). Accuracy, however, can be degraded by several sources of error. Atmospheric errors occur because the troposphere and ionosphere slow the transmitted signal, thereby increasing the time between satellite and collar resulting in erroneous distances. Multipathing errors occur when satellite signals are redirected by terrestrial objects causing multiple receptions of the same signal. Receiver and ephemeris errors result from imprecise clocks and the transmission of incorrect satellite positions, respectively. Selective availability was the intentional introduction of error to satellite positions and signal transmission times to prevent the unauthorised use of the GPS system for applications that require sub-metre accuracy (Trimble Navigation Ltd. 1994). Although selective availability was in place during this study, it was deactivated 1 May 2000.

The errors resulting from atmospheric distortion and selective availability can be accounted for with a process known as differential correction. This process involves using a second GPS receiver (base station) located at a surveyed location to compare how long it should have taken to receive the signal from each satellite versus how long it actually took to receive the signal. Correction factors are then applied to the distances calculated by the GPS collar for the same satellites monitored by the base station. In the absence of differential correction, locations are expected to be within 100 m 95% of the time (Lotek Engineering 1998). The number of satellite signals acquired by a collar also affects location accuracy. If signals are received from only three satellites, the collar can not calculate an elevation at that time and is forced to use previous elevations or a default elevation to calculate a horizontal two-dimensional (2-D) location. For every incorrect metre in the assumed elevation of the collar, the horizontal location may be miscalculated by 0.5 - 2 m (Trimble Navigation Ltd. 1994). For example, a collar assumed to be at sea level, but which is actually at 1,000 m could have a horizontal error of 500 - 2,000 m. Collars that acquire at least four satellite signals can calculate an elevation, generating a three-dimensional (3-D) location. For animals that range over a large topographic gradient, 3-D locations are more accurate than 2-D locations.

Number of satellite signals that a collar can acquire will be determined by the satellite constellation during the location attempt and the ability of the collar to 'see' and track the satellites. Topography and vegetation can block or weaken transmitted signals. A GPS-collared mountain goat (*Oreamnos americanus*) on a near vertical cliff can only acquire satellite signals from approximately one-half of the sky. Likewise, a caribou standing in an alpine meadow will receive signals from a greater number of satellites over a longer time than a caribou standing in a dense patch of large-diameter trees. Collar hardware also will influence number of unique satellite signals acquired by a collar. For example, a six-channel receiver can track only six satellites simultaneously whereas a 12-channel receiver can track up to 12 satellite signals, selecting the combination of signals that results in the lowest HDOP and most accurate location (Moen *et al.* 1997).

Why Did We Choose GPS Collars?

Our study was designed to explain the responses of caribou to environmental variables at several spatial scales. We anticipated that frequent locations would allow us to reconstruct movement routes, identify discontinuities in the spatial scales of movement behaviours, and examine responses to environmental heterogeneity at spatial scales larger than those that can be investigated by trailing caribou from the ground. In central and northern Canada, limited road development and large distances from rural airports often make it difficult to access study areas and frequently relocate wide-ranging species. The caribou we monitored ranged over a large area (5,100 km²) with little development and few roads. Ground access was extremely limited, thereby necessitating the use of aircraft for relocating collared animals. This, however, offered its own suite of logistical difficulties. The study area is 200 – 300 km from the nearest departure airport resulting in a 1-hr transit time. Additionally, frequent periods of often unpredictable inclement weather and the propensity of caribou to range from valley bottoms to high-elevation habitats made relocation from aircraft difficult and costly in terms of time and money. Considering our need for frequent accurate animal relocations, the logistical limitations of ground, air or remote VHF telemetry, and the relatively poor accuracy of the Argos system (Fancy *et al.* 1988), GPS collars appeared to be the most appropriate choice to meet our data requirements.

GPS Animal Location System

We used GPS 1000 collars from Lotek Engineering, Inc. (Newmarket, Ontario, Canada) weighing 1.8 or 2.2 kg depending on battery size. Although currently available collars operate with a Motorola VP Oncore eight-channel receiver, our collars were manufactured with a Motorola PVT-6 six-channel receiver. Collars were constructed to perform all positioning, communication, maintenance, and sensor functions to -30 °C and were designed to withstand repeated complete immersions in water (Lotek Engineering 1995). A temperature transducer in each collar measured ambient temperature ($\pm \frac{1}{2}$ °C) each time a location was recorded. A dual-axis motion sensor recorded upward and downward movements (tips) of the head and neck. Tips were totalled for each minute of activity and averaged over the scheduled sampling period, resulting in a single activity value per location. Each collar had sufficient non-volatile random access memory to store 1,680 records. Memory retention is guaranteed to -50 °C and designed to retain information even if the collar ceases to function (Lotek Engineering 1995). All data were differentially correctable and were processed with the most current version of the vendor specific software N3WIN (V. 2.412). In addition to temperature and activity, each processed record contained a longitude and latitude, elevation for 3-D locations, date, time, HDOP, the identification of satellites used in calculating the position, and a measure of satellite convergence.

The 1.8-kg collars were equipped with small battery packs and were scheduled to record one location every 3 hr for a total of eight locations per day (56/week). The 2.2-kg collars were equipped with large battery packs and were scheduled to record one location every 4 hr Saturday to Thursday and every 20 min on every fourth hour for each Friday (60/week). We specified an 8-hr communication window seven days per week to allow data retrieval via UHF modem in the collars and the system command unit connected to a laptop computer. Based on those location and communication schedules, the communication software (GPS 1000 HOST, V. 3.04) indicated that the 1.8- and 2.2-kg collars would function for 249 and 549 days, respectively.

OUR EXPERIENCES: SUCCESSES AND FRUSTRATIONS

Collar Reliability

Between March 1996 and April 1999 we put 11 collars (three 1.8-kg and eight 2.2-kg) on 23 individual female caribou of greater than one year of age for a total of 26 collar deployments (Table 4.1). For 22 of those deployments, collars with new batteries were placed on animals and were retrieved when the batteries were exhausted. Only four of the completed

	Days in	% of Expected	No. of	% of Expected	3D Locations	2D Locations	% Location Success
Deployment [*]	Field	Days	Locations	Locations ^b	(% of total)	(% of total)	(≥3 satellites)
04L1	83	15	364	8	52	48	58
04L2	652*	119	3228	69	59	41	64
77LI	301	55	1183	25	49	51	49
77L2	474	86	3281	70	75	25	90
83S1°	172	69	716	36	59	41	53
83S2	307*	123	1238	62	47	53	51
84S1	158	64	505	25	47	53	41
84S2	308*	124	1934	97	64	36	79
84S3 ^d	209	84	1012	51	56	44	61
85L1ª	96	18	565	12	65	35	69
85L2	149	27	891	19	64	36	78
88S1 ^d	103	~83	511	51	54	46	63
OELI	0	0	0	0	0	0	0
OEL2	38	7	35	1	86	14	12
OEL3	129	24	876	19	83	17	93
IDLI	26	5	110	2	56	44	55
IDL2	335	61	1293	28	50	50	50
B9L1	318	58	1856	39	55	45	74
B9L2	197	36	778	17	53	47	52
B9L3	213	39	1077	23	70	30	66
B9L4	205	37	83	2	49	51	9
BALI ^d	87	16	491	10	67	33	72
BAL2	4	1	15	1	53	47	56
BAL3	134	24	471	10	41	59	46
BAL4	158	29	658	14	63	37	54
E4L1	617*	112	2487	53	49	51	52
Total or X %	5473	51	25658	29	59	41	59

Table 4.1. Success rate of GPS collars deployed on woodland caribou in northcentral British Columbia over 37 months (March 1996 - April 1999).

^a Collars are named according to manufacturer identification labels followed by battery size (L=large, S=small), and number of successive deployments.

^b % of total locations that would have been recorded if collars had performed for expected lives and 100% location acquisition rate was achieved.

^cCollars 83, 84, and 88 were equipped with single small batteries (1.8-kg) and had an expected battery life of 249 days while the remaining collars were equipped with large batteries and had an expected life of 549 days. ^d Collars that were retrieved before battery had exhausted power or were deployed with partially used battery.

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* Symbol represents collars that functioned normally for the expected period; deviations from 100% of Expected Days are due to time of deployment in field versus time of battery connection as well as number of communication sessions.

deployments lasted as long or longer than their expected battery life. Furthermore, results were highly variable. Deployment 04L2 collected the greatest number of days of data (652, 119% of its expected life); in contrast, one deployment collected no useable data, and 11 others functioned for less than one-half of their expected lives (Table 4.1).

All collars that failed prematurely (n = 18) were returned to the manufacturer for repair, refurbishment, and software/hardware upgrades if available. Most collars performed slightly better following servicing by the manufacturer, but on average individual collars functioned only 92 days longer (17% of the expected life of a collar with a large battery) than they had on their previous deployment (SD = 174, n = 15, range = -121 – 569 days). Only three collars (84S2, 83S2, 04L2) met or exceeded their expected battery lives on subsequent deployments.

Collars failed in one of three ways. In most instances collars failed completely and entered into a mortality mode where the VHF transmitter emitted a double beep signal. Less frequently, the VHF beacon did not indicate a malfunctioned collar. Although data on temperature and activity were collected for each scheduled location, the collar failed to collect the satellite data necessary to calculate a location. We diagnosed this type of failure only following the remote retrieval and subsequent screening of data. This type of failure occurred for four collars, resulting in 417 days of failed operation. Two collars functioned normally, but we were unable to retrieve stored data because the collar modern failed. Those animals had to be recaptured to obtain stored data.

In most instances the manufacturer did not volunteer reasons for collar failures. We are reasonably confident, however, that failures were not the result of incorrect collar initialisation, scheduling, or data retrieval. Temperatures recorded by our collars averaged 4.1° C (SD = 9.33, n = 25,658) and ranged from 44° C (inside vehicle) to -36° C. The cold climate may have influenced collar reliability.

The consequences of a collar malfunction on data collection were exacerbated by several factors. First, we often did not diagnose a malfunction immediately. With the exception of winter (December to March), monitoring was infrequent because we examined collar status only every four to six months. Following detection of a collar failure, additional time was needed to arrange a recapture operation. Poor weather or unsuitable terrain (i.e., no suitable capture location) also delayed some recapture attempts. Once collars were recovered, there was an additional delay associated with the diagnosis, repair, and return of the collar by the manufacturer. This delay often was at least one month, but exceeded two months for six collars. In combination with organisation, logistics, and weather delays, collar malfunction contributed to a significant loss of potential data.

Data Retention, Recovery, and the Risks of Catastrophic Loss

Lotek GPS collars are "designed to give data retention the highest priority, so that stored information will be preserved even if the unit ceases to operate (e.g., through battery exhaustion or under extreme low temperature conditions)" (Lotek Engineering 1995:7). Our experience showed this to be true in all but one instance. The exception was a collar with a failed modem and a dislodged backup battery (used to maintain an electrical current and retain all stored information following the failure of the main battery). Once we disconnected the main battery to allow safe shipping to the manufacturer, all stored data were lost (approximately six months). Generally, data retrieved from all other returned collars were free of errors and could be differentially corrected. Less than 0.5% of the retrieved data were corrupted.

Modem communication between the command unit and collar was not always successful, but was an asset because the costs and limitations associated with capturing animals to retrieve data would have been prohibitive. Except for modem failures, communication difficulties were not a product of collar design, but resulted from a poorly mounted whip antenna, slight abrasions in the connector cables, and failed laptop and command-unit batteries. Because we retrieved data infrequently, relocation of collared animals was difficult. Thus, our data-retrieval costs using fixed and rotary winged aircraft were considerably more than predicted. For far-ranging animals such as barren-ground caribou or polar bears (*Ursus maritimus*), data-retrieval costs should be a serious consideration. A collar containing 1,680 records took approximately 25 min to upload once a link was established (≤ 10 min).

Location Bias and Realised Accuracy

Over 37 months, the collars attempted 41,822 locations, collecting 15,247 3-D and 10,411 2-D locations for an average acquisition rate of 59%. For the 22 deployments with \geq 100 locations, 3-D locations ranged from 41 – 83% of the total and location success ranged from 41 – 93% (Table 4.1). We suspect that variation in location success was caused by differences in habitat use, with collars on caribou living primarily in the alpine having higher rates of location acquisition than those on caribou living in the forest.

Three-dimensional locations had lower HDOP values ($\bar{x} = 6.7$, SD = 4.12, n = 15,247) than 2-D locations ($\bar{x} = 10.3$, SD=75.74, n = 10,411) (t = -5.86, df = 25,656, P < 0.001). An HDOP threshold of no greater than four, which is quoted as excellent satellite geometry for survey purposes, and in theory should achieve a horizontal accuracy of ~5 metres (Trimble Navigation Ltd. 1994, British Columbia Ministry of Environment, Lands, and Parks 1995), would require us to discard 72% of our 3-D and 36% of our 2-D locations. Contrary to the findings of Rempel and Rodgers (1997), these examples illustrate that the expectation of high accuracy can be met only by rejecting a large percentage of locations.

We chose differential correction because of greater location accuracy. This choice, however, came with both financial and temporal costs. Software (i.e., N3WIN) and base

station data were obvious costs. We contracted a privately operated base station to prepare the data necessary for our post-processing needs. Base station data were edited to provide just the first 5 min of every hour within which a location was recorded by the collars. This resulted in considerably smaller file sizes and reduced data storage costs (for one day 570,000 bytes compressed versus 2.5 megabytes compressed if unedited). For differential correction to be accurate, the base station must be located within 500 km of the deployed collar (Trimble Navigation Ltd. 1994). Although base station data is available without fees across most of the United States, there would be additional hardware, monitoring, and data management costs for users of differentially correctable GPS collars in more remote areas lacking established base stations.

The hidden costs of differential correction were the time necessary to process and manage base station and corrected collar data, the potential for irretrievable locations, and reduced battery life due to the greater memory requirements of differential data. Using N3WIN to process six weeks of collar data for five animals, a Pentium II 333 with 64 megabytes of RAM and sufficient hard-drive space took approximately 1.5 hr of computing time. Differential correction resulted in 12 files, all of which were archived so the procedure could be repeated or revisited. When base station data were missing, N3WIN did not provide a non-differentially corrected location. To ensure that all locations were processed, we spent considerable time replacing base station data that were corrupt or not provided by the contractor. Differential records required more memory, per location, than non-differential records. A collar collecting non-differential locations could store 3,640 records, whereas a collar collecting the data necessary for correction could store only 1,680 records. Differential correction requires more frequent retrieval of data, greater power demands, and, therefore, results in a reduction in the collar's field-life.

Animal Welfare

The Lotek 1000 is one of the largest collars available. Nonetheless, we did not witness any adverse effects on the collared female woodland caribou (-91 - 136 kg). Caribou were captured with a hand-held net-gun fired from a helicopter. All collars were snugly attached to minimise any side-to-side pendulum movement of the collar during running. Upon recapture, we observed some hair loss and hair breakage around the neck, but no bare or abraded skin. On several occasions during winter, we recaptured animals with battery packs that were encapsulated in ice. Of the 23 animals we collared, three died of natural causes at least three months after the capture date.

LESSONS LEARNED: RECOMMENDATIONS FOR FUTURE STUDY DESIGNS

Our experience with GPS collars has been restricted to one manufacturer and a relatively small number of collars. Over the 37 months that we deployed and maintained GPS collars, however, several reoccurring issues occurred that are of contemporary importance and can be generalised to GPS collars of other types.

Collar Reliability

Premature collar failure should not be unexpected; GPS collars are complex devices required to work under extreme conditions (Moen *et al.* 1996b, Merrill *et al.* 1998). For example, the Lotek 1000 has three internal computers that manage its multiple functions. In our study area, this sophisticated package of electronic hardware was subjected to variations in temperature as extreme as 45° C in 24 hrs, rapid changes in humidity, and complete immersion in water. Reliability in this context must be redefined outside that of traditional VHF collars, which are much simpler hermetically sealed devices expected to perform fewer less sophisticated functions.

At what point do reliability concerns force the researcher to reject the use of this technology? Large amounts of money and time may be sacrificed and despite best efforts insufficient data may be collected to answer pre-defined research questions. In our study, only 18% of the collars functioned properly until battery exhaustion. Despite these setbacks, we did collect nearly 26,000 locations over a wide enough period to meet our study objectives. At our average location acquisition rate of 59%, normal operation of all collars with field replacement of batteries would have resulted in approximately 48,000 locations. To ensure that study objectives are met, the reliability of a specific collar should be estimated based on the best available information, and a pre-determined number of collars should be kept in reserve to replace collars that fail prematurely. This strategy will maintain a minimum number of collars in the field while failed units await replacement and repair.

GPS Performance and Location Bias

Depending on terrain and vegetation, a GPS receiver may or may not be capable of obtaining signals from a minimum of three satellites and calculating a location. This is an inherent quality of all GPS devices, but can have significant implications for the interpretation of use versus availability statistics and other frequency-related measures (Dussault *et al.* 1999). Before electing to use this technology, we recommend that researchers assess the performance of GPS devices across the habitat types animals are expected to use. In general, large diameter, dense and tall vegetation, and steep topography will degrade signal reception (Rempel *et al.* 1995, Moen *et al.* 1996a, 1997; Edenius 1997, Rempel and Rodgers 1997, Dussault *et al.* 1999). Hence, large variation could be expected within and among study areas. For example, a collar on a tundra-dwelling animal would be expected to have a high rate of location acquisition and little habitat-related bias. Alternatively, GPS collars on animals that range across steep, vegetated mountains may have a low success rate and high bias depending on how frequently the animals venture from forests with large diameter trees into openings

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such as riparian areas or meadows. Possible solutions include generating correction factors for individual habitat types, analysing movement vectors between relocations (Rempel *et al.* 1995), or using habitat-use indices that are not dependent on the frequency of relocations.

Functionality of User-collar Communication

Capability to remotely retrieve data and diagnostics is an option available from three of the four manufacturers of GPS collars (Lotek Engineering, Newmarket, Ontario, Canada; Televilt International AB, Lindesberg, Sweden; Telonics, Inc., Mesa, Arizona, USA). Additionally, GPS collars from Lotek Engineering can be reprogrammed remotely with new location and communication schedules. The utility of these features depends on the focal species and study duration. If animal capture is inexpensive and can be performed year-round, or information about animal movement is required only for short periods, then costs related to user-collar communication may not be warranted. The heavier electronics and battery package associated with modem communication (e.g., Lotek 1000) may also be impractical for smaller mammals such as wolves (Merrill *et al.* 1998). We recommend remote data retrieval when study length exceeds collar memory and animals are difficult to capture or where animals periodically move large distances and are difficult to relocate. Ability to alter collar activity schedules is an asset where sampling strategies need to be adjusted in accordance with unpredictable animal behaviour.

Differential Correction

Differential correction is an appealing option for purchasers of GPS collars. The added precision of animal locations may be worth the additional software and base station data costs. Although differential correction can increase precision, sub-optimal satellite geometry can degrade the accuracy of many locations beyond that quoted by the manufacturer. Differential correction also has many often unforeseen drawbacks that can add to project costs, or reduce immediate usefulness of the data. The recent deactivation of selective availability (the main source of controllable error) reduces the utility of differential correction substantially, but differential correction would still reduce error associated with atmospheric distortion. Considering this, researchers should not assume that differential correction is necessary for all projects employing GPS collars, but rather should consider the utility of differential correction within the context of the hypotheses to be tested (Rempel and Rodgers 1997).

The spatial resolution of GPS without differential correction may not be sufficient to capture the movements or behaviours at the scale necessary to meet study objectives. Furthermore, there may be nothing to gain by employing differential correction to generate home range statistics or measure large-scale habitat use patterns. Where fine-scale movements can be measured, maximising accuracy may involve discarding some portion of the data (2-D locations and locations with a high HDOP), increasing vegetation and topography associated bias. If relating GPS locations to mapped features, additional accuracy gained with differential correction may be lost within the scale or error tolerances of the maps (Goodchild and Gopal 1989, Stoms 1992, Cherrill and McClean 1995). We undertook a lengthy and expensive mapping project to take advantage of the accuracy and precision offered by differential correction. We did not consider those costs when initially evaluating differential versus non-differential collars.

The utility of differential correction needs to be evaluated on a project by project basis. We opted for differential correction because we wanted to address questions relative to finescale movements and habitat use, but we underestimated the time, effort, and financial resources necessary to differentially correct location data. Users also need to consider the functionality of the post-processing software. Although we are now confident with the ability of N3WIN to provide the expected information, errors were identified in earlier versions of the software (Moen *et al.* 1998).

GPS COLLARS: A USEFUL TOOL FOR WILDLIFE SCIENTISTS?

Several of the published works discussing GPS collars have concluded with statements such as "GPS radio-telemetry has great promise for expanding our knowledge about hourly, daily, and annual patterns in moose movements and habitat selection" (Moen et al. 1996a:667-668); and "GPS-based animal-location systems will set a new standard for habitat-resource utilisation studies of large animals over the next five to 10 years." (Rodgers et al. 1996:565). Our research, although not reported here, also has demonstrated that GPS collars can provide insights into small-scale movements, infrequent behaviours such as migration events, and activities during dark and inclement weather. There is a trade-off, however, between location frequency and cost. At this point in their development, field-operation and GPS-collar maintenance require large amounts of time and money. Furthermore, there are still limitations related to the performance and reliability of GPS collars. Although we suspect that collar design will improve with time, there was little evidence of this over the 37-month duration of our study. In some instances, broad management objectives such as home range determination or habitat use may be achieved with frequent monitoring of conventional VHF-collars. Aerial or ground telemetry has fewer data-related risks (i.e., catastrophic loss) and complications, has more predictable costs, and will likely result in a larger number of individuals collared at any one time. Those advantages, however, must be weighed against the utility of relatively frequent accurate locations regardless of daylight or weather. Ultimately, the wildlife professional must chose the tool that best meets study and budget objectives.
CHAPTER 5 - MOVEMENT PARAMETERS OF UNGULATES AND SCALE-SPECIFIC RESPONSES TO THE ENVIRONMENT¹

SUMMARY

Breadth of biotic and abiotic factors that affect individual animals and ultimately populations occurs across a wide range of spatial and temporal scales that are logistically difficult to define. Most studies of animal movements and habitat selection infer biological meaning from maps of vegetation, and usually do not recognise analytically that different variables are important to animals at different scales. Researchers should, however, strive to identify breaks in scale with interpretable biological parameters if they are to imply explanatory reasoning for why animals select or move to certain parts of their range. We used a nonlinear curve-fitting model of movement rates to identify discontinuities in the scales of movement by woodland caribou collared with Global Positioning System (GPS) collars. We differentiated intra-patch from inter-patch movements, but for most combinations of individual caribou by season, we were unable to distinguish inter-patch from migratory-type movements. The bout criterion interval (t_c) used to distinguish inter- from intra-patch movements varied among seasons, and among animals except during winter. Patch heterogeneity may explain inter-animal and inter-season variation. Land-cover type, energetic costs of movement, predation risk, and spatial autocorrelation differentiated the two scales of movement when we applied logistic regressions. Small-scale movements were highly correlated, had a lower cost of movement, and were associated with cover types where foraging behaviours likely occurred. Responses by caribou to the environment are scale-dependent. We discuss the merits of the nonlinear model and the implications of these findings to the study of resource selection and animal behaviour.

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INTRODUCTION

Since the early 1980s, the spatial and temporal patterns of animal behaviour and resource selection have received considerable attention (e.g., Johnson 1980, Morris 1987, Wiens 1989, Levin 1992, Fragoso 1999, Saab 1999). With the recognition that the observed variability of an ecological system depends on the grain and extent of description, much emphasis has been placed on identifying the appropriate scale or scales of observation (Wiens 1989, Levin 1992, Bowyer *et al.* 1996). Multi-scale, hierarchical study designs have been presented as approaches that can be used to observe the scale-specific responses of animals to the environment (Legrende and Demers 1984, Addicott *et al.* 1987, Blondel 1987, Senft *et al.* 1987, Kotliar and Wiens 1990, Lavorel *et al.* 1993, Wiens *et al.* 1993*a*, Lima and Zollner 1996). Typically, however, scales of study chosen by researchers to describe and explain ecological associations of large herbivores are arbitrarily defined or coincide with plant community composition or physiognomy (e.g., feeding location, patch, home range). Those definitions may not agree with how animals perceive or respond to the environment (Wiens 1989).

Studies conducted at arbitrarily defined multiple scales may suffer from one or more important limitations. First, an incorrect definition of scale, relative to the perception of space by an animal, may result in the failure to measure responses to variables and variation relevant to the processes of interest. Small-scale processes or patterns may be averaged or large-scale variables missed depending on the scope of the measurements (Dunning *et al.* 1992, Bowers *et al.* 1996). Second, assuming measured responses are scale-independent may result in the erroneous extrapolation of processes or patterns to larger or smaller scales (Gardner *et al.* 1989, Turner *et al.* 1989, Turner 1990). Third, defining availability is ultimately a function of scale (Knight and Morris 1996). Studies that define the patch as an individual unit isolated from neighbouring patch types or beyond the dispersal distance of the organism may be incapable of assessing resource selection (Morris 1992). Fourth, arbitrary choice of scale may not permit a comparison of scale-specific processes among organisms or studies (Collins and Glenn 1997). For example, patterns of foraging behaviour or patch selection may differ greatly between studies depending on the choice of patch size. Ecologists should begin searching for ways to relate different landscapes or species to one another in common terms (Milne 1991). By successively identifying scale, describing patterns, and postulating processes, we can compare animal behaviour and resource selection among species.

Movement paths of individual animals reflect behavioural responses to environmental heterogeneity and may serve as an index of shifts in scale-dependent processes (Kotliar and Wiens 1990, With 1994). Studies of insects have drawn on measures such as fractal patterns, movement rate, length, duration, direction, and turning angle to quantify movement paths (Dicke and Burrough 1988, Aluja *et al.* 1989, Milne 1991, Turchin 1991, Turchin *et al.* 1991, Johnson *et al.* 1992, Wiens *et al.* 1993b, 1995, 1997, With 1994). Except for trailing studies at relatively small scales (e.g., Ward and Saltz 1994, dorcas gazelles (*Gazella dorcas*)), those approaches have not been used to understand behavioural patterns of far-moving organisms simply because of the logistical limitations of obtaining continuous, accurate location data. The recent advent of global positioning system (GPS) collars allows the frequent and accurate relocation of large mammals and the reconstruction of movement paths.

We modified a previously published technique (Sibly *et al.* 1990) to identify scales of movement of far-ranging large mammals over seasons. We demonstrate this approach using the movement rates generated from frequent relocations of woodland caribou collected with GPS collars. Scales of movement are compared among individuals and seasons. We discuss the application and importance of a multi-scale approach to the study of resource selection and animal behaviour.

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We followed GPS-collared caribou on the ground during winter (Chapter 2) and tracked caribou with fixed- and rotary-wing aircraft throughout the year. Based on those observations, we developed and tested two predictions relative to the identification of multiple scales of movement:

- The responses of caribou to the environment are reflected in three spatio-temporal scales of movement: feeding site, patch, and migration. Each of those scales can be defined both by the frequency of events and the rate of movement of each event. Caribou make frequent short distance moves within patches while moving between feeding sites with terrestrial and arboreal feeding lichens (Johnson *et al.* in press). Caribou move longer distances less frequently when travelling between patches containing accessible forage or to meet other requirements such as predator vigilance (Skogland 1978, Antifeau 1987, Bradshaw *et al.* 1995). Caribou infrequently move long distances at the scale of migration to take advantage of plant physiognomy, to avoid environmental conditions (e.g., deep snow) that may limit access to forage, or to reduce the risk of predation (Pruitt 1959, Bergerud *et al.* 1984, Cumming and Beange 1987, Seip 1992, Poole *et al.* in press).
- The scale-specific response of caribou to the environment will differ among animals and seasons.

METHODS

Identifying Scales of Movement: The Model

We adapted a nonlinear curve-fitting procedure developed by Sibly *et al.* (1990) to identify scales of movement. The model accommodates two-processes, or behaviours, where time between events serves as a measure by which the processes can be differentiated. Typically, the model identifies a frequent and a less frequent process (for application to foraging bout dynamics, see Gillingham *et al.* 1997). To apply the model, a nonlinear curve is fit to data, which are in the form of a log_e transformed frequency distribution of events. The model takes the form:

$$y = \log_e(N_f \lambda_f e^{-\lambda_f t} + N_s \lambda_s e^{-\lambda_s t})$$
(1)

where f and s represent fast (intra-patch) and slow processes (inter-patch), respectively, N represents the total number of events of each process, t represents time between events, and λ represents the probability that an event occurs in the next time interval. A bout criterion interval (t_c) is calculated and used to classify individual points as members of the slow or fast process:

$$t_{c} = \frac{1}{\lambda_{f} - \lambda_{s}} \log_{e} \frac{N_{f} \lambda_{f}}{N_{s} \lambda_{s}}$$
(2)

To assess whether movement rates of woodland caribou could be represented by three scales of movement (i.e., intra-patch, inter-patch, migratory), we modified the original two-process model to account for a third process:

$$y = \log_e(N_p \lambda_p e^{-\lambda_p t} + N_p \lambda_p e^{-\lambda_p t} + N_m \lambda_m e^{-\lambda_m t}), \qquad (3)$$

where f, p, and m now represent foraging, patch, and migration scales of movement, respectively.

In our modification of the Sibly *et al.* (1990) model, we did not use the frequency distribution of time between events (i.e., bites), but instead the rates of movement (v_i) between successive animal relocations:

$$v_i = l_i / t_i, \tag{4}$$

where l_i represents the distance from location *i* to location i + 1 and t_i represents the time between the acquisition of location *i* and location i + 1. We assumed that frequency of rates identified intra-patch, inter-patch or migratory scales of movement within the two- or threeprocess model.

Application of the Model

We applied both the two- and three-process models to one year of movement data collected from female woodland caribou in the Wolverine herd of northcentral British Columbia. Caribou locations were collected with two versions of GPS 1000 collars (small and large battery packs; LOTEK Engineering, Inc. Newmarket, Ontario, Canada). Locations were differentially corrected using N3WIN (V. 2.412, LOTEK Engineering). We scheduled collars equipped with small battery packs to record one location every 3 hr for a total of eight locations per day, and collars with large battery packs to record one location every 4 hr Saturday to Thursday and every 20 min on every fourth hour for each Friday (60/week).

We applied the model to the five caribou for which we had location data over an entire year (1997-98). Relocations for each animal were divided into four seasons: winter (December 1 – March 31), spring (April 1 – June 30), summer (July 1 – August 31), and autumn (September 1 – November 30). We chose the start and end dates of the seasons to match ecological events that may influence the movements and behaviour of caribou. Winter corresponded with the first lasting snowfall; spring with the melting of snow on south-facing slopes and in tree wells and the emergence of green vegetation; summer with the disappearance of snow from the study area and the most active period of vegetative growth; and autumn with the senescence of green plants.

Depending on the number of unique signals acquired by the receiver during a location attempt, and the configuration of the transmitting satellites, differentially corrected GPS locations can be as accurate as 3 - 8 m 95% of the time (Chapter 4). We omitted all locations with a horizontal dilution of precision (HDOP = index of satellite configuration) of >25, and locations generated with three satellites (2-Dimensional locations) that were not differentially

correctable. The remaining 2- and 3-Dimensional locations were used in the following analyses.

We used rates of movement, as opposed to distances, to standardise differences in sampling interval resulting from the inability of collars to acquire GPS locations for all scheduled attempts, differences in collar schedules, and slight differences in acquisition times. A missed location is the result of the GPS receiver failing to acquire signals from at least three satellites during an attempt and may lead to vegetation and topography-related bias (Rempel *et al.* 1995, Moen *et al.* 1996, Edenius 1997). Successive relocations of caribou varied from 20 min – 16 hr. We used Kolmogorov-Smirnov tests for each temporally separate combination of relocations (e.g., four versus 16 hr) to assess the affect of time between relocations on recorded movement rates (Hollander and Wolfe 1973). Those data drawn from the same population, as indicated by the Kolmogorov-Smirnov tests, were pooled for each analysis. A conservative a of 0.01 was used to control the experiment-wise error rate resulting from multiple comparisons.

We performed all analyses by individual caribou for each season. Each combination of data was fit to both the two- and three-process models (equations 1,3), and a least squares linear regression. We assessed model fit by comparing explained variation between the two- and three-process models and the linear regression. A linear fit is the expected distribution of data collected from a scale-independent process. Nonlinear regression routines and evaluations were performed in accordance with Bates (1998).

Model Effectiveness and Ecological Inference

We developed logistic regressions to assess whether the scales determined by the nonlinear model represented ecologically meaningful relationships of caribou to the environment. We compared measures for cover type (vegetation), predation risk, the costs of movement, and spatial autocorrelation of locations at different scales of movement. Logistic analyses were conducted only for winter, during those periods when we collected detailed information on foraging behaviours by following caribou on the ground (Chapter 2). Geographic information system (GIS) analyses were conducted with IDRISI (V. 4.1, V. 2, V. 32; Clark Labs 1999).

Cover Type. – We used LANDSAT V Thematic Mapper satellite imagery and Terrain Resource Information Management (TRIM) elevation data to classify the geographic area used by all collared caribou. We identified 13 cover types of unique vegetative and topographical association (Table 5.1, Appendix A).

Distance to Predation Risk. – We monitored the movements and feeding habits of 19 collared wolves from eight packs throughout the duration of the study. After excluding individuals travelling together or multiple relocations at den or kill sites, 200 relocations and seven kill sites were considered independent and located within the range of the collared caribou. Selection of habitat by wolves was inferred through a comparison of relocations and kill sites to random locations drawn from the 95% minimum convex polygon of wolf relocations. We centred an error buffer with a radius of 125 m on all wolf relocations and extracted the proportion of each cover type (Leptich *et al.* 1994). Because wolves select certain habitats for hunting versus other behaviours (Kunkel and Pletscher 2000), we arbitrarily weighted kill sites (where predation was confirmed) to have twice the influence as nonkill relocations (where wolf presence was a potential risk to caribou).

We used logistic regression to determine which cover types were most associated with wolves, and, therefore, associated with high risk of predation (Mladenoff *et al.* 1999). Predation risk is defined as the probability of encountering or being captured by a predator during some time period (Lima and Dill 1990). The significant positive coefficients of the logistic regression were used to develop a spatial surface describing the weighted distance of

Cover Type	% of Study Area	Description
Aspen/	5.8	Primarily (97%) stands of Populus tremuloides that may be associated with Pinus contorta; includes
Cottonwood		floodplains dominated by Populus balsamifera, Salix spp., and Alnus incana.
Pine Terrace	3.0	Level glaciofluvial terraces and other well-drained soils consisting of <i>P. Contorta</i> and an understory of <i>Cladina</i> and <i>Cladonia</i> spp.
Pine	7.5	Dominated by P. contorta (80%), but may occur with some component of Picea mariana or Picea engelmannii x P. glauca in older stands; prevalence of feather mosses (Pleurozium schreberi, Hylocomium splendens, Ptilium crista-castrensis), some wetter lichen types (e.g., Peltigera apthosa), and to a lesser extent Cladina or Cladonia spp.
Spruce	7.0	Dominated by <i>P. engelmannii</i> x <i>P. glauca</i> (80%), but may be a minor component of <i>P. mariana</i> , <i>P. contorta</i> , <i>P. tremuloides</i> or <i>P. balsamifera</i> ; typically at lower elevations (<1,100 m) on wetter sites.
Pine-Spruce	4.5	Level to steep slopes at lower elevations consisting of <i>P. engelmannii</i> x <i>P. Glauca</i> and <i>P. contorta</i> ; poorly to moderately developed shrub and herb layers and a continuous cover of feather mosses.
Pine-Black Spruce/ Black Spruce	9.6	Primarily (78%) older P. contorta – P. mariana stands found on level to moderate slopes associated with patches of Cladina and Cladonia spp., but characteristically feather mosses; also areas consisting of open stunted forests of P. mariana with abundant arboreal lichens.
Wetland	5.3	Shrub/sedge and forb dominated wetlands on depression landscapes with high water tables.
Lakes/Rivers	7.2	Permanent and ephemeral water bodies.
Mid-elevation Coniferous	36.1	Mid-elevation stands (1,100 – 1,600 m) composed of <i>Abies lasiocarpa</i> , <i>P. Engelmannii</i> , and <i>P. contorta</i> found on moderate to steep slopes.
Krummholz	6.8	Shrub cover of <i>A. lasiocarpa</i> on gentle to moderate slopes at elevations (1,300 – 1,600 m) just below the alpine tundra zone; associated with abundant arboreal lichens.
Alpine-Shrub	2.1	Moderate to steep slopes with extensive cover of <i>Betula glandulosa</i> or <i>Salix reticulata</i> ; <i>Altai fescue</i> , <i>Carex, Stereocaulon</i> , and <i>Cetraria</i> spp. found in openings.
Alpine-Grass	0.3	Wind-swept slopes and ridges dominated by A. Fescue, associated with Stereocaulon, Cetraria, and Cladina spp.
Alpine-Little Vegetative Cover	4.8	Flat to steep rocky terrain with sparse vegetation restricted to pockets of soil among rock outcrops; lichen-dominated cover of Umbilicaria, Cetraria, Cladina, and Stereocaulon spp.

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Table 5.1. Description of cover types found across the range of the Wolverine caribou herd in northcentral British Columbia.

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every cell to high-risk cover. This operation involved three steps: 1) for each cover type with a positive coefficient, we generated a GIS surface where every 25 x 25-m cell in the study area was assigned a risk value equal to the shortest distance to that cover type; 2) each risk value was then multiplied (weighted) by the inverse of the coefficient produced from the logistic regression; and 3) the risk values of all cells were averaged to produce one surface representing the overall proximity to risk for each cell within the study area. The greater this value, the greater the distance to high-risk cover types, and the lower the risk of predation for the animal.

Costs of Movement. - Because energetic costs of movement are related to the distance and terrain an animal travels, we used equations developed by Fancy and White (1987) to model the energy expended by a 100-kg female caribou moving across variable terrain. We used a digital elevation model (DEM) generated from TRIM data to estimate whether an animal was moving up or down slope, the mean slope of the movement path, and the change in elevation between caribou relocations (25 x 25-m pixel resolution, British Columbia Ministry of Crown Lands 1990). The energy costs (kJ·kg^{-0.75}) of walking on a horizontal snow-covered surface were calculated as the distance travelled multiplied by the cost per km (1.696 kJ \cdot kg⁻ 1 km⁻¹) corrected for sinking depths in snow of 12 - 47 cm ((0.02416 x e^{0.0635}) +1) (Fancy 1986). The net energy costs of moving uphill were calculated as the mean cost of lifting 1 kg of body weight $(1.957 \text{ kJ} \cdot \text{kg}^{-1} \cdot \text{m}^{-1})$ adjusted for slope of terrain, multiplied by the total vertical distance ascended. Energy recovered during downhill movements was calculated as the efficiency of recovery $(0.412 \text{ kJ} \cdot \text{kg}^{-1} \cdot \text{m}^{-1})$ corrected for slope, multiplied by the potential energy stored while lifting 1 kg of body weight 1 vertical m (9.79 kJ) and total vertical distance (Fancy 1986).

Spatial Autocorrelation. – We developed a distance-weighted estimate of the spatial correlation of relocations of individual caribou (Augustin *et al.* 1996). We assumed that autocorrelation decreased as distance between relocations and rate of movement increased. Spending a relatively long period in one area leads to an aggregation of caribou relocations and indicates that the animal is attracted to some suite of localised environmental characters. As distances among relocations increase, the strength of the relationship between behaviour and place decreases. Creation of the autocorrelation surface was a four-step process: 1) we stratified the caribou relocation data by animal; 2) a surface was then created where the inverse distance from each cell to the nearest relocation was calculated; and 3) a weighted averaging filter of variable size was passed over the distance surface; filter size ranged from 3 by 3 to 13 by 13 pixels with larger filters applied to animals with faster median rates of movement (Augustin *et al.* 1996). Autocorrelation values are relative and increase as density of relocations increases and distance between relocations decreases.

Data Treatment. – We stratified caribou relocations by movement rate according to the t_c . The mid-point of each vector between successive relocations was calculated and a circular buffer with a diameter equal to the distance between those two relocations was generated. We assumed the circular buffer represented the potential area over which a caribou may have ranged between relocations and that it accommodates bias associated with the failure of the GPS collars to acquire signals from at least three satellites at each attempt. The buffer was superimposed on each data layer (cover type, predation risk, cost of movement, spatial autocorrelation) and the mean value or, for cover type, the percentage of each cover type within that buffer, was extracted for analysis.

We developed a logistic regression for each animal; scale served as the dichotomous dependent variable (i.e., large- versus small-scale), and 13 cover types, cost of movement, and predation risk were the independent variables. We used Akaike's Information Criterion (AIC)

to rank and identify the cover-type variables that were most reliable for making inferences about the movement processes (Burnham and Anderson 1998). This method is best suited for a small subset of *a priori* hypotheses, but the large number of cover types and inter-animal variability led us to use a best subsets approach. We ranked all cover-type regressions from lowest AIC score to highest. For those with a difference in scores of less than two from the lowest, we calculated Akaike weights (*w*), which serve as a normalised measure, and summed the *ws* for each cover type (Burnham and Anderson 1998). Cover types that occurred frequently or with low AIC scores would, therefore, have a large summed *w* value. Those cover types with a *w* greater than 0.15 were retained and used with the other two independent variables (predation risk, cost of movement) for final regression comparisons. Because of high collinearity (tolerance <0.2) among independent variables, we developed a univariate logistic regression for each animal using scale as the dependent and degree of autocorrelation as the independent variables (Menard 1995).

We used Log Likelihood χ^2 tests, non-cross validated classification accuracy, and Nagelkerke R^2 values to assess the reliability of the logistic regressions (Menard 1995). We used the likelihood ratio test to evaluate individual coefficients. Leverage statistics and Pearson standardised residuals served to diagnose animal relocations that fit the model poorly or had a large influence on model coefficients. Independence of residuals was assessed using Durbin-Watson tests of the linear equivalents of the logistic models (Logit transform) (Neter *et al.* 1990). Independent variables were log-ratio transformed to reduce the effects of collinearity and decrease the influence of large values (Aebischer *et al.* 1993). All statistical analyses were performed with STATISTICA (V. 5.5) (Statsoft, Inc.1997). We considered tests to be statistically significant at an α of 0.05.

RESULTS

Fitting the Nonlinear Model: Distinguishing Scales of Movement

Two-process model. - Movement data of >40-min sampling intervals were drawn from similar populations (i.e., GPS relocation intervals, P < 0.001). Consequently, all data with a sampling interval >40 min were used in subsequent analyses. The nonlinear model fit the log. frequency distribution of movement rates for caribou well for most combinations of caribou by season, suggesting that large-scale processes can be differentiated from small-scale processes. A typical fit of the nonlinear model to the log, frequency distribution of caribou movement rates is shown in Fig. 5.1. In that example, a movement rate of 2.18 m/min (t_c) is used to differentiate small- from large-scale movements for caribou 042B. Variation explained by the nonlinear model ranged from 77% for caribou 042B during summer to 95.8% for caribou E41A during winter and, on average, significantly differed from the corresponding linear regression models (t = -6.667, df = 37, P < 0.001) (Table 5.2). The nonlinear model did not fit the movement data for caribou E41A during the summer (Table 5.2). In that instance, examination of the log, frequency versus movement rate plot revealed a linear relationship, whereas the other caribou-season combinations illustrated nonlinear relationships with distinct bout criteria (t_c). Average t_c values differed between seasons and individual caribou (Fig. 5.2). Absolute values ranged from 1.89 m/min for caribou 772B during spring to 13.8 m/min for caribou 1D2B during summer (Table 5.2). Mean t_c differences among animals were greatest between caribou 042B (2.96 m/min \pm 0.33 SE) and 1D2B (6.78 \pm 2.78 m/min) and among seasons between winter $(2.6 \pm 0.29 \text{ m/min})$ and summer $(8.24 \pm 3.14 \text{ m/min})$.

Three-process model. – The three-process model fit most combinations of caribou by season poorly or not at all. In several instances, the t_c values designed to separate the between-patch from migratory movements were large negative or positive numbers. In other

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Figure 5.1. Example of frequency (A) and \log_{e} frequency (B) distribution of movement rates by caribou 042B during winter (December 1997 – April 1998). A nonlinear two-process model was fit to (B) and the bout criterion (t_c) was calculated using the parameters of the fitted equation. For comparison, a linear regression (dashed line) serves as the null model of a nonscalar response.

Table 5.2. Movement rates (t_c) that differentiate small- and large-scale movements as determined by a two-process model and compared to linear regressions for five caribou across four seasons in northcentral British Columbia (1997 – 1998). Bout criterion (t_c) was calculated as m/min, %Var represents percent variation explained by each model, and NF (no fit) represents t_c values that were non-sensical or could not be calculated because of poor model fit.

· · · · · · · · · · · · · · · · · · ·	Spring		Summer		Autumn			Winter				
	Two	Proc.	Linear	Two	Proc.	Linear	Two	Proc.	Linear	Two	Proc.	Linear
Animal		%Var	r^2	$\overline{T_c}$	%Var	r^2	t _c	%Var	r^2		%Var	r^2
042B	3.72	85.0	65.8	2.77	77.0	74.4	3.17	88.1	64.9	2.18	89.0	67.5
ID2B	8.70	88.2	81.2	13.80	86.9	81.7	2.45	92.6	75.5	2.18	87 .8	52.4
772B	1.89	87.4	65.6	2.83	83.1	74.8	4.55	86.2	79.7	2.87	89.3	72.6
B91A	3,19	88.7	74.2	13.54	87.6	84.0	4.43	84.7	76.7	2.13	87.5	69.7
E41A	2.81	87.7	68.5	NF	NF	79.7	5.46	88.6	86.0	3.62	95.8	81.0



Figure 5.2. Average rate of movement (t_c) used to differentiate small- from large-scale movements calculated from nonlinear two-process models for 5 caribou of the Wolverine herd in northcentral British Columbia (1997 – 1998) by season (A) and animal (B). Error bars Represent ± 1 SE; sample sizes of the number of animals (A) or seasons (B) are included in parentheses.

instances, inspection of the fitted curves indicated that the nonlinear models overfit data. This outcome was characterised by one of the two t_c values being slightly less and the other slightly greater than the two-process t_c .

Model Effectiveness and Ecological Inference

Data on movement rates for caribou collected during winter (December 1 – March 31) were stratified by their corresponding two-process t_c values (Table 5.2). Caribou E41A had the highest ratio of small- to large-scale movements at 114.5 (229:2), followed by 1D2B at 17.6 (351:20), 772B at 6.2 (526:85), 042B at 6.2 (505:82), and B91A at 5.6 (316:56). Large-scale movements were characterised by a significantly greater distance travelled and were sampled from a different statistical population than small-scale movements (P < 0.001, locations with only a 3- or 4-hr interval; insufficient sample sizes to test caribou E41A).

With only two large-scale movements, we could not compare the two scales of movement for caribou E41A. Because of high collinearity between independent variables, we performed both a multivariate model with cover type, cost of movement, and predation risk, and a univariate model of autocorrelation for each of the other caribou. Cover types that significantly increased the risk of predation included Pine, Spruce, and Wetland/Lakes/Rivers.

All logistic regressions were statistically significant (Tables 5.3, 5.4). Caribou 042B had the highest R^2 and 772B the lowest (Table 5.3). Classification accuracy was greater for small-scale movements. Greater use of Lakes/Rivers discriminated large- from small-scale movements of caribou 042B, 772B, and B91A. Large-scale movements also were associated with patches of Mid-elevation Coniferous forest, Krummholz, and Pine-Spruce. Three of the four caribou demonstrated greater energetic costs while making large-scale movements (Table 5.3). Caribou 1D2B and 772B experienced a lower risk of predation during large-scale compared to small-scale movements. Given that the weighting factor for kill sites may have

Table 5.3. Statistical summary of logistic regression models using cover type, cost of movement, and predation risk to differentiate large- from small-scale movements by caribou 042B, 1D2B, 772B, and B91A of the Wolverine herd in northcentral British Columbia (December 1997 – April 1998).

Caribou 042B: $\chi^2 = 96.92$, $df = 6$, $P < 0.001$; $n = 580$, $R^2 = 0.28$; Class.								
$\frac{\text{accuracy} = 88.0\% \text{ (small scale = 98.0\%, large scale = 50.0\%)}}{\text{Variables Retained in Model}} \frac{B}{B} = \frac{\chi^2}{P}$								
Intercept	-3.106							
Lakes/Rivers	0.052	8.55	0.004					
Alpine-Little Vegetative Cover	-0.064	6.48	0.011					
Mid-elevation Coniferous	0.008	3.90	0.048					
Pine	-0.195	0.04	0.843					
Cost of Movement	0.002	77.27	<0.001					
Predation Risk	0.014	0.69	0.407					

Caribou 1D2B: $\chi^2 = 34.53$, df = 6, P < 0.001; n = 368, $R^2 = 0.28$; Class.

accuracy = 95.1% (small scale = 99.4%, large scale = 11.1%)						
Intercept	-6.630					
Krummholz	0.151	6.25	0.012			
Spruce	-0.022	2.02	0.155			
Lakes/Rivers	0.036	1.99	0.158			
Alpine-Grass	0.208	1.02	0.313			
Cost of Movement	0.002	19.04	<0.001			
Predation Risk	0.114	4.22	0.040			

Caribou 772B: $\chi^2 = 38.17$, df = 11, P < 0.001; n = 605, $R^2 = 0.11$; Class.

accuracy = 85.8	% (small scale =	= 99.4%,	large scale	= 0%)
•				

Intercept	-2.681		
Lakes/Rivers	0.076	8.13	0.004
Pine-Spruce	0.131	5.51	0.019
Pine Terrace	-0.052	4.01	0.045
Mid-elevation Coniferous	0.020	3.31	0.069
Alpine-Little Vegetative Cover	-0.148	3.13	0.077
Wetland	0.065	2.80	0.095
Aspen/Cottonwood	-0.188	2.44	0.119
Alpine-Shrub	0.099	0.77	0.379
Pine	-0.114	0.24	0.623
Cost of Movement	0.001	1.45	0.229
Predation Risk	0.024	6.40	0.011

Caribou B91A: $\chi^2 = 28.05$, df = 7, P < 0.001; n = 366, $R^2 = 0.13$; Class. accuracy = 85.3% (small scale = 98.4%, large scale = 7.6%)

		,	
Intercept	3.167		
Lakes/Rivers	0.101	6.55	0.011
Alpine-Grass	0.088	2.96	0.086
Alpine-Little Vegetative Cover	0.066	1.25	0.264
Mid-elevation Coniferous	0.102	0.80	0.371
Cost of Movement	0.001	15.83	<0.001
Predation Risk	0.014	7.37	0.414

Table 5.4. Statistical summary of logistic regression models using the spatial autocorrelation
of movements to differentiate large from small-scale movements by caribou 042B. 1D2B,
772B, and B91A of the Wolverine herd in northcentral British Columbia (December 1997 -
April 1998). All logistic regressions were statistically significant ($P < 0.001$).

Statistic	Caribou				
	<u>042B</u>	1D2B	<u>772B</u>	<u>B91A</u>	
Classification Accuracy (%)					
Total	91.7	95 .7	93.9	92.6	
Small Scale	96.8	99.7	96.2	96.2	
Large Scale	60.0	16.7	79.5	71.7	
R^2	0.64	0.46	0.73	0.76	
χ^2	254.47	59.08	309.07	203.17	
Ν	580	368	605	366	
Intercept	3.531	1.500	5.210	5.380	
B (autocorrelation index)	-0.215	-0.107	-0.391	-0.164	

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influenced the results relative to predation risk, we also determined that a non-weighted logistic model had little influence on these conclusions. Small-scale movements occurred in patches of Alpine-Little Vegetative Cover and Pine Terrace. Relative to the multivariate logistic regressions, the univariate regressions had noticeably larger R^2 values and higher classification accuracy for the large-scale movements (Table 5.4). For all of the animals, small-scale movements were more highly autocorrelated than large-scale movements.

DISCUSSION

Model Fit and Interpretation

We adapted the Sibly *et al.* (1990) nonlinear model to delineate scale-specific movements of woodland caribou because of its founding in applied behavioural research and the intuitive nature of the measured parameters. Rates and frequencies are observable biological phenomena that can be directly related to use of the environment. We predicted that changes in the frequency of movements would reflect particular behaviours that are interpreted as scale-specific responses to the environment. This interpretation and the workings of the model are consistent with much of the theory concerning the hierarchical relationships of ecological phenomena. Hierarchy theory is premised on the assertion that scale can be identified using the frequencies and rates of activities (Allen and Star 1982). Senft *et al.* (1987) adopted those principles and identified an ecological hierarchy of large foragers using the frequencies of foraging events (i.e., selection of diet, feeding-area, home range).

In our study, we predicted that caribou would respond to the environment in a hierarchical fashion, with frequency of movements of a particular rate defining within-patch, between-patch, and migratory-type behaviours. For most combinations of caribou and season, the three-process model was ineffective at discriminating scales of movement that occur when caribou migrate. Nonsensical t_c values or overfitting of the model to the data indicated that

either the technique is insensitive to events with a very low frequency (e.g., migration), or that those events were absent from the data. The variability in t_c values further suggested that this form of the model was not useful relative to the data we analysed.

The negative result does not imply that a three-process model is inappropriate for all situations. We encourage researchers to apply the nonlinear model according to their knowledge of the subject species and its behaviour. Although not demonstrated by Sibly *et al.* (1990), the technique will accommodate more than three processes. In our study, the two-process model achieved a good fit to all but one combination of data for caribou by season. We interpret all movements less than the t_c threshold as frequent small-scale intra-patch movements, which likely correspond with foraging behaviours, and all movements greater than the respective t_c as less frequent inter-patch and migratory movements.

Although sample sizes were too small to perform statistical tests, t_c values visibly differed between some combinations of animal and season (Fig. 5.2), supporting our second prediction. Caribou demonstrated a wide range of within-season behaviours and life-history strategies. For example, over the four winters that we monitored animals, some remained exclusively within alpine or within forested habitats, whereas others ranged across both habitats. Inter-season differences were likely a product of the temporal and spatial variation in forage distribution and accessibility and other biological determinants such as calving and rutting.

In summer, the two-process model did not fit data for caribou E41A and t_c values for two of the other four caribou were notably greater than t_c values in other seasons. The linear and near linear fits (i.e., as t_c increases, the data approaches linearity) for those animals suggest that woodland caribou may respond to the environment in a nonscalar fashion during the summer. Forage is relatively abundant during that season and the environment less patchy, resulting in a continuum of movement over the range of scales we measured. In contrast, t_c values during winter were small and exhibited little variability. This is consistent with a relatively patchy environment, where snow conditions and lichen distribution restrict foraging activity to small discrete patches. During two winters of tracking caribou on the ground (Chapter 2), we observed caribou in both the alpine and forest foraging intensely over relatively small areas and then moving some distance to new patches. Similarly, during the spring and autumn, green vegetation is in a state of flush, or sequestration and dormancy, respectively, leading to a patchy environment. Calving and rutting also may lead to scale-dependent movement behaviours. Others have noted a behavioural response by *Rangifer* to variations in environmental patchiness. This includes the tracking of vegetation release following snow melt (Skogland 1980, 1984), selection of feeding areas and sites where the snow conditions are favourable for cratering (Adamczewski *et al.* 1988, Nellemann 1996, Chapter 2), the use of areas with relatively high biomass or proportion of most nutritional plants (White and Trudell 1980, Helle and Tarvainen 1984), and the selection of snow patches for behavioural thermoregulation or as relief from insect harassment (Ion and Kershaw 1989).

Although we have discussed a few possible explanations for scale-explicit responses to a patchy environment, we acknowledge that the suite of biotic and abiotic factors that influence the movements of caribou are too numerous to parameterise and understand all possible interactions. Environmental heterogeneity is, however, well documented as a causal agent in the movement and distribution of terrestrial and aquatic animals and can result in scale-dependent behavioural responses (Fahrig and Paloheimo 1988, Kotliar and Wiens 1990, Schaefer and Messier 1995, Wallace *et al.* 1995, Bellamy *et al.* 1998, Logerwell *et al.* 1998). The nonlinear model appears to reflect the response of caribou to environmental heterogeneity, where heterogeneity occurs within spatial and temporal domains. Patches that differ in size, composition, and configuration across time and space elicit that response.

Ecological Inference: The Importance of a Multi-scale Approach

Our assertion that the two-process nonlinear model is an effective means of differentiating scales of movement is supported by logistic regression analyses. If the logistic regressions had not fit data on movement, we would conclude that either a scaling relationship was not present, the nonlinear model was ineffective at discriminating scales, or the scale of patchiness that we mapped misrepresented the scale of patchiness to which caribou respond. For the multivariate regression models, R^2 values were relatively low and there was a high misclassification of large-scale movements. When animals move between patches they probably do not avoid cover types associated with small-scale movements. At the level of detail we mapped the landscape, perfect separation of movements based on cover type is highly unlikely and some discrimination error should be expected. Misclassification of cover types (see Appendix A) and the resulting errors in the map of predation risk (i.e., based on cover type) also could obscure relationships between movements and those independent variables.

The R^2 values and large-scale classification accuracy were the lowest for the multivariate regression of caribou 772B (Table 5.3). This animal travelled over the greatest area and likely transited patches of all cover types at both scales. The relatively high t_c value indicates a less localised or patchy response to the environment, further reducing our ability to precisely differentiate small- from large-scale behaviours. Relative to the three other caribou, the movement data for 1D2B had a poor fit to the univariate model. This animal made few large-scale movements while ranging over a relatively small area that encompassed two hillsides. This behaviour resulted in little contrast between the spatial correlation of small-and large-scale movements. Caribou B91A also had a small range spending a large portion of the winter moving across the alpine. This animal, however, made several large-scale movements into the forest providing a strong contrast with the smaller-scale behaviours.

Variation in the fit of the regression models between animals illustrates a key consideration for studies measuring animal responses to heterogeneity: the grain, extent, and number of patch types should be organism-defined as opposed to observer-defined (Kotliar and Wiens 1990, Knight and Morris 1996). Our trailing studies revealed finer scales of patchiness (e.g., distribution of terrestrial lichens) (Chapter 2). There also may be larger scales of heterogeneity consisting of collections of patches (Stuart-Smith *et al.* 1997). The land-cover map that we used appears to represent one patch scale that is relevant to the foraging decisions of woodland caribou. For example, alpine dwelling woodland caribou forage on patches of terrestrial lichens within larger patches identified as Alpine–Little Vegetative Cover. The two-process model identified the small intra-patch movements within those patches and the larger inter-patch movements between those and other cover types.

The behavioural tendency of caribou to spend time concentrating foraging across a relatively small area followed by a move to another patch was captured by the autocorrelation variable. Repeated small-scale movements are a response to a spatially correlated environment (i.e., forage or snow conditions). This pattern also has been observed for moose fitted with GPS collars (Rodgers *et al.* 1996, Pastor *et al.* 1997). We acknowledge that because of the inability of GPS collars to acquire locations equally across all cover types, this variable may be biased toward those cover types with little vegetative cover (i.e., more locations = higher autocorrelation). We inspected plots of relocations collected in the alpine and forest and are confident that cover-type bias was not strong enough to obscure differences in the relative frequency of relocations at small and large scales.

The energetic costs of movement were greatest at large scales for three of the four caribou tested (Table 5.3). As would be expected, caribou making large-scale movements traversed greater distances and topographic variability than animals making small-scale movements. This is consistent with our assumption that rate is correlated with distance. As

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previously discussed, caribou 772B had a more uniform distribution of movement events and was the exception to this trend.

Decisions such as habitat selection, time dedicated to predator vigilance, and animal positioning relative to escape cover may all be modified by the presence of predators or the perceived risk of predation (Hirth 1977, Hughes *et al.* 1994, Roberts 1996, Cowlishaw 1997, Frid 1997, Kramer and Bonenfant 1997). Risk-adverse behaviours may result in significant time and energy costs and direct consequences for individual fitness (Lima and Dill 1990). Of four caribou we analysed, 1D2B and 772B demonstrated that risk differed between large- and small-scale movements. In those instances, distance to risk was greater, and the risk of predation lower, during large-scale movements. This difference is likely the result of those caribou foraging across high-risk, low-elevation areas and then making large-scale movements across lower-risk forest types to access alpine or mid-elevation habitats.

This research demonstrates that the response by animals to the environment may vary depending on the scale of measurement and highlights the importance of defining perception of scale by the animal (Knight and Morris 1996, Pastor *et al.* 1997). We identified two scales of movements that we hypothesise are consistent with a broad group of within-patch behaviours (e.g., foraging, ruminating, social interaction) and movement to other patches. Adopting a single-scale approach in conventional use versus availability (Thomas and Taylor 1990) or analyses of resource selection functions (Boyce and McDonald 1999) would result in the intra-patch movements being lumped with the inter-patch movements. The overall affect on the conclusions of those analyses would depend on the frequency of inter-patch movemental variables may still be apparent, but relocations collected while those animals were engaged in inter-patch movements would add 'noise' to the prediction process (Gardner *et al.* 1989). Caribou B91A had the lowest ratio of intra- to inter-patch movements and would be most

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susceptible to the effects of pooling locations. Further, a single-scale approach may result in the loss of infrequent events. For example, we attempted to identify migratory movements with the three-process model, but were unsuccessful. Despite sample size limitations to modelling habitat selection in our study, identification of large-scale movements may provide insight into the use of corridors and the importance of habitat connectivity (Lord and Norton 1990, Keitt *et al.* 1997).

Description of animal movements and habitat selection at large spatial scales is largely concerned with the question of *where*. Biological meaning often is inferred from animal relocations related to maps of vegetation (Bradshaw *et al.* 1995) or differences in home-range size (Stuart-Smith *et al.* 1997). The assumption is made that animal distribution is correlated to vegetation and that specific vegetation types drive animal movements at all scales. Using a two-process nonlinear model, we demonstrated that different variables are important to caribou at different spatial scales. These findings suggest that to imply explanatory reasoning for *why* animals select or move to certain portions of their range, it may be necessary to identify the scales at which animals respond to the environment. By using scale to delimit behaviour, we can begin to infer mechanisms that drive movement and resource selection and ultimately population processes.

CHAPTER 6 - A BEHAVIOURAL APPROACH TO UNDERSTANDING THE MOVEMENTS OF WOODLAND CARIBOU AT LARGE SPATIAL SCALES1

SUMMARY

Different factors affect habitat selection at different scales. Choosing an inappropriate scale for habitat analyses may result in patterns that are artefacts of scale as opposed to those that actually reflect selection. Most previous studies of woodland caribou-habitat relationships have concentrated strictly on vegetation and topography, with little emphasis on spatial and temporal dynamics associated with animal behaviour. We used a nonlinear curve-fitting model of frequent locations collected with Global Positioning System (GPS) collars to identify discontinuities in the scales of movement by woodland caribou found in forested and alpine (above tree-line) habitats. We differentiated intra- from inter-patch movements, and identified collections of patches (multiple-patch scale) where caribou concentrated intra-patch movements. We assessed the response of caribou to land-cover type (vegetation), predation risk, energetic costs of movement, and patch configuration. Our multi-scale approach provided insights into the processes that govern caribou-habitat relationships not revealed by previous studies conducted at single or arbitrary spatial scales. Intra-patch movements were highly correlated, indicative of a strong relationship between behaviour and place. Caribou in the forest selected patches of Pine Terrace, whereas caribou in the alpine selected patches of Alpine-Little Vegetative Cover. Predation risk was not a factor influencing the intra-patch scale. Selection of cover types was more variable during inter-patch movements. At that scale, caribou selected patches of Pine Terrace, Lakes/Rivers, Alpine-Little Vegetative Cover, and Alpine-Grass. The routes selected by caribou had lower energetic costs relative to surrounding terrain, and during some winters caribou were subjected to higher levels of

predation risk during those movements. At the multiple-patch scale, selection was more specific and encompassed patches of Alpine-Little Vegetative Cover, Alpine Grass, and Pine Terrace. Predation risk was relatively unimportant at the multi-patch scale, but animals that moved from forested to alpine habitats reduced their relative risk of predation over winter. Patch configuration, consisting of patch adjacency and contagion, was a poor predictor of those areas where caribou concentrated intra-patch movements. There was some evidence of caribou selecting patches of Pine Terrace within a matrix of Wetlands and Pine-Black Spruce/Black Spruce patches. Caribou in the alpine avoided patches of Alpine-Little Vegetative Cover adjacent to forest types. Our results, relative to conservation strategies for woodland caribou, indicate that forest managers should maintain widely distributed patches of Pine Terrace and ensure that low-elevation areas used for inter-patch movements are not fragmented, relative to increased moose and predator populations, by forest management operations.

INTRODUCTION

Woodland caribou in British Columbia and across North America are a high-priority management species (Cumming 1992). Historical trends of declining populations or extirpated herds have necessitated management schemes that not only conserve and stabilise existing populations, but possibly enhance others (Edmonds 1988). In British Columbia, Canada, an increased demand for merchantable timber has led to a heightened awareness of the potential conflict between human encroachment and the requirements of caribou. To meet the needs of both industry and caribou, resource managers, planners, and biologists must understand the processes governing movements and distribution of those animals relative to

¹ Chapter will be submitted for publication with the following authorship: C.J. Johnson, K.L. Parker, D.C. Heard, and M.P. Gillingham.

several potentially limiting factors including forage, predators, the energetic costs of movement (i.e., movement routes), and snow (Stevenson and Hatler 1985).

Previous studies of woodland caribou have taken relatively coarse-grained approaches to explaining caribou-habitat relationships. Caribou locations at one or several arbitrarily defined scales have been related to generalised maps of vegetation and topography (Bradshaw *et al.* 1995, Steventon 1996, Terry and Wood 1999, Poole *et al.* in press), with little emphasis on how limiting factors vary at different scales. Because processes were not investigated and can only be assumed, the inferences of those studies are limited to time and site-specific events, and therefore have limited predictability.

As with those studies, the habitat requirements of large mammals are often inferred through studies of use versus availability (e.g., Alldredge and Ratti 1992). Typically, we measure use of resources (e.g., habitat, forage) relative to resource availability; a positive ratio suggests selection and a negative ratio is presumed to be avoidance. Although widely used by wildlife ecologists, use versus availability approaches suffer from several shortcomings (Aebischer et al. 1993). One conceptual limitation is defining used and available resources appropriately. Analyses are frequently designed to recognise habitat selection as hierarchical and patterns of selection as differing between scales or levels within the hierarchy (Johnson 1980). The definitions of those scales, however, are often arbitrary or based on criteria with little direct relationship to the ecological responses of the study species (e.g., choice of study area boundary) (Porter and Church 1987). Because the observed variability of an ecological system is conditional on the scale of description, detection of appropriate scales of study is key to understanding processes (Stommel 1963). Thus, studies should be designed to measure effects at scales specific to the response of species to the environment (Morris 1987, Wiens 1989).

Many use versus availability analyses implicitly assume that habitat is the vegetation or cover types occurring across the study area. Habitat is "the resources and conditions present in an area that produce occupancy - including reproduction and survival - by a given organism" (Hall et al. 1997:175). Processes that govern the movements, distribution, and habitat use of a species, however, also include dynamic factors such as predation risk, snow, parasites, and population density. By including a larger suite of explanatory variables than vegetative associations and assessing their importance across a range of scales, our study encompassed what Lima and Zollner (1996) termed "a behavioral ecology of ecological landscapes." We adopted a multi-scale behavioural approach to investigate processes that govern caribou-habitat relationships. Our premise was that different factors affect selection and behaviour by caribou at different scales. For example, animals may forage in relatively predator-safe areas with respect to the overall landscape, but select feeding sites where forage is most available at a microsite scale. Similarly, animals may concentrate foraging efforts in forests, but rest on open frozen lakes where predators can be detected. Therefore, our approach included an animal-based measure to identify three scales of habitat use and availability, employing maps of vegetation based on ecological criteria, and investigating previously unexplored effects of predation risk, landscape configuration, and the energetic costs of movement. Such a process-based approach will allow us to more confidently generalise results to other populations of caribou, while better estimating the effects of environmental perturbations such as forest harvesting (Hobbs and Hanley 1990).

Our objectives were to use frequent relocation data to identify three spatiotemporal scales of movement by caribou that were not arbitrarily defined (i.e., not defined *a priori* by the researchers, but rather by the animals; see Chapter 5), and to evaluate selection of environmental features at each of those scales. At the smallest scale, we assessed the influence of correlated movements, and selection of cover types and relative predation risk on

short small-scale intra-patch movements that we assumed were representative of foraging bouts within a patch. We considered a patch to be all levels of heterogeneity larger than the feeding site, but not extending beyond the most dominant and observable ecotone. At a larger scale, we assessed selection of cover types, areas of low predation risk, and terrain (relative to energetic costs of movement) on longer movements that we inferred to be inter-patch movements. At the third scale, we assessed selection of multiple patches relative to composition and configuration of cover types and predation risk. At each of those scales, we used movements by the animals to delineate resource availability. Because the variety and availability of forage is most limited during the winter and caribou typically spend the summer months at high elevations distant from forest harvesting (Seip 1998), we focused our investigations on the activities of female caribou during winter.

METHODS

Caribou and Wolf Relocations

We conducted analyses using movement data collected from a group of female woodland caribou referred to as the Wolverine herd (Heard and Vagt 1998) between March 1996 through March 1999 (Appendix B: Fig. B.1; Appendix C: Fig. C.1). Animals were captured, collared, and sampled as in Chapters 4 and 5. We also used very high frequency (VHF, Lotek Engineering, Newmarket, Ontario, Canada; Telonics, Inc., Mesa, Arizona, USA), Argos satellite (Telonics, Inc., Mesa, Arizona, USA), and GPS collars (Televilt International AB, Lindesberg, Sweden) to monitor the movements and feeding habits of 19 collared wolves from eight packs throughout the duration of the study.

Identifying Scales of Movement

We used a nonlinear curve-fitting model of rates of movement between successive caribou relocations (developed in Chapter 5, sensu Sibly *et al.* 1990) to identify two scales of movement. Small-scale intra-patch movements were assumed to occur at a greater frequency and with lower movement rates relative to inter-patch movements. Using this approach, we calculated a bout criterion (t_c) and used it to classify movements according to membership within one of the two scales. Movement rates of caribou $< t_c$ were considered to be small-scale movements; rates $> t_c$ were large-scale movements. We distinguished the third scale of selection (areas where caribou concentrate small-scale movements) as the area of all smallscale movements that occur following and before the next large-scale inter-patch movement.

Habitat Attributes

We developed a series of geographic information system (GIS) routines to quantify environmental features that may influence the distribution of caribou at three scales of movement. Cover type, predation risk, the costs of movement and the autocorrelation variables were generated with procedures outlined in Chapter 5. For these analyses, we also a priori selected two measures of patch configuration that may be related to caribou behaviour. We used a contagion index to determine if caribou selected areas dominated by large patches of a single land-cover type (Baskent and Jordan 1995). Large values are generated for collections of patches that predominantly consist of few cover classes; small values arise from collections of patches that comprise many different cover types in approximately equal proportions. We also calculated adjacency matrices to determine if caribou select arrangements of juxtaposed cover types (Mladenoff and DeZonia 1999). Values ranged from 0 - 100% and represented the proportion of cells of one cover type that were neighboured by a second cover type. We used APACK (V. 2.11) to calculate the contagion and adjacency metrics (Mladenoff and DeZonia 1999). All other GIS analyses were conducted with IDRISI (V. 4.1, V. 2, V. 32; Clark Labs 1999).

Selection Analyses

Caribou relocations were stratified by individual, year, and scale of selection according to the corresponding *t_c*. For intra- and inter-patch movements, the mid-point of each vector between successive relocations was calculated and a circular buffer with a diameter equal to the distance between the two relocations was generated (Fig. 6.1). We assumed the circular buffer represented the potential area over which a caribou may have ranged (i.e., used habitat) between relocations and accommodated bias associated with the failure of the GPS collars to acquire signals from at least three satellites at each attempt. The buffer was superimposed on each data layer (cover type, predation risk, spatial autocorrelation, cost of movement) and the mean value or, for cover type, the percentage of each cover type within that buffer, was extracted for analysis as used habitat. Multiple-patch composition consisted of the proportion of cover types or predation risk averaged across all successive intra-patch movements separated by large-scale inter-patch movements. Metrics for multiple-patch configuration were calculated from a rectangular area of pixels bounding all of those intra-patch movements (Fig. 6.1).

To identify selection for habitat variables at each scale, we compared used areas with corresponding random areas. The spatial area of the random area was set to not exceed the maximum expected linear distance a caribou could move relative to the paired used area. For intra-patch movements, this was calculated as the t_c multiplied by the relocation interval (e.g., 4 hr); for inter-patch movements, the third quartile of inter-patch rates was multiplied by the corresponding relocation interval (Fig. 6.1). We considered the third quartile rate to be more conservative and representative than the maximum recorded rate because maximum rates could be related to larger scales than we examined (e.g., migration). The buffer size of each random location was equal in area and did not overlap the paired caribou relocation. For

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Figure 6.1. Schematic representation of the sampling design used to define small-scale intrapatch movements, large-scale inter-patch movements, and areas used for multiple-patch configuration metrics, using GPS relocations collected from caribou of the Wolverine herd in northcentral British Columbia (March 1996 – April 1999). selection of multiple-patch areas, a location was randomly chosen from the circumference of a circle centred on the last recorded intra-patch movement and of a radius equal to the distance of the next inter-patch movement. The random location was equal in size to the summed area of all previous intra-patch locations.

We pooled locations for animals by scale, year, and occupation of forested habitats, alpine habitats or both. Exclusive occupation of one habitat was arbitrarily defined as a ratio of 5:1 locations below or above 1,650 m (tree-line). Where sample sizes permitted, we developed a logistic regression for each component of the landscape (i.e., forest, alpine, forestalpine) for each of the four winters (Manly *et al.* 1993, Type III Analysis). Selected and random locations served as the dichotomous dependent variables for each regression. We tested the influence of correlated movements, cover types and predation risk on intra-patch movements; cover types, predation risk, and the energetic costs of movement on inter-patch movements; and cover types, predation risk, and land-cover configuration (patch contagion and adjacency) on the selection of areas consisting of multiple patches. Relative to configuration, we tested whether cover types selected at that scale occurred in a matrix of lesser-used types, as identified by published reports and our on-site field investigations (Chapter 2). We used Akaike's Information Criterion (AIC), as in Chapter 5, to identify and rank the cover types used in the final regression comparisons.

We evaluated reliability of logistic regressions using Log Likelihood χ^2 tests, non-cross validated classification accuracy, and Nagelkerke R^2 values (Menard 1995). We used a derivation of the Relative Pratt index to assess the importance and relative strength of independent variables (Thomas and Zumbo 1997, Thomas *et al.* 1998). Explained variation of each logistic model was partitioned amongst the independent variables; all variables with a score of >1/(2p) were considered important, where p represents the number of variables in the model (Thomas and Zumbo 1996). We used tolerance scores to reveal variables with

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excessive collinearity (threshold of <0.2, Menard 1995), and leverage statistics and Pearson standardised residuals to diagnose cases that fit the model poorly or had a large influence on model coefficients. Independent variables were log-ratio transformed to reduce the effects of collinearity and decrease the influence of large values (Aebischer *et al.* 1993). All statistical analyses were performed with STATISTICA (V. 5.5) (Statsoft, Inc. 1997). Unless otherwise noted, we considered tests to be statistically significant at an α of 0.05.

Snow Depth

Throughout three of the four winters (excluding 1995-96), we collected snow depths at 12 stations located across the range of the collared caribou; measurements, however, were inconsistently made because of travel logistics. Data were insufficient to model regional snow depths and include as a variable within the logistic-regression analyses. We, therefore, used linear regression to explore those data for trends in depth from south to north, east to west, and over time. Snow depths were averaged across two-week periods resulting in eight periods for each winter (December 1 – March 31). Only those snow stations with data for at least four periods in a year were analysed.

RESULTS

Caribou Locations

Over four winters (December 1 – March 31) we collected 7,218 caribou locations from 16 individual caribou (Appendix B: Fig. B.1). We collected GPS data from seven of the 16 animals for more than one winter. Because animals ranged over a large study area $(5,100 \text{ km}^2)$ with variable topography (Appendix B), snow conditions differed between years (Appendix E), and collared caribou did not consistently select the same habitat (forest, alpine, forest-alpine) across winters, we considered data from each winter to be independent. Consequently, we developed models of selection for 25 'animals' (Table 6.1).
Model	Caribou	Date Collected	t _c	t _c Number of		Forest:Alpine	
		(dd/mm)		SS	LS	· · · · ·	
95-96 - Forest-Alpine	771A	01/03-31/03	1.26	136	59	62:133	
95-96 - Forest-Alpine	BAIA	01/03-31/03	1.33	120	25	100:45	
95-96 - Alpine	831A	13/03-31/03	1.88	9 4	27	8:113	
95-96 - Alpine	851A	12/03-31/03	1.88	127	15	0:142	
95-96 - Alpine	B 91A	12/03-31/03	1.88	118	16	0:134	
96-97 - Forest	041A	01/12-11/02	1.25	168	58	226:0	
96-97 - Forest	1DIA	01/12-23/12	1.88	59	13	72:0	
96-97 - Forest	771A	01/12-25/12	1.88	37	12	49:0	
96-97 - Forest	772 B	21/02-31/03	0.95	146	33	179:0	
96-97 - Forest-Alpine	0E2B	23/02-27/03	1.88	68	22	31:59	
96-97 - Forest-Alpine	E41A	01/12-31/03	1.47	369	108	103:374	
96-97 - Alpine	852 B	01/12-25/03	1.53	420	55	6:4 6 9	
96-97 - Alpine	B 91A	01/12-31/03	1.45	521	62	0:583	
97-98 - Forest	1D2 B	01/12-24/03	2.18	351	20	371:0	
97-98 - Forest	832 B	10/12-31/03	3.89	516	32	547:1	
97-98 - Forest	E41A	01/12-31/03	3.62	229	2	231:0	
97-98 - Forest-Alpine	772 B	01/12-31/03	2.87	526	85	433:178	
97-98 - Alpine	042B	01/12-31/03	2.18	505	82	43:544	
97-98 - Alpine	B 91A	01/12-31/03	2.13	316	56	40:332	
98-99 - Forest	852B	11/12-31/03	1.40	247	64	271:40	
98-99 - Forest-Alpine	042B	10/12-31/03	1.13	297	59	98:258	
98-99 - Forest-Alpine	1 D2B	19/12-31/03	1.59	338	39	223:154	
98-99 - Forest-Alpine	843C	01/12-31/03	1.69	528	100	155:473	
98-99 - Forest-Alpine	B94D	26/03-31/03	1.88	22	5	11:16	
98-99 - Alpine	B91A	11/03-31/03	1.88	9 8	8	0:106	

Table 6.1. Summary of movements of caribou of the Wolverine herd in northcentral British Columbia (March 1996 – April 1999) and bout criteria (t_c) used for logistic regression analyses.

¹ SS and LS refer to small-scale intra-patch and large-scale inter-patch movements, respectively.

² All movements above 1,650 m were considered to occur in alpine habitats.

Eight caribou spent most of their winters in forested habitats, eight spent winter in alpine habitats, and nine spent some portion of winter in both alpine and forested habitats. Of those animals with continuous location data over a winter (approximately four months), four, four, and five resided in the forest, alpine, and mixed forest and alpine habitats, respectively. Bout criteria (t_c) separating small- from large-scale movements ranged from 0.95 – 3.89 m/min. For animals with few locations, model fit often was inconclusive (See Chapter 5 for a discussion of model assessment). In those instances for which there were <150 relocations or data collection occurred for less than one month (n = 8), we applied the mean t_c of the models fit to the other caribou (1.88 m/min).

Predation Risk

We recorded 650 wolf relocations and 13 kill sites (Appendix D: Fig. D.1). Of the total, 200 relocations and seven sites where moose had been killed by wolves were treated as independent (excluding individuals travelling together or multiple relocations at den or kill sites) and were located within the range of the collared caribou and used for these analyses. Because there were no differences in the percentage of cover types used during snow or snow-free periods (Rao's R = 0.907; df = 11,402; P = 0.533), we pooled all wolf relocations for logistic regression analysis (Table 6.2; $\chi^2 = 99.452$, df = 11, P < 0.001, $R^2 = 0.28$;

Classification Accuracy = 72%). Patches of Pine, Spruce, and Wetlands/Lakes/Rivers (with significant positive regression coefficients) were areas most likely for caribou to encounter wolves, and consequently be subjected to greater risk of predation (Fig. 6.2).

Intra-patch Selection

Small-scale movements by caribou were observed in each of the three habitats (forest, alpine, forest-alpine) in all four winters, except for the forest during the first year of the study (1995-96). Results from the forest likely reflect low sample size. All logistic models of

Variable	В	χ ²	P
Intercept	0.341		
Mid-elevation Coniferous	-0.185	24.315	<0.001
Wetland/Lakes/Rivers	0.071	22.113	<0.001
Pine	0.037	18.147	<0.001
Spruce	0.068	14.601	<0.001
Alpine	-0.206	7.925	0.005
Krummholz	-0.077	4.783	0.029
Aspen/Cottonwood	-0.039	3.272	0.071
Pine-Black Spruce/Black Spruce	0.047	2.379	0.123
Spruce-Pine	-0.073	1.169	0.280
Pine Terrace	-0.094	0.741	0.389
Roads/Clear Cuts	0.006	0.007	0.935

Table 6.2. Logistic regression model differentiating wolf relocations and kill sites from random locations relative to cover types in the Wolverine caribou herd study area of northcentral British Columbia (March 1996 – April 1999).



Figure 6.2. Distribution of predation risk, as determined from wolf relocations, across the range of the Wolverine caribou herd of northcentral British Columbia (March 1996 - April 1999). Predation risk decreases as distance from high-risk patch types (Pine, Spruce, and Wetlands/Lakes/Rivers) increases.

intra-patch selection were significant (Table 6.3). While in the alpine, caribou selected patches of Alpine-Little Vegetative Cover (Table 6.4). Animals in the forest consistently selected Pine Terrace, whereas caribou ranging across both the forest and alpine selected a combination of the former two cover types. To a lesser extent, small-scale movements occurred in Wetlands and Pine-Black Spruce/Black Spruce areas. During winter 1995-96, caribou also demonstrated selection for Mid-elevation Coniferous patches. Predation risk had little influence on selection at the intra-patch scale, but during the winter 1998-99 caribou occurring in the alpine selected areas with a relatively greater distance to high-risk cover types (i.e., $d_j >$ importance criterion). The autocorrelation variable explained a large amount of the variation captured by all models. That variable had a mean importance rating (i.e., $\sum d_j$ / Total Number of Models [Alpine or Forest or Mixed]) across all winters of 0.74, whereas patches of Pine Terrace and Alpine-Little Vegetative Cover had values of 0.13, and in order of decreasing importance: 0.030 for Pine-Black Spruce/Black Spruce, 0.021 for Mid-elevation Coniferous, and <0.02 for Wetland, Alpine-Grass, and Distance to Predation Risk.

Inter-patch Selection

Large-scale movements by caribou occurred in the same habitats as intra-patch selection and were significant for all combinations of year and habitat, but sample size was insufficient to test movements recorded for alpine habitats during winter 1998-99 (Table 6.3). Cover types selected by caribou for inter-patch movements included Pine Terrace and Alpine-Little Vegetative Cover, as well as Lakes/Rivers, Alpine-Shrub, Alpine-Grass, Wetland, Pine-Black Spruce/Black Spruce, and Aspen/Cottonwood (Table 6.5). Costs of movement were typically less across selected terrain. Caribou making inter-patch movements through alpine during the winter of 1995-96 and through forest during the winters of 1996-97 and 1997-98 chose routes with a greater risk of predation, although caribou moving across forest and alpine Table 6.3. Statistical summary of logistic regression models of selection by caribou in northcentral British Columbia (March 1996 – April 1999) at scales of intra-patch movements, inter-patch movements, and collections of patches relative to composition and configuration.

					Classificatio	on Accuracy
Model	χ^2	df	P	R^2	Random	Caribou
		•			Locations	Locations
Intra-Patch Selection						
95-96 - Forest-Alpine	110.53	9	<0.001	0.26	63.8	64.1
95-96 - Alpine	234.35	8	<0.001	0.39	78.1	70.0
96-97 - Forest	149.87	9	<0.001	0.22	66.3	64.2
96-97 - Forest-Alpine	258.97	12	<0.001	0.34	74.1	64.1
96-97 - Alpine	765.90	9	<0.001	0.34	76.9	73.1
97-98 - Forest	708.14	13	<0.001	0.28	77.3	71.7
97-98 - Forest-Alpine	304.65	10	<0.001	0.34	71.5	69 .2
97-98 - Alpine	332.63	10	<0.001	0.18	71.1	64.6
98-99 - Forest	132.91	9	<0.001	0.32	77.i	67.9
98-99 - Forest-Alpine	427.70	12	<0.001	0.17	68.5	62.5
- 98-99 - Alpine	76.40	6	<0.001	0.44	78.7	75.3
Inter-Patch Selection						
95-96 - Forest-Alpine	38.80	7	<0.001	0.28	57.3	78.1
95-96 - Alpine	71.41	7	<0.001	0.64	82.1	88.9
96-97 - Forest	33.63	9	<0.001	0.18	60.9	74.6
96-97 - Forest-Alpine	76.07	11	<0.001	0.35	67.7	79.2
96-97 - Alpine	84.36	8	<0.001	0.41	70.7	92.0
97-98 - Forest	19.76	6	0.003	0.23	57.7	73.6
97-98 - Forest-Alpine	50.39	7	<0.001	0.35	65.1	80.5
97-98 - Alpine	56.56	8	<0.001	0.25	57.4	76.8
98-99 - Forest	31.88	7	<0.001	0.30	65.6	87.3
98-99 - Forest-Alpine	91.05	9	<0.001	0.26	60.2	74.9
Patch Composition						
95-96 - Forest-Alpine	27.85	7	<0.001	0.35	75.6	76.6
95-96 - Alpine	44.34	8	<0.001	0.59	81.6	89.5
96-97 - Forest	50.28	7	<0.001	0.44	70.3	79 .0
96-97 - Forest-Alpine	67.66	9	<0.001	0.52	73.5	88.6
96-97 - Alpine	76.24	7	<0.001	0.54	69.4	93.4
97-98 - Forest	21.26	8	0.007	0.34	83.8	80.0
97-98 - Forest-Alpine	25.67	6	<0.001	0.27	64.9	64.4
97-98 - Alpine	43.10	7	<0.001	0.29	59.6	79.8
98-99 - Forest	31.86	7	<0.001	0.43	70.7	70.7
98-99 - Forest-Alpine	27.62	7	<0.001	0.12	58.5	70.2
Patch Configuration						
95-96 - Forest-Alpine	6.30	5	0.278	0.09	53.3	55.3
95-96 - Alpine	2.08	3	0.557	0.04	45.7	61.5
96-97 - Forest	7.46	4	0.114	0.08	59.4	67.7
96-97 - Forest-Alpine	22.55	8	0.004	0.20	38.0	87.5
96-97 - Alpine	31.30	4	<0.001	0.25	47.4	89.3
97-98 - Forest	7.27	5	0.201	0.13	67.6	54.3
97-98 - Forest-Alpine	19.95	6	0.003	0.21	67.2	54.2
97-98 - Alpine	11.71	5	0.0 39	0.08	46.7	63.4
98-99 - Forest	5.98	4	0.200	0.09	64.3	58.1
98-99 - Forest-Alpine	12.77	5	0.030	0.06	33.3	83.0

Table 6.4. Variables affecting small-scale intra-patch movements by caribou in northcentral British Columbia (March 1996 – April 1999) as determined by logistic regression models of cover types, distance to predation risk, and correlated locations. Variables are considered important where d_i is greater than the importance criterion shown in brackets.

Model	Variable ¹	B	SE	d_j
95-96 - Forest-Alpine (0.056)	Autocorrelation	0.034	0.005	0.71
	Mid-elevation Coniferous	0.104	0.025	0.15
	Alpine-Grass	0.076	0.021	0.05
95-96 - Alpine (0.063)	Autocorrelation	0.050	0.005	0.86
•	Alpine-Little Vegetative Cover	0.123	0.026	0.17
96-97 - Forest (0.056)	Autocorrelation	0.024	0.003	0.66
	Pine Terrace	0.088	0.014	0.31
96-97 - Forest-Alpine (0.042)	Autocorrelation	0.044	0.005	0.61
	Alpine-Little Vegetative Cover	0.132	0.025	0.13
	Pine Terrace	0.167	0.034	0.12
	Wetland	0.085	0.035	0.03
96-97 - Alpine (0.056)	Autocorrelation	0.051	0.003	0.82
	Alpine-Little Vegetative Cover	0.142	0.017	0.14
	Alpine-Grass	0.118	0.014	0.04
97-98 - Forest (0.039)	Autocorrelation	0.068	0.004	0.75
	Pine Terrace	0.106	0.012	0.17
	Wetland	0.095	0.014	0.06
97-98 - Forest-Alpine (0.05)	Autocorrelation	0.092	0.008	0.69
	Alpine-Little Vegetative Cover	0.119	0.020	0.11
	Pine-Black Spruce/Black Spruce	0.097	0.019	0.08
	Pine Terrace	0.073	0.019	0.06
	Distance to Predation Risk	-0.011	0.005	0.03
97-98 - Alpine (0.05)	Autocorrelation	0.038	0.003	0.63
	Alpine-Little Vegetative Cover	0.123	0.013	0.37
98-99 - Forest (0.056)	Autocorrelation	0.119	0.015	0.75
	Pine Terrace	0.150	0.026	0.23
	Pine-Black Spruce/Black Spruce	0.047	0.021	0.04
	Distance to Predation Risk	0.032	0.016	0.03
98-99 - Forest-Alpine (0.042)	Autocorrelation	0.028	0.002	0.83
	Pine-Black Spruce/Black Spruce	0.164	0.022	0.09
	Alpine-Little Vegetative Cover	0.031	0.011	0.03
98-99 - Alpine (0.083)	Autocorrelation	0.140	0.023	0.86
	Distance to Predation Risk	0.095	0.035	0.10
	Alpine-Little Vegetative Cover	0.129	0.054	0.09

¹ Only those cover types associated with selection (i.e., positive regression coefficient B) and variables with an importance value ≥ 0.025 are listed.

Table 6.5. Variables affecting large-scale inter-patch movements of caribou in northcentral British Columbia (March 1996 – April 1999) as determined by logistic regression models of cover types, movement terrain, and distance to predation risk. Variables are considered important where d_i is greater than the importance criterion shown in brackets.

Model	Variable ¹	B	SE	<i>d</i> ,
95-96 - Forest-Alpine (0.071)	Alpine-Grass	0.088	0.040	0.37
·····	Cost of Movement	-0.001	0.001	0.29
	Alpine-Shrub	0.076	0.049	0.22
	•			
95-96 - Alpine (0.071)	Alpine-Little Vegetative Cover	1.24	0.347	0.52
	Distance to Predation Risk	-0.188	0.052	0.20
	Cost of Movement	-0.001	0.001	0.11
	Wetland	0.398	0.168	0.10
96-97 - Forest (0.056)	Pine Terrace	0.130	0.103	0.17
	Lakes/Rivers	0.093	0.049	0.17
	Distance to Predation Risk	-0.016	0.032	0.06
	Spruce	0.024	0.056	0.05
	Aspen/Cottonwood	0.066	0.052	0.05
	Cost of Movement	-0.001	0.001	0.03
96-97 - Forest-Alpine (0.046)	Alpine-Grass	0.148	0.052	0.21
·····	Distance to Predation Risk	0.065	0.035	0.21
	Pine Terrace	0.138	0.071	0.13
	Cost of Movement	-0.001	0.001	0.11
	Wetland	0.068	0.071	0.03
96-97 - Alpine (0.063)	Alpine-Little Vegetative Cover	0.918	0.265	0.60
	Cost of Movement	-0.001	0.001	0.22
97-98 - Forest (0.083)	Pine Terrace	0.166	0.063	0.46
	Distance to Predation Risk	-0.091	0.04	0.43
	Cost of Movement	-0.001	0.001	0.07
	Krummholz	0.146	0.071	0.04
97-98 - Forest-Alnine (0.071)	Pine Terrace	0 289	0.098	0 38
	Lakes/Rivers	0 211	0.108	0.18
	Cost of Movement	-0.001	0.001	0.18
97.98 Almine (0.063)	Cost of Movement	0.001	0.001	0.43
97-98 - Alpine (0.003)	Lokes/Divers	-0.001	0.001	0.42
	Pine Terrace	0.096	0.049	0.07
		0.220	0.114	0.04
98-99 - Forest (0.071)	Lakes/Rivers	0.223	0.075	0.33
	Cost of Movement	-0.001	0.001	0.17
	Pine-Black Spruce/Black Spruce	0.133	0.113	0.15
	Pine Terrace	0.040	0.075	0.06
	Alpine-Little Vegetative Cover	0.184	0.076	0.04
98-99 - Forest-Alpine (0.056)	Cost of Movement	-0.001	0.001	0.38
	Alpine-Grass	0.064	0.025	0.17
	Aspen/Cottonwood	0.118	0.038	0.16
	Lakes/Rivers	0.046	0.041	0.04

ⁱ Only those cover types associated with selection (i.e., positive regression coefficient B) and variables with an importance value ≥ 0.025 are listed.

areas during the winter of 1996-97 were subjected to lower risk of predation. Of all the independent variables across all models and winters, the cost of movement was most important (mean $d_j = 0.198$), although patches of Pine Terrace (mean $d_j = 0.177$) and Alpine-Little Vegetative Cover (mean $d_j = 0.166$) contributed almost equally.

Composition of Multiple-patch Areas

Caribou selected multiple-patch areas that were on average 182 ha, but extremely variable (SD = 2,844 ha), for intra-patch movements. Composition of cover types and distance to predation risk differed between selected and random areas (Table 6.3). Caribou in the forest chose collections of patches consisting of Pine Terraces, whereas animals in the alpine selected areas of Alpine-Little Vegetative Cover (Table 6.6). Animals ranging across both the forest and alpine selected collections of patches consisting of the former two cover types. During the winters of 1995-96 and 1998-99, caribou in Forest-Alpine areas were farther from high predation-risk areas than were randomly available. Across winters, areas of Alpine-Little Vegetative Cover had the largest mean importance rating (0.379) to models describing multiple-patch selection, followed by Pine Terraces (0.313).

Configuration of Multiple-patch Areas

In general, configuration of patches was most important when caribou ranged across alpine habitats. In contrast to the other three scales of selection, several of the models (including all forest models) describing differences in the configuration of patches across selected and random areas were nonsignificant (Table 6.3). Patches of Alpine-Little Vegetative Cover adjacent to Krummholz or Mid-elevation Coniferous areas were consistently avoided. Caribou in the alpine selected patches of Alpine-Grass adjacent to Mid-elevation Coniferous patches, but animals in forest-alpine areas avoided that juxtaposition of patch types (Table 6.7). Instead, those caribou selected for Pine Terraces adjacent to Wetlands and Pine-Black Spruce/Black Spruce areas, and in the winter of 1997-98 avoided patches adjacent to Table 6.6. Variables affecting selection of multiple-patch areas by caribou in northcentral British Columbia (March 1996 – April 1999) as determined by logistic regression models of cover types and distance to predation risk. Variables are considered important where d_j is greater than the importance criterion shown in brackets.

Model	Variable ¹	B	SE	d _j
95-96 - Forest-Alpine (0.071)	Alpine-Little Vegetative Cover	0.150	0.055	0.53
	Alpine-Grass	0.074	0.055	0.18
	Distance to Predation Risk	0.034	0.035	0.12
	Pine Terrace	0.080	0.132	0.03
95-96 - Alpine (0.063)	Alpine-Little Vegetative Cover	0.505	0.153	0.70
96-97 - Forest (0.071)	Pine Terrace	0.181	0.039	0.61
96-97 - Forest-Alpine (0.056)	Pine Terrace	0.399	0.107	0.30
-	Alpine-Little Vegetative Cover	0.226	0.076	0.29
	Alpine-Grass	0.150	0.061	0.03
96-97 - Alpine (0.071)	Alpine-Little Vegetative Cover	0.4 9 7	0.144	0.54
97-98 - Forest (0.063)	Pine Terrace	0.141	0.085	0.33
	Pine-Black Spruce/Black Spruce	0.047	0.100	0.09
	Distance to Predation Risk	-0.020	0.041	0.07
	Pine	0.117	0.130	0.03
97-98 - Forest-Alpine (0.083)	Alpine-Grass	0.252	0.096	0.28
-	Pine Terrace	0.094	0.042	0.25
97-98 - Alpine (0.063)	Alpine-Little Vegetative Cover	0.128	0.048	0.39
-	Alpine-Grass	0.050	0.042	0.05
98-99 - Forest (0.071)	Pine Terrace	0.242	0.070	0.63
	Spruce	0.108	0.057	0.12
	Alpine-Little Vegetative Cover	0.101	0.136	0.05
	Distance to Predation Risk	0.050	0.040	0.04
98-99 - Forest-Alpine (0.071)	Distance to Predation Risk	0.020	0.022	0.23
	Alpine-Little Vegetative Cover	0.021	0.035	0.15
	Alpine-Grass	0.039	0.039	0.10
	Pine Terrace	0.058	0.036	0.04

¹ Only those cover types associated with selection (i.e., positive regression coefficient B) and variables with an importance value ≥ 0.025 are listed.

Table 6.7. Variables affecting selection of multiple-patch areas by caribou in northcentral British Columbia (March 1996 – April 1999) relative to patch configuration, as determined by logistic regression models of patch adjacency and contagion; \rightarrow indicates patch type 1 adjacent to patch type 2. Variables are considered important where d_j is greater than the importance criterion shown in brackets.

Model	Variable ¹	B	SE	d_i
96-97 - Forest-Alpine (0.063)	Alpine-Little Vegetative Cover → Krummholz	-0.124	0.055	0.64
	Alpine-Little Vegetative Cover -> Mid- elevation Coniferous	-0.078	0.081	0.16
	Pine Terrace → Wetland	0.022	0.025	0.13
	Alpine-Grass -> Mid-elevation Coniferous	-0.080	0.178	0.05
	Contagion	0.291	0.337	0.04
96-97 - Alpine (0.125)	Alpine-Little Vegetative Cover → Krummholz	-0.0 9 4	0.041	0.43
	Alpine-Grass -> Mid-elevation Coniferous	0.160	0.081	0.27
	Contagion	0.493	0.310	0.17
	Alpine-Grass → Krummholz	-0.032	0.024	0.14
97-98 - Forest-Alpine (0.083)	Pine Terrace → Pine-Black Spruce/Black Spruce	0.023	0.012	0.34
	Pine Terrace → Wetland	0.068	0.042	0.22
	Alpine-Grass -> Krummholz	0.323	0.255	0.16
	Contagion	-0.574	0.410	0.15
	Pine Terrace → Lakes/Rivers	-0.128	0.094	0.09
	Alpine-Grass → Mid-elevation Coniferous	0.163	0.286	0.03
97-98 - Alpine (0.1)	Alpine-Little Vegetative Cover -> Krummholz	-0.033	0.015	0.47
	Contagion	-0.450	0.272	0.25
	Alpine-Grass -> Krummholz	-0.014	0.013	0.14
	Alpine-Grass → Mid-elevation Coniferous	0.073	0.053	0.13
98-99 - Forest-Alpine (0.1)	Alpine-Grass -> Krummholz	-0.031	0.015	0.49
	Alpine-Little Vegetative Cover → Mid- elevation Coniferous	-0.028	0.017	0.30
	Alpine-Grass → Mid-elevation Coniferous	-0.029	0.050	0.07
	Contagion	0.243	0.218	0.07
	Alpine-Little Vegetative Cover -	-0.004	0.008	0.06
	Krummholz			

ⁱ Only those cover types associated with selection (i.e., positive regression coefficient B) and variables with an importance value ≥ 0.025 are listed.

Lakes/Rivers. Patch contagion was important for three of the five significant models. There was no consistent trend, however, to suggest that caribou chose multiple-patch areas consisting of larger patches of fewer cover types (i.e., with positive contagion values).

Snow Depth

Snow depths were recorded during at least four of eight two-week periods in winter during 1996-97 (seven stations), 1997-98 (nine stations), and 1998-99 (three stations) (Appendix E: Table E.1, Figs E.1, E.2, E.3). During winter 1996-97 we did not collect snow depths at the most southern portion of the caribou range, as we did in 1997-98 and 1998-99. In 1996-97, snow depths did not differ between stations relative to their north to south (F =2.88, df = 1, 49, P = 0.096, $r^2 = 0.06$) or east to west (F = 2.51, df = 1, 49, P = 0.12, $r^2 = 0.05$) orientations, but increased significantly over time (F = 41.95, df = 1, 49, P < 0.001, $r^2 = 0.46$). The average range of depths between stations was 25.8 cm (\pm 4.9 SE). Snow depths increased in 1997-98 from north to south (F = 10.66, df = 1, 45, P = 0.002, $r^2 = 0.19$) and over time (F =37.49, df = 1, 45, P < 0.001, $r^2 = 0.46$), but showed no trends relative to the east to west direction (F = 1.91, df = 1, 45, P = 0.174, $r^2 = 0.04$). The average range of snow depths between stations was 31.7 \pm 6.6 cm. Sample size was insufficient to perform analyses for the 1998-99 winter.

DISCUSSION

Relative to other boreal and sub-boreal ungulates, woodland caribou characteristically demonstrate frequent movements and seasonal or inter-seasonal migrations (Cumming 1992). Movements may be in response to predation risk, avoidance of insects, forage accessibility as dictated by snow, forage availability as dictated by grazing intensity and season, or social aggregations such as during rut (Helle and Tarvainen 1984, Bergerud and Page 1987, Ion and Kershaw 1989, Nellemann 1996). Caribou in northcentral British Columbia spent some time at locations making a series of small-scale movements, presumably while foraging, followed by less frequent moves of longer distance to other patches or locations on the landscape (Table 6.1). Others have noted similar patterns of movements of ungulates using GPS-collar data (Rodgers *et al.* 1996, Pastor *et al.* 1997) and direct observations (Ward and Saltz 1994).

Scales of Selection

We used movement rate as an index of animal behaviour to identify scales of selection, and were able to compare selection at spatial scales defined by caribou as opposed to the researcher (Morris 1987, Pastor *et al.* 1997). Where previous habitat studies on caribou identified multiple scales of selection, analyses specifically differentiated use and availability of habitat types within and outside home ranges (Bradshaw *et al.* 1995, Terry and Wood 1999, Poole *et al.* in press), but with little attention to temporal and spatial dynamics. The movement rates of caribou permitted us to explicitly define availability relative to the behaviour of an individual caribou.

Depending on the questions asked and phenomena measured, the scale of investigation may determine findings and alter conclusions. Choosing an inappropriate scale for use or availability may result in the reporting of patterns that are artefacts of scale as opposed to the actual dynamics of interest (Wiens 1989). We recognise that our study only examined a subset of the possible scales representing the movements and selection habits of caribou (Allen and Starr 1982). For example, while trailing caribou through winter habitats, we observed finer scales of selection that were a response to heterogeneity greater than our habitat maps (Chapter 2).

Caribou also make choices that result in scales of selection larger than those measured at a series of individual movements. Animals may choose alpine habitats over forested habitats or migrate to portions of their range to meet seasonal requirements (e.g., calving). Terry and Wood (1999) and Wood and Terry (1999) reported that caribou in the south of our study area made northerly movements from early to late winter ranges and that caribou were more likely to winter in the forest during years of less snow. Six of our collared caribou also spent December in the south of the study area before moving north towards areas with alpine habitats. We had insufficient data to model snow depths, but during 1997-98, snow depths decreased from the south to the north of the study area. Although the absolute differences in snow depths between snow stations were small, they may have exceeded a threshold for which the energetic gains of cratering were less than the costs (Fancy and White 1985). During our on-site field investigations we observed alpine habitats with shallower snow relative to forested habitats (Chapter 2). Those animals that moved to the alpine may have selected snow conditions that permitted greater access to terrestrial lichens. That scale of selection is larger than the scales of movement we identified, and would only be apparent after several cumulative inter-patch movements.

Selection of Cover Types

Particular cover types were selected consistently across the four winters and three spatial scales that we identified. Patches of Pine Terrace and Alpine-Little Vegetative Cover were prevalent at intra-patch, inter-patch, and multiple-patch scales. Our smaller-scale site investigations revealed that caribou selected feeding sites across Pine Terraces that provided abundant *Cladina* and *Cladonia* lichens (Chapter 2). Similarly, within patches of Alpine-Little Vegetative Cover and Alpine-Grass, caribou selected feeding sites on wind-swept ridges with *Stereocaulon, Cladina, Cetraria,* and *Thamnolia* lichens. There also were notable among-scale differences in selection of cover types. Wetlands and patches of Pine-Black Spruce/Black Spruce were selected during intra- and inter-patch movements more frequently than at the multiple-patch scale. Lakes/Rivers and patches of Alpine-Shrub and Aspen/Cottonwood were important cover types exclusively during inter-patch movements.

The cover types selected by caribou in our study during winter are in general agreement with other studies of woodland caribou in central British Columbia. Terry and Wood (1999) also reported that caribou of the Wolverine Herd selected stands of lodgepole pine, wetlands, and alpine habitats. Caribou in westcentral British Columbia selected stands of dry lodgepole pine, meadows, and alpine habitats (Cichowski 1993), or were associated with old forest on sites of poor productivity and with wetland mosaics (Steventon 1996). Caribou of the Takla herd, south of our study animals, selected spruce-fir forests and alpine habitats during winter (Poole et al. in press). Our multi-scale approach, however, revealed differences in cover type between scales and allowed us to test a wider range of variables while linking the behaviour (movement patterns) of the animals at smaller scales to those areas selected (Chapter 2). Furthermore, where previous studies used forest inventory data with little sensitivity to caribou-vegetation relationships, our map of cover types was developed to represent ecological types (e.g., Pine Terraces), with likely relevance to caribou biology (Appendix A). Further, large numbers of relocations per individual allowed us to consider a greater number of cover types during the analyses.

Distance to Predation Risk

Relative to predation risk, the spatial separation hypothesis (James 1999) asserts that to minimise risk, caribou should distance themselves from moose and their principal predator, wolves. Studies of caribou-moose-wolf interactions in Alberta, British Columbia, and Ontario showed that caribou and moose selected different habitats, wolves and moose were associated with similar habitats, and moose were the primary prey of wolves (Bergerud 1985, Seip 1992, Cumming *et al.* 1996, James 1999). We did not monitor the locations of moose, but assumed wolves mimicked the habitat affinities of their principal prey species, as was observed by James (1999). The premise of our risk variable is that caribou have knowledge of, and avoid locations where the probability of encountering a predator is high. Three assumptions govern this relationship: 1) wolves preferentially select specific locations to hunt, inferring that wolves can not be everywhere at one time and, therefore, concentrate their efforts in the most productive locations for prey abundance or ease of capture: 2) prey location is related to vegetation; and 3) independent of cover type, actual or perceived wolf distribution encompasses the entire study area. Bouskila and Blumstein (1992) assumed that knowledge of predation risk was exercised through simple rules. Using an optimisation model, they concluded that animals attempt to track fluctuations in predation risk despite incomplete or inaccurate knowledge, but rules that overestimate risk should lead to lower mortality. Jedrzejewski and Jedrzejewska (1990) demonstrated that bank voles (*Clethrionomis glareolus*) were just as likely to avoid pens scented with weasel (*Mustela nivalis*) as those that actually contained weasel. Similarly, caribou may use vegetation to evaluate risk (sensu Hirth 1977). Because wolves can not be in all patches of a similar vegetation type at all times, such a rule would overestimate actual risk, but perhaps represent perceived risk.

Particular cover types in our study area presented a greater risk to caribou or moose of encountering a predator, as demonstrated by logistic regression analysis of wolf relocations and kill sites (Table 6.2). By weighting the distance from any one place across the landscape to risk-prone cover types, we were able to measure the risk of inhabiting a patch adjacent to a high-risk cover type and to lessen sharp transition areas at patch boundaries. With the exception of one winter, predation risk was unimportant at the scale of intra-patch movements. Although distance from high-risk patches will differ among locations within any one patch, variation over what was considered available might have been too small to detect selection or avoidance of low-risk areas. This outcome is consistent with our implicit assumption that caribou evaluate predation risk at scales larger than the patch (i.e., we assigned risk values to patches of a specific type). Predation risk was most important during inter-patch movements. This resulted from animals transiting higher risk cover types such as Lakes/Rivers, patches of Spruce, and Wetlands (Table 6.2, 6.5) when moving between patches. Fuller and Keith (1980) reported that most wolf kills of moose during the winter occurred in lowland habitats despite an equal distribution of moose across lowland and upland areas. Nelson and Mech (1991) noted that white-tailed deer (*Odocoileus virginianus*) were more vulnerable to wolf predation during large-scale migratory movements.

Predation risk at the scale of multiple-patches was unimportant for three of the four winters. Only in 1997-98 did caribou in the forest tend to be in areas of higher predation risk (Table 6.6). Alternatively, during the winters of 1995-96 and 1998-99 caribou occupying both forest and alpine habitats selected areas of lower predation risk. This result likely reflects the contrast between high-risk valley bottoms and low-risk alpine areas where caribou moving to high-elevation habitats reduced their overall risk across the winter. Those data represent the cumulative movements and relative risk experienced by caribou that transit the forest and alpine landscapes.

Our data illustrate that risk is scale-dependent and that it must be considered relative to the range of cover types occupied by caribou. For movements at the inter-patch scale, risk occurs relative to short-term occupancy of risk-prone cover types. Caribou also may respond to predation risk at scales beyond what we defined as multiple-patch selection. Distance to risk was the greatest between low- and high-elevation habitats (Fig. 6.2, Appendix B: Fig. B.1). Selection of alpine habitats may be a strategy to maximise the distance from high-risk valley bottoms (Bergerud and Page 1987). Small differences in risk across low-elevation forested areas and strong selection by wolves for particular patch types suggest that the advantages of spatial separation to caribou are not simply proportional to distance and that the hunting behaviour of wolves is also a product of more than just distance to prey (e.g., predictability). To minimise risk, caribou should avoid patches where moose are typically found or occupy alpine or mid-elevation habitats.

Research across a large number of terrestrial and aquatic species has demonstrated that predation risk is an important component of animal behaviour (see Lima and Dill 1990 for review). We can, however, only speculate about how individuals perceive or measure risk (Lima and Dill 1990). Our results do not reveal whether caribou were actively choosing lowrisk habitats or fortuitously experienced lower risk through the selection of habitats associated with a greater abundance or accessibility of desirable forage species. Furthermore, if caribou were actively reducing their risk, we are unsure whether they were avoiding moose or wolves. Within the constraints of available data, we are confident that wolves were not hunting within habitats strongly selected by caribou as foraging areas (i.e., Pine Terrace, Alpine-Little Vegetative Cover, Table 6.2). From our observations, wolves appeared to hunt more abundant and spatially predicable moose. Caribou selecting low-risk patches adjacent to high-risk cover types or travelling through high-risk patches, however, may decrease their distance from wolves and increase the probability of becoming secondary prey (Holt 1984). The complexity of choice increases when animals attempt to minimise risk while meeting daily or seasonal nutritional requirements (Ferguson et al. 1988, Hughes et al. 1994, Heard et al. 1996, Bowyer et al. 1999, Kie et al. 1999).

Correlated Movements

Small-scale intra-patch movements of caribou were highly correlated relative to random locations (Table 6.4). Frequent sampling of animal relocations for movement analyses can violate the statistical assumption of independence of error terms. One solution has been to use a statistical test based on Schoener's ratio (Schoener 1981) to decrease the sampling interval to the point where relocations are considered independent (Slade and Swihart 1983, Swihart and Slade 1985*a*,*b*,1986). McNay *et al.* (1994) demonstrated that for animal movements with skewed distributions, an independence interval based on Schoener's ratio was excessive and led to the classification of most data as dependent. They recommended that researchers sample systematically through time rather than identify a time interval representative of independent locations. Although our average relocation interval (~7.5 hr) was greater than used to indicate independence for pronghorns (*Antilocapra americana*. >4 hr), coyotes (*Canis latrans*, >6 hr), and white-tailed deer (>4 hr) (Reynolds and Laundré 1990, Holzenbein and Marchinton 1992), we still chose to explicitly model autocorrelated movements. This reduced the potential for violating statistical assumptions (Neter *et al.* 1990) and permitted an exploration of the biological meaningfulness of autocorrelation.

A large portion of the variation between random and recorded intra-patch movements by caribou was explained by autocorrelation. This outcome suggests that caribou responded to resource heterogeneity at a finer scale than we mapped ($<25 \times 25$ -m pixel or 625 m^2). These findings also suggest that resources have a patchy rather than random distribution (Kotliar and Wiens 1990). Our investigations at smaller scales showed that caribou are selective at fine scales (i.e., feeding sites) based on the presence of certain lichen species and snow depth, density, and hardness, which may limit access to those lichens (Chapter 2).

Energetic Costs of Movement

Anecdotal observations and published reports suggested that, independent of predation risk, caribou should transit flat valley bottoms with little topographic relief during large-scale movements (Wiens *et al.* 1993, Wiens *et al.* 1997). Relative to surrounding mountainous terrain, those areas offer the lowest energetic costs relative to distance travelled and are more likely be associated with foraging habitats (e.g., Pine Terrace) (White and Yousef 1978, Fancy and White 1987). Our approach of calculating the energetic costs of moving up slope, down slope, or across flat terrain may not have considered all factors affecting those costs (e.g., sinking depth in snow, speed of travel), but we believed it to be more representative than comparisons based only on differences in slope and elevation (Krist and Brown 1994). For all winters, caribou moved across topography with lower energetic costs relative to what was available (i.e., caribou selected terrain that facilitated level or downhill movements more often than uphill movements). This is consistent with features such as valley bottoms and lowlands associated with Lakes/Rivers, a cover type prevalent at that scale (Table 6.5). Selection of topography may be more important for alpine-dwelling caribou because of the greater topographic extremes across smaller areas.

Composition and Configuration of Patches

Researchers typically quantify the composition of available and selected habitats, but do not report spatial configuration of those same habitat patches. Numerous landscape metrics, however, are available to quantify spatial arrangement, size, and shape of individual patches and collections of patches (Baskent and Jordan 1995, McGarigal and Marks 1995, Gustafson 1998). Most tests of patch configuration have been relative to habitat requirements of avian species (Coker and Capen 1995, McGarigal and McComb 1995, Bellamy *et al.* 1998, Saab 1999), although Stuart-Smith *et al.* (1997) calculated several measures for distinct landscapes occupied by caribou in northeastern Alberta.

We did not describe patterns of patch configuration, but tested for differences in configuration between what was selected by caribou and what was available. Our analyses were designed using information from previous studies and our observations (Paré and Huot 1985, Cichowski 1993, Terry and Wood 1999). We tested whether cover types selected at the scale of multiple-patch areas occurred in a matrix of lesser used Wetlands, Pine-Black Spruce/Black Spruce areas, or Lakes/Rivers. Wetland complexes consisting of those cover types contain sedges (*Carex* spp.), abundant arboreal lichens (*Bryoria* spp.), and mineral licks, all of which may have value to caribou. We also assessed whether cover types selected in the

alpine occurred adjacent to forested patches (Krummholz or Mid-elevation Coniferous) containing arboreal lichens.

Relative to patch composition, and in contrast to studies of other fauna (Hokit *et al.* 1999, Saab 1999), indices of patch configuration served as poor indicators of those collections of patches chosen by caribou. For those significant logistic models containing forest adjacencies (1996-97, 1997-98), caribou selected patches of Pine Terrace adjacent to Wetlands and Pine-Black Spruce/Black Spruce stands. Site investigations revealed some foraging activity within those cover types, but it was less frequent than cratering for terrestrial lichens in adjacent Pine Terrace patches (Chapter 2). We speculate that, although their distribution is limited, sedges in wetlands may serve as a protein supplement (Skoog 1968, Klein 1982, Bradshaw *et al.* 1995) for a diet dominated by high-energy, but low-protein lichens (Thing 1984, Russel *et al.* 1993, Dannell *et al.* 1994).

Patch configuration was more important to caribou ranging across the alpine. Caribou consistently avoided patches of Alpine-Little Vegetative Cover adjacent to forest patches (Table 6.7). This suggests caribou selected Alpine-Little Vegetative Cover while at high elevations and avoided patches of that type at low elevations near forest cover. This may be a strategy to maximise distance from predators, or to select more exposed wind-swept slopes. Adjacencies of Alpine-Grass were inconsistent across winters. During some winters, animals selected areas adjacent to forest cover whereas in others, they avoided them. We observed caribou foraging in Krummholz patches on arboreal lichens on only one occasion, and Midelevation Configuous cover was important at the intra-patch scale during only one winter (1995-96) (Chapter 2). Differences between winters may be due to inter-animal variation in selection.

During some winters, large patches of a single type (i.e., positive coefficients for contagion, Table 6.7) dominated areas selected by caribou, whereas other winters were

characterised by collections of smaller patches. This suggests that the distribution of patch types and sizes varies across the study area and that caribou selected a range of patch collections.

CONSERVATION IMPLICATIONS

Resource managers attempting to meet conservation objectives for woodland caribou are concerned principally with the negative effects of forest practices. Relative to natural disturbance, forest harvesting alters the composition and seral distribution of commercial tree species across large areas, leading to at least a temporary reduction in the availability of suitable forage for caribou while increasing that available for moose (Cumming 1992, Seip 1998). The distribution and abundance of wolves can be expected to increase in proportion to moose (Messier 1994). Studies of caribou-forestry interactions have reported that caribou may abandon or avoid harvested and partially harvested areas for >12 years (Darby and Duquet:c 1986, Chubbs *et al.* 1993, Cumming and Beange 1993).

Our research suggests that caribou respond to the environment hierarchically and that forest practices should recognise a range of scale-dependent requirements. Caribou occurred in either forest, alpine or a combination of forest and alpine habitats during any one winter. Across those broad geographic areas, caribou were most restrictive in their general choice of collections of patches, but within those areas selected a wider variety of cover types for making intra- or inter-patch movements. For forest-dwelling caribou, patches of Pine Terrace, comprising only 3% of the study area (Table 5.1), were important at the three scales we analysed. There also was weak evidence that patches of Pine Terrace contained within a matrix of Wetlands and Pine-Black Spruce/Black Spruce stands were desirable. Caribou in the alpine used patches of Alpine-Little Vegetative Cover (<5% of the study area), which were spatially distinct from the forest. Although alpine habitats are not of interest to the forest industry, mining development and the needs of animals occupying both forest and alpine habitats must be recognised. Road building adjacent to alpine and krummholz habitats may also facilitate the movements of predators and increase the risk of predation to caribou occupying high-elevation areas (James 1999).

Connectivity of cover types across the landscape should be defined relative to animal responses to cover type and arrangement (Wiens *et al.* 1997). The female caribou we monitored were selective when making inter-patch movements, but chose a wider range of cover types than at the other two scales. This indicates that animals may be less constrained by cover type during large-scale movements. The prevalence of Lakes/Rivers and level topography indicates that valley bottoms may serve as movement corridors, although large-scale movements were not restricted to low-elevations. When animals did make inter-patch movements they were subject to a greater risk of predation. Successional changes influencing moose and wolf numbers would have their greatest influence on caribou at that scale, and could possibly create population sinks, fragment their range, or isolate alpine from forested habitats (Lord and Norton 1990, Harrison and Voller 1998). Low-elevation areas that connect disparate portions of a caribou range should be recognised during forest development planning and treated as special management zones.

Our results and recommendations are in agreement with the more general coarse-filter ecosystem management approach of Seip (1998). He recommended that areas managed for caribou maintain large unfragmented patches of older forest that support terrestrial lichens and serve to spatially separate caribou from early seral habitats where moose and wolves may be encountered. To provide such a distribution of stand ages, Seip (1998) suggested a harvesting regime of large clearcuts (i.e., 250 – 1000 ha) that mimic the natural disturbance patterns (i.e., fires) of boreal and sub-boreal forests inhabited by northern caribou. The breadth of biotic and abiotic stimuli that affect individual animals and ultimately populations occurs across a wide spatial and temporal range. Failing to account for such spatial and temporal variation may have implications for study objectives, results, and conservation initiatives (Bergin 1992). In our study, we used animal-centred measures to distinguish between different scales of selection, and included dynamic attributes such as predation risk and the energetic costs of movement with vegetative characteristics to identify how selection by caribou varied between scales. The knowledge gained from identifying scale-dependent factors can be used to improve conservation strategies for caribou inhabiting heterogeneous landscapes.

CHAPTER 7 - GENERAL CONCLUSIONS: CONSERVATION OF WOODLAND CARIBOU AND FOREST MANAGEMENT

INTRODUCTION

Prior to the 1800s, woodland caribou ranged across most of northern North America and were reported as far south as northeastern Vermont, northern New Hampshire, and across northern Michigan, Wisconsin, Minnesota, Montana, Idaho, and northeastern Washington (Banfield 1961). Caribou also were more abundant and widespread in Canada, occurring in the southern portions of all the provinces except Prince Edward Island. Many of those populations, however, have since disappeared or contracted northwards (Banfield 1961, Bergerud 1974b). Today, woodland caribou are a species requiring special management for many of the provinces (Cumming and Beange 1993, Cumming 1998, Edmonds 1998, Rettie et al. 1998). In British Columbia, wildlife managers have focussed their attention on conserving the endangered (red-listed) mountain ecotype for which four of the 11 identified herds are thought to be declining (Heard and Vagt 1998). In contrast, only two of the 28 northerncaribou herds are in a reported state of decline, but the population status of many of those herds (18) is unknown (Heard and Vagt 1998). Declining herds are a contemporary reflection of historical trends and illustrate that the maintenance of viable woodland caribou populations will benefit most from proactive management strategies. Reactive policies such as translocations or moratoriums on development are expensive and do not guarantee positive results (Dauphiné 1975, Warren et al. 1996, Jordan et al. 1998). Our lack of knowledge of the population dynamics of the northern caribou ecotype is matched by our comparatively simplistic understanding of the movements and behaviour of those animals. Knowledge of both individual interactions with the environment and the effects of those responses at the

level of the population are necessary if we are to develop and assess effective management strategies.

Reasons for present and historic declines are debated, but include habitat alteration and loss, increased predation, uncontrolled hunting, and disturbance, or some combination of those factors. Population-level effects are exacerbated by the relatively low reproductive potential of caribou (Bergerud 1974b). In British Columbia, management objectives are focussed on mitigating the actual or potential effects of timber harvesting. This includes providing sufficient winter range to ensure that caribou can disperse over large areas, minimising early seral stage habitats that allow moose and consequently wolf populations to flourish, and controlling access in specific areas to limit unregulated hunting (Seip 1998).

The objective of this study was to enhance our understanding of the processes that influence the habitat relationships of northern woodland caribou so that management guidelines relative to forest practices in northcentral British Columbia could be refined. Specifically, we addressed many of the assumptions that limited inferences from earlier studies (appropriate definition of scale, small sample sizes (per individual), generalised forestry-based vegetation maps) and explored a number of potentially important habitatrelated factors including snow, predation risk, patch configuration, and the energetic costs of movement at multiple spatial scales.

FINDINGS

We employed a hierarchical scale-explicit approach to understand some of the mechanisms influencing caribou behaviour relative to resource selection. At small-scales, data were collected through detailed investigations of feeding areas, and at larger scales Global Positioning System (GPS) collars were used to record the movements of caribou in the Wolverine herd of northcentral British Columbia. We identified six spatial scales across which caribou demonstrated a unique response to the environment: forage species, feeding site, patch, inter-patch movement, collections of patches, and landscape. In the context of our work, scale represents the spatial and temporal heterogeneity of the environment and the functional implications of heterogeneity to the choices animals make. Rather than focussing on the definitions of time or space, we concentrated on how animal behaviour changes across those scales.

Selection of Landscapes

At the largest spatial scale, we observed that the general movements and habitat occupancy of caribou were classified into one of three types: wintering exclusively within forested habitats, alpine habitats, or spending some portion of the winter in both the forest and alpine. Terry and Wood (1999) suggested that broad-scale movements are in response to some change in snow gradient and that during deep-snow winters, animals show a propensity for wind-swept alpine habitats. For those caribou with GPS collars that functioned throughout a complete winter in this study, animals were distributed evenly across the three broad habitats. Data were sparse relative to repeat winters, but only one animal (B91A) spent all four winters in the same habitat (alpine), whereas others demonstrated variability in choice over successive winters.

At the landscape scale, snow depths increased over time and for 1997-98, we detected a decrease in snow depths from south to north. A number of collared caribou spent the early winters in the southern portions of the study area before moving north in early January. This pattern indicates that there was a response to snow depth, even though absolute differences between any of the snow stations across the study area were small (1996-97: $\bar{x} = 25.8 \pm 4.9$ SE cm; 1997-98: $\bar{x} = 31.7 \pm 6.6$ cm). Examination of foraging areas revealed that abundance and accessibility of terrestrial lichens differed between the alpine and forest. Relative to the

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alpine, caribou in the forest foraged at feeding sites and patches with greater amounts of less variably distributed lichens, but deeper less variable snow depths. Alpine areas also had a lower risk of predation. Caribou selecting alpine habitats may have foregone forage abundance in favour of forage accessibility and low predation risk. Although we can speculate on the consequences to reproductive fitness of selecting one area over the other or a combination of both, caribou are a dynamic species that has adapted to a wide range of circumpolar conditions. Relative to snow and forage conditions, there may be no distinct advantage to occupying alpine over forested landscapes.

Selection of Collections of Patches

Caribou made repeated small-scale movements, likely associated with foraging, across collections of patches. At that scale, caribou were relatively selective. Animals in the forest chose pine-lichen woodlands with understories of abundant *Cladina* and *Cladonia* lichens, whereas caribou in the alpine selected rocky ridges and slopes with sparsely distributed lichens, and wind-swept ridges with more productive, deeper soils dominated by grass communities. There was some evidence that caribou did not select those cover types in isolation of the surrounding landscape matrix. Patches of pine-lichen woodland were adjacent to wetlands and patches of black spruce or mixed stands of black spruce and pine. In the alpine, caribou selected rocky ridges and slopes that were not contiguous with forested patches.

Vegetation was a more important consideration for caribou than predation risk. The level of risk across any one area depended on the surrounding matrix of cover types. For example, occupancy of pine-lichen woodlands was relatively high-risk if they were adjacent to lower risk mid-elevation coniferous stands, but relatively low-risk if they were found in a matrix of lakes and wetlands.

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Selection of Movement Paths

Inter-patch movements occurred less frequently, and at a greater movement rate and over a greater distance, than intra-patch movements. During those movements, caribou selected a wide range of cover types. Patches of pine-lichen woodland, rocky-alpine ridges and slopes, lakes, rivers, grassy-alpine ridges, and hybrid white spruce stands were important. Caribou chose areas with little elevation change or grade and, therefore, achieved a lower energetic cost of movement. This, in combination with the before-mentioned cover types, suggests that caribou often chose valley bottoms as movement routes. Relative to the other scales of selection, predation risk had the greatest influence during inter-patch movements.

Selection of Patches

We observed patch-level selection while trailing caribou on the ground and using GPSrelocation data, and considered a patch to be all levels of heterogeneity larger than a feeding site, but no larger than the most dominant and observable ecotone (i.e., forest stand). Intrapatch movements were related to cover types of $\geq 625 \text{ m}^2$. At that scale of patchiness, caribou illustrated weak selection for cover types. Pine-lichen woodlands, and rocky-alpine ridges and slopes were used predominantly, followed by patches of black spruce or mixed stands of black spruce and pine, mid-elevation coniferous species, and wetlands. Predation risk was not important at the intra-patch scale, but movements were highly correlated, indicating that animals were responding to some scale of heterogeneity more detailed than we mapped. While trailing caribou, we focussed on foraging areas across forested and alpine habitats. In forested 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. In the alpine, there was no discernible relationship between patch selection and terrestrial lichen abundance and snow conditions. Most of our site investigations were conducted in pine-lichen woodlands (66%) and more productive, wetter pine stands with lesser amounts of terrestrial lichens (15%). In the alpine, caribou foraged across rocky (80%) and grass (15%) dominated ridges and slopes. Measurements made on the ground were in agreement with the GPS data, except that through constant monitoring we were able to identify a number of less frequently used cover types (e.g., mid-elevation coniferous stands and wetlands).

Selection of Forage Species and Feeding Sites

Over two winters of trailing caribou, we observed consistent selection of several lichen species. Caribou in the forest selected *Cladina mitis* and *Cladonia* spp. and avoided mosses; caribou in the alpine selected *Cladina rangiferina*, *Cetraria cucullata*, *Cetraria nivalis*, *C. mitis*, *Thamnolia* spp., and *Stereocaulon alpinum*. We obtained similar results using measures of both percent cover and corrected biomass. Across forested and alpine areas, caribou selected cratering locations where the snow was less deep. When snow depth, density, and hardness limited access to terrestrial lichens in the forest, caribou foraged instead at those trees with the greatest amount of arboreal lichens (*Bryoria* spp.). Caribou appeared to be selecting the most abundant, not the most nutritious lichen species at both forested and alpine feeding sites.

LESSONS LEARNED: IMPLICATIONS FOR FOREST MANAGEMENT

This project was founded on an abstract concept: scale. Identifying nonarbitrary scales of movement and selection allowed us to comment on more than patterns of relocations on maps, but also to incorporate the behaviour of caribou towards understanding process-specific responses (e.g., snow, predation risk) to the environment. Those responses provide insights into the potential effects of forest harvesting and allow us to extrapolate results to other populations of caribou (Hobbs and Hanley 1990). We outline key points from this research relative to the potential consequences of forest harvesting: a reduction in the distribution and availability of forage and an increase in the distribution and abundance of predators. Rather than a general comment, review or speculation of forestry-caribou interactions (see Hristienko 1985, Cumming 1992, Cumming and Beange 1993), we focus on new or expanded insights.

Forage Distribution and Availability

- 1) Northern caribou have a strong propensity for pine-lichen woodlands during winter. Those areas were important at all scales of analysis and should be emphasised within management plans (Figure 7.1). They are characterised by poor productivity and well-drained soils, support abundant terrestrial lichens, and are easily discerned by satellite imagery. Although tree composition and age may be similar to the more productive and wetter pine and mixed pine/black spruce cover classes, efforts should be made to differentiate pine-lichen woodlands from forest types identified by more general classification schemes (e.g., mature lodgepole pine).
- 2) Other studies have observed associations between caribou and mosaics of pine-lichen woodlands, wetlands, and patches of black spruce (Cichowski 1993, Terry and Wood 1999). Whether caribou selected those associations or if they occurred consistently across the winter range was unclear. In this study, the presence of pine-lichen woodlands was a much stronger indicator of caribou habitat affinities, but there was weak evidence of caribou selecting lichen woodlands adjacent to patches of wetland and black spruce. Analyses at the intra-patch scale also showed selection for the former two cover types. Wetlands and black spruce stands support sedges and arboreal lichens, which may balance a high energy, low protein diet dominated by terrestrial lichens. Mosaics of pine-lichen woodlands, wetlands, and black spruce should be maintained across areas managed for caribou habitat values.



Figure 7.1. Distribution of pine-lichen woodlands (1992) within the range of the Wolverine caribou herd, as identified using a supervised classification of a Thematic Mapper satellite image.

- 3) Pine-lichen woodlands or site characteristics similar to those in lichen woodlands are variable in size and can occur as small patches that may not be represented on habitat maps. In those instances, the percent cover of *C. mitis* and *Cladonia* spp. serve as useful indicators of the potential of the stand to provide forage for caribou. *Cladina rangiferina* and *Stereocaulon* spp. were important species for alpine-dwelling caribou. Caribou may select or prefer a range of lichen species (DesMeules and Heyland 1969, Bergerud and Nolan 1970, Holleman and Luick, 1977, Dannell *et al.* 1994). If the successional progression of lichen communities across caribou winter range includes the two latter species, those lichens should also be considered during habitat assessments.
- 4) Researchers have hypothesised that forest-dwelling caribou begin foraging on arboreal lichens after some threshold in snow conditions makes cratering for terrestrial lichens unprofitable (Bergerud 1974*a*, Sulkava and Helle 1975, Helle and Saastamoinen 1979, Helle 1984, Vandal and Barrette 1985). We demonstrated that caribou actively select trees with the greatest amount of arboreal lichens following increases in snow depth, density, and hardness. To date, habitat research and silvicultural prescriptions concerning terrestrial-feeding woodland caribou have favoured the maintenance or regrowth of terrestrial lichens (Brumelis and Carleton 1989, Lessica *et al.* 1991, Harris 1992, Kranrod 1996, Webb 1998). Our data indicate that terrestrial lichens are of greater value to caribou, likely because of abundance, but foraging habits in late winter also encompass some component of arboreal lichens. If snow conditions restrict access, harvesting strategies that maintain terrestrial lichens, but retain no arboreal lichens, may not meet the full range of habitat requirements for caribou.
- 5) Snow is widely recognised as limiting to the movements and foraging efficiency of woodland caribou. Caribou of the Wolverine herd also demonstrated marked responses to snow conditions. Animals selected feeding sites based on snow depth, density, and

hardness and may have abandoned southern portions of their winter range for similar reasons. Management plans should, therefore, consider the distribution of pine-lichen woodlands relative to deep snow areas. Furthermore, abundance of terrestrial lichens needs to be assessed relative to its accessibility throughout the entire winter. Previous studies identified the threshold depth for cratering by caribou and reindeer to range from 50 to 80 cm (Formozov 1946, Pruitt 1959, Stardom 1975, LaPerriere and Lent 1977, Helle and Saastamoinen 1979, Darby and Pruitt 1984), although craters as deep as 123 cm have been reported (Brown and Theberge 1990). Over the two-year period of this study, the maximum crater depth we observed at a forested site was 97 cm.

Predation

- 1) Caribou inhabiting alpine habitats were subjected to lower risk of predation. From a forage perspective, alpine habitats are of little interest to forest managers. Forest practices that encourage early seral stages of vegetation that support moose and wolves, however, would have implications for caribou in both forested and alpine areas. Increased predation could eliminate forested areas as viable habitat and reduce some of the survival strategies available to caribou. Alpine-dwelling island populations of caribou would also have little opportunity for range expansion or gene exchange with adjacent caribou, as exemplified by the Chase herd (Terry and Wood 1999). Animals of the more southerly Takla herd also may be restricted to isolated alpine and mid-elevation habitats following moose and wolf expansion into low-elevation areas (Poole *et al.* in press).
- 2) Predation risk was relatively uniform across low-elevation forested habitats. Caribou had the highest exposure to risk when making inter-patch movements. At that scale, animals often moved across valley bottoms consisting of relatively high-risk cover types. Harvesting should be minimised in those areas, where possible. Increased predation across

movement routes may lead to population sinks or a reduction in winter range connectivity (Harrison and Voller 1998).

3) Caribou demonstrated little selection for mid-elevation coniferous or krummholz forests. This is in contrast to the mountain caribou ecotype, which typically winters in older-age coniferous stands while foraging on arboreal lichens (Terry *et al.* 2000). Logging those forest types would appear to have little effect on the forage base of northern woodland caribou when at typically low densities. High-elevation cuts, however, would be accompanied by road development that would allow wolves easier access to alpinedwelling caribou (James 1999). Vegetative regrowth in those cuts also may favour moose populations and increase the likelihood of caribou-wolf interactions.

Should we Manage Forests to Reduce Predation or Increase Forage?

Considerable debate has focussed on whether caribou populations are forage- or predator-limited. Bloomfield (1980) concluded that the decline of mountain caribou south of Prince George was primarily because of habitat destruction from logging and overhunting. Hatter (1999) has since seconded those conclusions, but added predation as a third cause. Others have stated that a reduction in foraging habitat was not a cause of decline (Bergerud *et al.* 1984), but rather that populations of northern caribou (Bergerud and Elliot 1986) and mountain caribou (Seip 1992) were regulated by predators. The Wolverine herd does not appear to be forage-limited. Animals ranged over an area of 5,100 km² with large expanses of pine-lichen woodland (-20,000 ha) and alpine habitats consisting of rocky (-28,000 ha) and grass-dominated (-2,200 ha) wind-swept ridges. Over the four winters that we monitored caribou, some pine-lichen woodlands appeared to be unused or used infrequently for short periods of the winter. These observations are largely anecdotal, but density-dependent regulatory pressures may result in a much more consistent and wider pattern of habitat occupancy with greater use of marginal habitats (e.g., pine, pine and black spruce stands). The high pregnancy rate (89%) observed by Wood (1994) further suggests that female caribou were not nutritionally limited (Thomas 1982, Skogland 1985). Densities $(0.06 - 0.12 \text{ caribou/km}^2$, Terry and Wood 1999) were below those reported by Bergerud (1992) for island $(2 - 16 \text{ km}^2)$ and mainland $(1 - 2 \text{ km}^2)$ populations of caribou and reindeer in predator-free systems.

Intuitively, managers faced with low-density populations should focus their efforts on increasing animal numbers. In the case of woodland caribou in general and the Wolverine herd specifically, this is likely not the best approach. Caribou range over large areas in small groups presumably to reduce the predictability of habitat occupancy (Bergerud 1992). That is a successful strategy for low-density populations only. It is unknown whether the Wolverine herd is decreasing or increasing (Heard and Vagt 1998), but our data suggest that wolves are concentrating their hunting efforts on the more predictable moose rather than caribou (Chapter 6). Contingent on the presence of some long-term dynamic equilibrium between wolves, moose, and caribou and a desire to retain a naturally-functioning ecosystem (i.e., including wolves), managers should aim to retain a low-density caribou population. The primary tool to achieve that goal would be to retain expanses of well-distributed pine-lichen woodlands across the range of the Wolverine herd (Seip 1998). Managers also need to be cognisant of changes in moose-wolf-caribou dynamics that may accompany any numerical response to increased moose populations. At present, forest-dwelling caribou appear to accommodate predation risk that is relatively constant across valley bottoms. Larger moose populations, however, may change the functional responses of wolves and increase the rate of predation on caribou. A logical outcome would be the exclusion of caribou from lichen rich, low-elevation habitats.
STUDY STRENGTHS AND LIMITATIONS

We adopted a multi-scale approach to investigate the behavioural responses of caribou to the environment. We assumed that an increased understanding of those processes would allow us to better predict the effects of forest practices on woodland caribou and more effectively generalise study results to other herds of northern woodland caribou. To accomplish that goal, we developed a series of explanatory models at spatial scales defined by the behavioural responses of caribou. The flexibility of that approach allowed us to measure the influence of correlated movements, the risk of predation, the energetic costs of movement, patch configuration, and cover-type on selection of habitat (intra-patch, inter-patch, and multiple-patch). We also contrasted the importance of those variables between scales, permitting us to consider the processes at the scale in question, processes that occur at a scale below to enlighten mechanisms, and processes that occur at a scale above to provide context (Allen and Hoekstra 1992). Previous studies of caribou-habitat relationships were conducted at one or several arbitrarily defined spatial scales and considered only vegetation and in some cases topography.

Our results, however, are limited to an understanding of the behaviour of individuals. We can only speculate about the cumulative effects of individual responses on population dynamics. The implications of our data depend on how the behaviours of an individual (i.e., the habitat use patterns that we describe here) influence its probability of survival and how survival rates affect population growth rates and ultimately population viability. For example, there may be implications to population viability of caribou choosing alpine versus forested habitats or of making high-risk inter-patch movements. Thus, we did not directly test the question of primary importance to the resource managers, foresters, and habitat biologists interested in the applied components of this work: does forest harvesting threaten woodland caribou populations? When trying to understand the effects of development on wide ranging species, such as woodland caribou, the more pragmatic yet less direct approach is to incrementally increase our knowledge of potentially limiting processes through carefully designed studies at a range of scales. Understanding the habitat relationships of individuals provides the foundation for interpreting and predicting the demographic consequences of environmental perturbations. A productive next step may be to measure survival rates of animals in relation to those factors that we determined to be important to habitat selection and that are most likely to be affected by logging and other land-use practices.

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APPENDIX A - MAPPING SUB-BOREAL AND BOREAL VEGETATION COMMUNITIES IN NORTHCENTRAL BC USING LANDSAT THEMATIC MAPPER AND DIGITAL TERRAIN DATA

INTRODUCTION

In British Columbia, forest inventory data has traditionally served as the basis for examining large-scale species-habitat relationships (e.g., Apps and Kinley 1996, Steventon 1996, Terry and Wood 1999). In some areas of the province, the inventory is out of date or is of inconsistent quality. Furthermore, biologists are forced to generate ecological associations using stand characteristics such as dominant tree type, age or site productivity, and areas that are unproductive for forest species are typically not mapped (e.g., alpine habitats). As a replacement, terrestrial ecosystem mapping (TEM) was conceived to capture the ecological associations of vegetation, soils, local and regional climatic conditions, and the resulting relationships with wildlife habitat. High costs and lengthy completion times, however, have hindered the implementation of TEM across the province. Landsat Thematic Mapper (TM) imagery and digital terrain data provide an alternative to map vegetative communities. Our principle objective was to use Landsat TM imagery and ancillary GIS data to accurately identify land-cover types with ecological meaning to caribou-habitat relationships across the range of the Wolverine caribou (*Rangifer tarandus caribou*) herd.

STUDY AREA

The Wolverine caribou range over an area of approximately 5,100 km², and are located to the west of the Wolverine mountain range approximately 220 km northwest of Prince George, British Columbia (Heard and Vagt 1998). The study area is characterised by numerous vegetation associations resulting from diverse topography, soils and succession, and is classified into eight biogeoclimatic variants (MacKinnon *et al.* 1990, Meidenger and Pojar 1991, DeLong et al. 1993) (Fig. A.1). The Boreal White and Black Spruce (BWBSdk1) subzone is located below 1,100 m in elevation. Dominant tree species include white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*) and occasionally black spruce (*Picea mariana*) on upland sites. Fire has had extensive successional influences within this subzone resulting in many lodgepole pine seral stages. Lowland and riparian areas are noted as excellent winter habitat for moose (*Alces alces*). Mature stands of pine and spruce are associated with dense arboreal, and often terrestrial lichens, and are presumed to be used by caribou throughout the winter (MacKinnon et al. 1990).

Three variants of the sub-boreal spruce (SBS) subzone characterise the remainder of the lower elevations of the study area. Dominant tree species of the SBSmk1 include lodgepole pine, trembling aspen (*Populus tremuloides*) and Sitka alder (*Alnus crispa* ssp. *sinuata*). Depending on site conditions, common shrubs include soopolallie (*Sheperdia canadensis*), velvet-leaved blueberry (*Vaccinium myrtilloides*), and black twinberry (*Lonicera involucrata*). Seral species of the SBSmk2 are similar to the mk1 variant except that paper birch (*Betula papyrifera*) may be an associate species. Characteristic understory species include highbush-cranberry (*Viburnum edule*), prickly rose (*Rosa acicularis*) and bunchberry (*Cornus canadensis*). *Cladina* lichen can be found on drier site units of both variants. The SBSwk2 is located on the eastern slopes of the Wolverine Range. Wetter cooler site conditions than the previous two SBS variants result in a greater prevalence of oak fern (*Gymnocarpium dryopteris*) and devil's club (*Oplopanax horridus*). Both black (*Ursus americanus*) and grizzly bear (*Ursus arctos*), caribou and moose can be found within the three variants during various times of the year.

The Engelmann Spruce – Subalpine Fir (ESSFmv2, mv3) subzone occurs between approximately 1,000 – 1,300 m. Climax forests have canopies of Engelmann spruce (*Picea*

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Figure A.1. Biogeoclimatic ecosystem classification variants found across the Wolverine caribou study area of northcentral British Columbia.

engelmannii) and subalpine fir (*Abies lasiocarpa*). A variety of wildlife inhabit that zone including moose, black bear and grizzly bear in moist subalpine meadows and avalanche tracks, and caribou in mature stands of pine and spruce that support dense arboreal lichens (MacKinnon *et al.* 1990).

The ESSFmv3p parkland occurs between 1,300 - 1,600 m. This variant is a transition between closed canopy forest and the non-forested subalpine vegetation. It consists of isolated patches of subalpine fir and Engelmann spruce and openings dominated by herbs, shrubs and sedges. Sedge wetlands provide summer forage for black and grizzly bear.

The Alpine Tundra (ATn) is the fourth biogeoclimatic subzone found within the study area and has the most severe climatic conditions. The subzone extends above ESSFmv3p elevations of 1,600 m. Vegetation is dominated by shrubs, herbs, bryophytes, and lichens with sporadic trees occurring in krummholz form. At the lowest elevations, plant communities include shrub-fields or scrub dominated vegetation, leading to grass and herbs, followed by lichen-dominated vegetation at the highest elevations. The ATn serves as important habitat for a variety of species. Moist herbaceous meadows are used by grizzly bear and caribou, with mountain goats (*Oreannos americanus*) making use of steep, rugged, vegetated alpine areas. Caribou have been noted to calve at high-elevation alpine sites that are often devoid of herbaceous forage (Bergerud and Page 1987).

MAPPING APPROACH

In 1997, we conducted a review of available vegetation or ecological mapping suitable for assessing habitat relationships of the Wolverine caribou herd. Existing sources were found to be inaccurate or were of insufficient area to meet project objectives. The most costeffective option was to use Landsat TM imagery to classify the vegetation communities and other cover types found across the caribou range. This resulted in a collaborative mapping

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project funded under Forest Renewal British Columbia contract OP98001 "Ecosystem Mapping Using Satellite Imagery" to Dr. Roger Wheate, University of Northern British Columbia. Nancy D. Alexander collected training site data, prepared the digital elevation model (DEM), performed the supervised classification, and was involved with most other aspects of map production. I established project objectives, georectified the Landsat image, identified ecological associations, collected the data used for the accuracy assessment, and with the assistance of N.D. Alexander developed the map legend.

The Peace/Williston Wildlife Compensation Fund and Fletcher Challenge Canada Ltd. had co-funded a biophysical mapping project in 1992 – 1993 that covered approximately 60% of the range of the Wolverine caribou herd (McKenzie 1993). Although this project did not meet all of our needs, it resulted in a comprehensive legend that encompassed the ecological types found across the larger study area. We used the legend and associated ecological data to develop an initial stratification of cover types with potentially unique spectral qualities. A fixed-wing aircraft was used to assess the study area and collect oblique photographs of vegetation associations. From 9 June – 15 July 1998, we visited and recorded the location and characteristics of suitable patches of vegetation to serve as training sites for the classification procedure. Field sites were accessed by road and helicopter.

A seven band Landsat Thematic Mapper dataset was acquired for 22 August 1992 (Track 50/Frame 21). This date was selected to optimise the photosynthetic potential of the vegetation while minimising snow cover at high elevations. Although we would have preferred more recent imagery, this was the most current cloud free day available within the months of July to September. A digital elevation model based on Terrain Resource Inventory Mapping (TRIM) (1:20,000) was used to generate models of slope, aspect, and elevation. Roads, trails, lakes, and rivers were extracted from 1:20,000 TRIM map-sheets. Slocan Forest Products and Finlay Forest Products provided digital files of clearcut boundaries. The study area was clipped from the full Landsat scene and georectified. Fifty-seven ground control points of road intersections and river junctions were selected from the TRIM data and referenced to the image (Kardoulas *et al.* 1996). A georectification Root Mean Square (RMS) error of 0.879 pixels was obtained (i.e., relative to UTM co-ordinates, pixel locations had a mean error of 26.4 m). Visual examination of the corrected imagery when overlaid with the stream and road coverages indicated that the model fit well. The data were corrected to the UTM projection based on the NAD 83 and the GRS80 ellipsoid. The image was resampled to a 25 x 25-m pixel size using a nearest-neighbour interpolation (Lillesand and Kiefer 1994).

We experimented with various combinations of Landsat bands, derivatives of Landsat bands, and topographic data to select the composite image with the greatest power to discriminate between predefined cover types (Hutchinson 1982). Histograms, coincident spectral plots, and visual interpretation led us to select an image mosaic consisting of Landsat bands TM 3 ($0.63 - 0.69 \mu m$, Red), TM 4 ($0.76 - 0.9 \mu m$, Near infrared), TM 5 ($1.55 - 1.75 \mu m$, Mid-infrared), elevation, slope, incidence, and a normalised differencing vegetation index (NDVI). The NDVI channel is a composite of TM 4 and TM 3 and measures variation in amount of green biomass. The image was classified using a supervised maximum-likelihood procedure (Lillesand and Kiefer 1994). Two hundred and seventy-eight training sites were used to define the spectral qualities of the identified cover types. Training classes were amended for statistical seperability, and merged where there was low discriminatory power, resulting in 27 cover types. Following classification, a modal filter removed abhorrent pixels and clustered small patches.

A second set of independent ground truth points was used to assess the accuracy of the classification. Four hundred and seventy-two independent assessment locations were gathered

from the original field data of the McKenzie (1993) project, vegetation data gathered during investigations of caribou foraging sites (Chapter 2), visits to sites accessible by road, and locations extracted from monochrome air photos and oblique colour slides. Statistics of overall accuracy, user's accuracy, producer's accuracy, and Kappa (κ) were produced (Congalton *et al.* 1983).

Landscape features of a small area (approximately two to three pixels), such as roads or minor waterways, can be difficult to capture with satellite imagery and may be lost during post-classification smoothing. To represent those features, which may be of use from both an ecological and interpretative sense, we extracted roads, trails, lakes, and rivers from the TRIM coverage and integrated them with the final map. Since the imagery was approximately six years old, clearcut boundaries recorded as of 1996 were applied to the final image. Classification and other digital procedures were performed with Easi/Pace software (PCI Inc., Richmond, Ontario, Canada).

RESULTS AND DISCUSSION

We distinguished 23 cover types using a supervised classification (Table A.1). Four additional types were created following the merging of the supervised classification and the TRIM Lakes, Roads/Trails, Rivers and Clearcut boundary GIS coverages (Figure A.2). This number of ecological associations was considerably less than the 72 habitat classes of various seral stages that McKenzie (1993) documented using 1:70,000 air photos. Much of that detail, however, would have had to be collapsed before performing a statistically tractable use versus availability analysis (Thomas and Taylor 1990). We improved upon ecological maps that could be constructed with forest inventory data. For example, we discriminated five alpine, two wetland, and a krummholz cover type, none of which are considered during forest

No. ¹	Cover Type	Area (ha)	Cover (%)	Description ²
1	Aspen	37,163	5.16	Shrub or closed stands of <i>Populus tremuloides</i> that may be associated with <i>Pinus contorta</i> ; on warm, southeast to west facing slopes; vigorous shrub understory including <i>Rosa acicularis</i> , Viburnum edule, Aster conspicuus, and Epilobium angustifolium.
2	Pine	49,804	6.92	Dominated by <i>P. contorta</i> (~80%), but may occur with a component of <i>Picea mariana</i> or <i>Picea engelmannii</i> x <i>P. glauca</i> in older stands; with the exception of southeast to west facing slopes, the understory is poorly developed and is characterised by feather mosses (<i>Pleurozium schreberi</i> , <i>Hylocomium splendens</i> , <i>Ptilium crista-castrensis</i>), wetter lichen types (e.g., <i>Peltigera apthosa</i>), and to a lesser extent <i>Cladina</i> or <i>Cladonia</i> spp., <i>Vaccinium caespitosum</i> , <i>Linnaea borealis</i> , and <i>Cornus canadensis</i> .
3	Spruce	46,357	6.44	Dominated primarily by P. engelmannii x P. glauca (~80%), but may be a minor component of P. mariana, P. contorta, P. tremuloides or Populus balsamifera; typically at lower elevations on wetter sites; variable understory development from feather moss- dominated to a variety of shrubs and herbs including R. acicularis, Lonicera involucrata, Cornus stolonifera, C. canadensis, V. edule, Equisetum spp., Alnus incana, L. borealis, Shepherdia canadensis, and Smilacina racemosa.
4	Lake	28,345	3.94	Permanent water bodies of all depths and sizes.
6	Avalanche Track	1,993	0.28	Active avalanche chutes and associated colluvial fans; sites are shrub-dominated with herbaceous openings including Salix spp., Alnus viridis, Calamagrostis canadensis, Heracleum lanatum, Aconitum delphiniifolium, P. engelmannii, Ribes hudsonianum, E. angustifolium, Valeriana sitchensis, and Carex spp.
8	Alpine-Little Vegetation	9,574	1.33	Wind-swept alpine ridge-tops or upper slopes with little vegetative cover and 40 - 60% rock; sparse Altai fescue, Betula glandulosa, Stereocaulon, Cetraria, Cladina and crustose lichens, Polytrichium piliferum, Silene acaulis, and Carex spp.
9	Alpine Shrub	13,780	1.91	Moderate to steep slopes with extensive cover (~75%) of <i>B. glandulosa</i> or Salix reticulata; A. fescue, Carex, Stereocaulon, and Cetraria spp. can be found in openings.
10	Black Spruce	14,248	1.98	Areas with water tables at or near the surface consisting of open stunted forests of <i>P. mariana</i> ; associated with <i>Salix</i> spp., <i>Equisetum</i> spp., <i>Sphagnum</i> spp., feather mosses, and abundant arboreal lichens (<i>Bryoria</i> spp.).

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Table A.1. Cover types produced from a supervised classification of a Landsat TM image of the Wolverine caribou study area.

Table A.1 Continued.

11	Sedge/ Sphagnum Bog	21,834	3.03	Shrub/sedge and forb dominated wetlands on depression landscapes with high water tables; sedge/moss dominated cover of Salix spp., Carex spp., Geum avens, Sitka burnet, Sphagnum spp, and Aster modestus.
12	Shrub Bog	12,893	1.79	Drier variant of Sedge/Sphagnum Bog with ~50% cover of <i>B. glandulosa</i> or Salix spp. and 5 - 10% stunted <i>P. mariana</i> .
13	Alpine-Moist Shrub	289	0.04	Moist meadow typically in alpine bowls or cirques dominated by V. sitchensis, Erigeron peregrinus, Carex, and Salix spp.
14	Rockfall	9,036	1.26	Steep rocky terrain with sparse vegetation restricted to pockets of soil among outcrops and in rock crevices; lichen-dominated cover of <i>Umbilicaria</i> , <i>Cetraria</i> , and <i>Cladina</i> spp., other associates include A. <i>fescue</i> and S. <i>acaulis</i> .
15	Krummholz	45,062	6.26	Shrub cover of subalpine fir on gentle to moderate slopes at lower elevations of the alpine tundra zone (parkland); understory of <i>Cassiope mertensiana</i> , <i>A. fescue</i> , crustose lichens, <i>Polytrichium</i> , and <i>Carex</i> spp.
16	Alpine-Grass Shrub	1,935	0.27	Sites with deep soil on gentle to moderate slopes; grass-dominated cover of A. fescue, S. reticulata, S. acaulis, C. mertensiana, Carex, and Polytrichium spp.; Stereocaulon, Cetraria, and Cladina spp. can be found in less productive openings.
17	Abies-Spruce	99,841	13.87	Mid-elevation stands on moderate to steep slopes dominated by Abies lasiocarpa and P. engelmannii; understory species include Rhododendron albiflorum, Vaccinium membranaceum, Lycopodium spp., and feather mosses.
19	Spruce-Pine	29,371	4.08	Level to steep slopes at lower elevations consisting of <i>P. engelmannii</i> x <i>P. glauca</i> and <i>P. contorta</i> ; poorly to moderately developed shrub and herb layers of <i>S. canadensis</i> , <i>R. acicularis</i> , <i>V. edule</i> , <i>L. borealis</i> , <i>C. canadensis</i> , <i>S. racemosa</i> , and a continuous cover of feather mosses.
20	Bedrock/No Vegetative Cover	12,984	1.8	Rocky terrain with sparse vegetation restricted to pockets of soil among outcrops and in rock crevices; lichen-dominated cover of <i>Umbilicaria</i> , <i>Cetraria</i> , and <i>Cladina</i> spp.; <i>A. fescue</i> and <i>S. acaulis</i> are associates.
21	Pine-Black Spruce	49,224	6.84	Older P. contorta – P. mariana stands found on level to moderate slopes that may occur with lesser components of A. lasiocarpa or P. engelmannii x P. glauca; associated with patches of Cladina and Cladonia spp., but characteristically feather mosses, C. canadensis, L. borealis, A. viridis, and S. canadensis dominate the understory.

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Table A.I. Continued

22	Cottonwood	1,279	0.18	Active floodplains dominated by <i>P. balsamifera</i> , Salix spp., and <i>A. incana</i> and associated with <i>L. involucrata</i> , <i>C. stolonifera</i> , <i>R. acicularis</i> , and <i>Equisetum</i> spp.
23	Abies	7,252	1.01	Mid-elevation stands on moderate to steep slopes dominated by A. lasiocarpa and with lesser components of P. engelmannii, and P. contorta; V. membranaceum, Rhododendron albiflorum, A. viridis, Lycopodium spp. and feather mosses compose understory.
24	Abies-Pine	21,257	2.95	Dry shedding ridge tops composed of open stands of A. lasiocarpa and P. contorta and mid-elevation stands found on moderate to steep slopes composed of A. lasiocarpa and P. contorta with lesser components of P. engelmannii; V. membranaceum, Rhododendron albiflorum, A. viridis, Lycopodium spp., and feather mosses compose understory with Cladina and Cladonia spp. found on dryer sites.
25	Pine-Lichen Terrace	19,949	2.77	Level glaciofluvial terraces and other features with well-drained soils that support stands of <i>P. contorta</i> and an understory of <i>Cladina</i> and <i>Cladonia</i> spp., <i>P. schreberi</i> , <i>C. canadensis</i> , <i>L. borealis</i> , and <i>V. caespitosum</i> .
26	Abies-Spruce- Pine	110,238	15.31	Mid-elevation stands composed of A. lasiocarpa, P. engelmannii, and P. contorta found on moderate to steep slopes; V. membranaceum, R. albiflorum, A. viridis, Lycopodium spp., and feather mosses compose understory.
99	Clearcut	51,965	7.22	Areas recently harvested (<20 years) and at an early stage of successional development.
100	River	19,082	2.65	Moving watercourses.
101	Road/Trail	5,220	0.73	Roads and trails primarily used for motor vehicle access.
104	Anthropogenic	25	0	Agricultural lands or areas disturbed by placer mining.

¹ Numbers are digital values assigned to cover types during the classification process. ² Descriptions of associate species are based on site investigations and McKenzie (1993), but are not exhaustive.

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Figure A.2. Distribution of 27 cover types across the Wolverine study area. Cover types were identified with a supervised classification of a Thematic Mapper satellite image or were generated from existing GIS data.

inventories.

We achieved an overall classification accuracy of 76.7% (Table A.2). A κ statistic of 0.748 indicates that the observed classification is nearly 75% better than chance. Accuracy was, however, variable across cover types. Pine-Lichen Terrace had a user's accuracy of 98.6% whereas the Spruce cover type had an accuracy of only 50% (Table A.2). For that cover type, Black Spruce, Abies-Spruce, Spruce-Pine, and Pine-Black Spruce were mistakenly classified as spruce (i.e., errors of commission) (Table A.3). Interpretation of the accuracy assessment was confounded by small sample sizes for some cover type. Because of our inability to reliably identify any assessment sites, the *Abies* cover type had an accuracy of zero percent. This is an extreme example, but it was also difficult to confidently assess the classification accuracy of some other cover types such as Alpine-Shrub, Alpine-Moist/Shrub, Rockfall, and Bedrock/No Vegetative Cover (Table A.3). Recommendations on sample size vary, but Congalton (1991) suggested that the minimum number of samples per cover type should range from 75 – 100. In our study, this would have required up to 2,300 independent, identifiable, and homogenous locations, far beyond the scope of this project.

We did not perform an accuracy assessment of the TRIM Lakes, Roads/Trails, and Rivers, but relative to the Landsat-derived cover types are confident in their associated planimetric accuracy. Terrain Resource Inventory Mapping is conducted at a scale (1:20,000) larger than the resolution of Landsat imagery (~1:50,000) and 90% of all well-defined planimetric features are within 10 m of their true position (British Columbia Ministry of Crown Lands 1990). Although the Landsat image revealed only discontinuous road or river pixels at many locations, these agreed with those contained on the GIS coverages. We are uncertain of the practices or accuracy standards used to survey and digitise the clearcut boundaries. In several locations we observed boundaries that extended one to two pixels

Number	Cover Type	Producer's	User's	Kappa
1	Aspen	93.9%	75.6%	0.738
2	Pine	82.4%	93.3%	0.925
3	Spruce	68.8%	50.0%	0.483
6	Avalanche Track	71.2%	97.4%	0.970
8	Alpine-Little Vegetation	84.6%	9 1.7%	0.909
9	Alpine-Shrub	50.0%	50.0%	0.494
10	Black Spruce	52.4%	61.1%	0.593
11	Sedge/Sphagnum Bog	76.5%	100%	1.000
12	Shrub Bog	93.3%	90.3%	0.897
13	Alpine-Moist Shrub	100%	100%	1.000
14	Rockfall	100%	77.8%	0.774
15	Krummholz	87.5%	71.8%	0.698
16	Alpine-Grass Shrub	75.0%	85.7%	0.855
17	Abies-Spruce	28.6%	40.0%	0.391
19	Spruce-Pine	62.5%	76.9%	0.761
20	Bedrock/No Vegetative Cover	66.7%	33.3%	0.329
21	Pine-Black Spruce	65.0%	38.4%	0.355
22	Cottonwood	77.8%	87.5%	0.873
23	Abies	0.0%	0.0%	0
24	Abies-Pine	100%	33.3%	0.332
25	Pine-Lichen Terrace	87.7%	98.6%	0.983
26	Abies-Spruce-Pine	68.8%	78.6%	0.778
104	Anthropogenic	100%	100%	1.000

Table A.2. Classification accuracy for individual cover types resulting from a supervised classification of the Wolverine caribou study area. Overall accuracy was 76.7% with a Kappa statistic of 0.748.

¹ Producer's accuracy represents the percentage of ground truth sites that were correctly classified (e.g., the percentage of Cottonwood sites correctly classified as Cottonwood).

² User's accuracy represents the number of correctly classified ground truth sites in a category relative to the total number of ground truth sites correctly and incorrectly classified as that category (e.g., the percentage of all sites classified as cottonwood that were actually cottonwood).

³ Kappa statistic represents the improvement in the observed classification over one based on chance. A κ of 0 suggests that a given classification is no better than a random assignment of pixels.

Table A.3. Matrix describing errors of omission (column = number of ground truth sites incorrectly excluded from cover type), commission (row = number of sites incorrectly included within cover type), and number of correctly classified ground truth sites (shaded values) for cover types resulting from a supervised classification of the Wolverine caribou study area.

Cover Type'	1	2	3	4	6	8	9	10	11	12	13	14	15	16	17	19	20	21	22	23	24	25	26	104	Total # of Classified Sites
1	31	0	1	0	16	0	0	0	1	2	0	0	0	0	0	0	0	0	2	0	0	0	0	0	53
2	0	42	0	0	0	0	0	1	0	0	0	0	0	0	0	I	0	1	0	0	0	0	0	0	45
3	0	0	11	0	0	0	0	3	0	0	0	0	0	0	3	2	0	3	0	0	0	0	0	0	22
4 ²	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3
6	0	0	0	0	25	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	26
8	0	0	0	0	0	33	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	36
9	0	0	0	0	1	0	3	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	6
10	0	2	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	2	0	0	0	3	0	0	18
11	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13
12	1	0	0	0	0	0	0	0	2	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	31
13	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	l l
14	0	0	0	0	0	2	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	9
15	0	0	0	0	9	0	0	0	0	0	0	0	28	0	0	0	0	0	0	0	0	0	2	0	39
16	0	0	0	0	0	1	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	7
17	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	1	0	5
19	0	0	l	0	0	0	0	0	0	0	0	0	0	0	1	10	0	0	0	0	0	0	1	0	13
20	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	6
21	0	5	3	0	0	0	0	5	0	0	0	0	0	0	0	3	0	13	0	0	0	5	0	0	34
22	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	8
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
24	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	71	0	0	72
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	11	0	14
104	0	0	0	0	_ 0	_ 0	0	0	_ 0	0	0	0	0	0	0	0	0	0	_0	0	0	0	0	7	7
Total # of Ground	33	51	16	0	52	39	6	21	17	30	1	7	32	8	7	16	3	20	9	0	1	81	16	7	472
Truth Sites		<u> </u>																							L

¹ See Table A.1 for a full description of cover types. ² The cover types Lake (4), Clearcut (99), River (100), and Road/Trail (101) were derived from TRIM data and were not tested for errors of omission.

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beyond the edge of clearcuts found on the composite image. This error of commission was likely less than would result from classifying clearcuts using a spectral signature that coincided with other deciduous cover types. Augmenting the classified image with ancillary GIS data enhanced the interpretability and usefulness of the final map.

Our results suggest that Landsat TM imagery, in combination with topographic data, can be used to map boreal and sub-boreal ecological types. The technique and data were successful at identifying vegetation associations important as caribou habitat (e.g., pine-lichen woodlands, wetlands, and alpine types). Although our method is of a lower resolution than other techniques such as TEM, it is relatively inexpensive and will meet the needs of largescale studies of caribou-habitat relationships.

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APPENDIX B – WINTER LOCATIONS OF GPS-COLLARED CARIBOU OF THE WOLVERINE HERD



Figure B.1. Locations of GPS-collared caribou of the Wolverine herd in northcentral British Columbia for the winters (December-April) of 1996-1999.

APPENDIX C - SPRING, SUMMER, AND AUTUMN LOCATIONS OF GPS-COLLARED CARIBOU OF THE WOLVERINE HERD



Figure C.1. Locations of GPS-collared caribou of the Wolverine herd in northcentral British Columbia for the :

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al British Columbia for the spring, summer, and fall of 1996-1999.

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APPENDIX D - LOCATIONS OF WOLVES AND WOLF KILL SITES IN THE WOLVERINE CARIBOU STUDY AREA



Appendix D.1 Locations of radio-, GPS-, and ARGOS-collared wolves and confirmed kill sites in the V

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and confirmed kill sites in the Wolverine caribou study area of northcentral British Columbia from March 1996 - June 19

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ea of northcentral British Columbia from March 1996 - June 1999.

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APPENDIX E - AVERAGE SNOW DEPTHS IN THE WOLVERINE CARIBOU STUDY AREA

Name	Description	UTM North	UTM East
SKL	Skunk Lake Forest Service road	6136884	434375
TSL	Tsaydaychi Lake Ministry of Environment Lands and	6142579	388169
	Parks snow station		
SQL	Squawfish Lake	6145831	403681
160	2 km of the 16000 spur line	6154428	433524
FSJ	Junction of Thutade and Finlay-Manson Forest Service	6156077	427225
	road		
MAN	Manson River	6160215	407308
106	106 km of the Finlay Forest Service road	6172600	443250
WOL	Wolverine Lakes	6173181	407419
GLA	Germansen Landing Environment Canada snow station	6183445	393080
12 M	12 Mile Creek	6188466	381192
BLL	Blue Lake	6193279	405904
148	148 km Finlay Forest Service road	6203633	421137
171	171 km Finlay Forest Service road	6217750	406000
LDC	Lower Donna Creek	6159253	423763
315	31.5 km Finlay-Osilinka Forest Service road	6225750	380250
MES	Mesilinka logging camp	6218512	412536

Table E.1. Name, description, and location of snow stations found in Figures E.1, E.2, and E.3.



Figure E. J. Average snow depths in the Wolverine caribou herd study area in northcentral British Columbia for two-week periods during the winter of 1996/1997. Asterix (*) indicates snow stations near, but outside of the study area and excluded from analyses in Chapter 6.



Figure E.2. Average snow depths in the Wolverine caribou herd study area in northcentral British Columbia for two-week periods during the winter of 1997/1998. Asterix (*) indicates snow stations near, but outside of the study area and excluded from analyses in Chapter 6.



Figure E.3. Average snow depths in the Wolverine caribou herd study area in northcentral British Columbia for two-week periods during the winter of 1998/1999. Asterix (*) indicates snow stations near, but outside of the study area and excluded from analyses in Chapter 6.