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# Managing fire for woodland caribou in Jasper and Banff National Parks

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*Abstract:* Woodland caribou (*Rangifer tarandus caribou*) populations in Jasper (JNP) and Banff National Parks (BNP) have declined since the 1970s, coincident with reduced fire activity in both parks, relative to historic levels. Some researchers have suggested that long periods without fire may cause habitat deterioration for woodland caribou, primarily by reducing available lichen forage. We examined winter habitat selection by woodland caribou at coarse and fine scales based on GPS-derived telemetry data and used models that included stand origin (decade), topography, and several stand structure variables that are related to time since fire, to explore relationships among caribou, lichen, and fire history. Based on the relationships illustrated by the models, we assessed how fire management could be applied to caribou conservation in JNP and BNP. At a coarse scale, caribou selected old forest (> 75 years) in landscapes that have likely experienced less frequent wildfire. While the abundance of *Cladonia* spp. influenced caribou use at fine scales, a preference for areas with older trees within stands was also significant. We conclude that short-term habitat protection for woodland caribou in JNP and BNP likely requires fire exclusion from caribou range.

**Key words:** *Cladonia*, fire management, forage, generalized linear models, habitat, lichen, multi-scale models, *Rangifer tarandus caribou*, resource selection functions.

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## Introduction

Woodland caribou (*Rangifer tarandus caribou;* hereafter caribou) in Alberta, Canada are listed federally and provincially as a threatened species (Alberta Wildlife Act, 2002; COSEWIC, 2003). Several factors have been implicated in recent population declines: (1) direct disturbance from human activities, (2) increased predation due to increased predator access along anthropogenic linear features and increased predator abundance due to alternate prey population increases, and (3) habitat loss, primarily as a result of industrial activity (Edmonds, 1988; Seip, 1992; James & Stuart-Smith, 2000; McLoughlin *et al.*, 2003; Wittmer *et al.*, 2005).

Jasper and Banff National Parks (JNP and BNP) contain the most southerly distribution of woodland caribou in Alberta. Despite protection from industrial development, the south JNP population is in serious decline, while the northern BNP population may consist of less than 6 animals (Flanagan & Rasheed, 2002; Mercer, 2002). In the national parks, caribou population declines could be caused by habitat deterioration due to human infrastructure (Parks Canada, 2000), displacement due to human use (Whittington & Mercer, 2004), increased predator pressure due to human activities (Mercer 2002) or recently reduced frequency in fire disturbance (Tande, 1979; Rhemtulla *et al.*, 2002; Van Wagner *et al.*, 2006), which has been hypothesized to result in a reduction of lichen forage (Schaefer & Pruitt, 1991; Thomas & Armbruster, 1996). Our research examines the latter possibility.

A low frequency of fire in the Rocky Mountain National Parks in the past century has been accompanied by a change from a relatively heterogeneous landscape, including a range of forest ages and composition along with non-forested areas, to a relatively even-aged and uniform, forest structure and composition (Tande, 1979; Rhemtulla *et al.*, 2002). This shift in forest age and structure, which could be attributed to fire supression activities, should have benefited caribou, given that they have generally been found to prefer older forests (Apps *et al.*, 2001; Szkorupa, 2002; Joly *et al.*, 2003; Saher, 2005). However, populations have declined in recent decades (Mercer *et al.*, 2004).

An assessment of fire effects on caribou requires consideration of temporal effects on habitat. Fires can make forests unsuitable for caribou for at least several decades (Thomas *et al.*, 1996a; Joly *et al.*, 2003), but some researchers have suggested that a lack of fire eventually leads to degradation of caribou habitat as terrestrial lichen cover declines (Schaefer & Pruitt, 1991; Coxson & Marsh, 2001). The immediate effect of fire on lichens is destruction through combustion (Johnson, 1981; Schaefer & Pruitt, 1991; Joly *et al.*, 2003). Over time, following fire, lichen genera re-establish in a sequential pattern; usually *Cladonia spp.*, followed by genera more commonly preferred by caribou (e.g., *Cladina* spp., *Cetraria* spp.*;* Johnson, 1981; Klein, 1982; Snyder & Woodard, 1992; Thomas & Hervieux, 1994; Thomas *et al.*, 1996a). In the longer term, terrestrial lichens may decline as litter accumulates and forest floor bryophyte cover develops (Klein, 1982; Payette *et al.*, 2000; Coxson & Marsh, 2001). Arboreal lichen is usually only found in abundance in older, presumably long-unburned stands (Edwards *et al.*, 1960; Schaefer & Pruitt, 1991; Apps *et al.*, 2001). Structural changes accompanying forest development post-fire, such as declining stand density (Arseneault, 2001; Schoennagel *et al.*, 2003) and development of continuous forest canopy (Bessie & Johnson, 1995) may create stand structures preferred by caribou.

Terrain affects stand structure and fire behavior (Hirsch, 1996; Gray *et al.*, 2002), and has been shown to influence caribou habitat selection (Johnson *et al.*, 2004; Saher & Schmiegelow, 2005). Elevation can influence fire return intervals, with older stands tending to occur at higher elevations (Tande, 1979; Rogeau, 1996; Schoennagel *et al.*, 2003) while aspect affects both fire frequency and intensity, with south and southwest aspects having more frequent and more intense fire events (Tande, 1979; Gray *et al.*, 2002).

Over the last decade, Parks Canada has adopted a policy of trying to achieve annual burning of an area that would eventually emulate 50% of each Park's average long-term fire cycle (Parks Canada, 2000; 2001; 2005). Per hectare average burn rates are calculated across the extent of a park, ignoring topographic variation in the fire cycle (Parks Canada 2005). Prescribed burning is employed to meet multiple management objectives in parks and elsewhere (Van Wagner & Methven, 1980; Achuff *et al.*, 1996), with effects on caribou largely unknown. Our objective was to develop and evaluate emprical models to determine whether stand age affects caribou habitat selection. We were specifically interested in whether caribou use forests younger than 75 years during winter, as this cohort is underepresented in our study region, relative to natural, historic levels; thus, restoration of this age class has become an objective of fire management efforts in the parks. Following on recent studies that have highlighted the importance of examining caribou habitat selection at different spatial scales (Rettie & Messier, 2000; Apps *et al.*, 2001; Johnson *et al.*, 2001; Szkorupa, 2002; Saher, 2005), we wanted to develop both fine- and coarse-scale models. At a coarse scale, we evaluated habitat selection models using variables related to time since fire along with those that may influence fire regime. Our fine scale modeling efforts focused on caribou selection related to lichen abundance, given the importance of forage availability to caribou (Rettie & Messier, 2000; Saher, 2005), but also included topography, stand age, and forest composition and structure.

## Material and methods

### *Study area*

We conducted our study in the southern half of JNP (52.5°N, 118.08°W) and the northern portion of BNP (51.3°N, 116.15°W; Fig. 1), in the Rocky Mountains of Alberta, Canada. Both areas are immediately east of the continental divide and include wide, glacier-carved valley systems. In JNP, a significant proportion of the park area consists of rock and glacial ice (19%; Holland & Coen, 1983). Forested areas include the montane (7%), lower subalpine (30%), and upper subalpine (37 %) ecological regions (Holland & Coen, 1983). The BNP valley systems for this study were all higher elevation valleys and did not include any montane zones. In the vegetated portion of the BNP study area, 44% was alpine, 30% was upper subalpine, and 25% was lower subalpine (Holland & Coen, 1983). Montane forest was primarily composed of dominant and mixed stands of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), Douglas-fir (*Pseudotsuga menziesii*), and trembling aspen (*Populus tremuloides*). Subalpine forests included lodgepole pine, subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), black spruce, whitebark pine (*Pinus albicaulus*), and subalpine larch (*Larix lyallii* - BNP only). Stand boundaries in both study areas were determined primarily by stand initiating fire events (Tande, 1979; Achuff *et al.*, 1996). Stands were up to 400 years old in the study area in JNP, (Tande, 1979; Parks Canada, unpublished data), and generally older in the BNP study area, some as old as 600 years (Rogeau, 1996; Parks Canada, unpublished data). Elevations of sample locations ranged from 1019 m to 2393 m above sea level (ASL) in JNP and 1494 m to 2589 m ASL in BNP. While not the emphasis of this study, we note that both parks support diverse predator populations, including wolf (*Canis lupus*), grizzly bear (*Ursus arctos horribilis*), black bear (*Ursus americanus*), wolverine (*Gulo gulo*), and cougar (*Felis concolor*) (Holland & Coen, 1983). For wolves, the primary ungulate prey species in both JNP or BNP is elk (*Cervus elaphus*) (White *et al.,* 2003); in contrast to other forested systems where moose (*Alces alces*) represent the primary prey (Lessard *et al.*, 2005; Wittmer *et al.*, 2005).

### *Study design*

We used a mixed modeling approach to create a candidate set of Resource Selection Function (RSF) models at coarse and fine scales, using telemetry based animal location data. RSF models quantify habitat selection patterns based on the use of potential habitat attributes (independent variables) relative to their availability. We treated individual animals as a random effect in our models to address issues of pooling location data from multiple animals (Otis & White, 1999), and elimated correlated independent variables ($r$>0.50) using univariate regression to identify the variables with greatest potential explanatory power among correlated pairs. S-PLUS v.6.2 was used for all analyses (Venables & Ripley, 1999).

### *Animal location data*

We used Global Positioning System (GPS) telemetry collar data (GPS 2200 and GPS 3300 Lotek, Inc.) from 2001-2004, collected between October 15 and April 15 of each year. From late April-October, caribou remained primarily in alpine areas in JNP and BNP, for which there is no measured fire cycle (Tande, 1979; Rogeau, 1996). We thus restricted our analyses to the period where caribou occurred primarily below treeline, yielding a total of 8124 caribou locations, collected over 3 years. Data were supplied by Parks Canada, from the first 3 years of a 5-year caribou study in JNP (Mercer *et al.*, 2004) and from the first year of BNP's caribou telemetry monitoring (Dibb, 2004). Caribou were captured in late fall each year, with 11 animals collared from 2001-03, and 8 in the winter of 2003-04. Locations were collected every 6 hours, with an average successful fix rate of 81.8%. Habitat-induced bias has been cited as a confounding factor in selection studies using GPS telemetry data (D'Eon *et al.*, 2002; Frair *et al.* 2004). Frair *et al.* (2004) found that closed conifer forest cover resulted in a GPS habitat-induced data loss that biased coefficients if data loss was ≥ 30%. Our overall GPS data loss was less than 20%, thus we did not feel it necessary to account for bias in parameter estimation. Furthermore, Hebblewhite *et al.* (in press) report that Lotek 12 channel GPS collars, as used in this study, do not have significant habitat-induced data loss, and do not require correction when used in the Central Canadian Rockies.

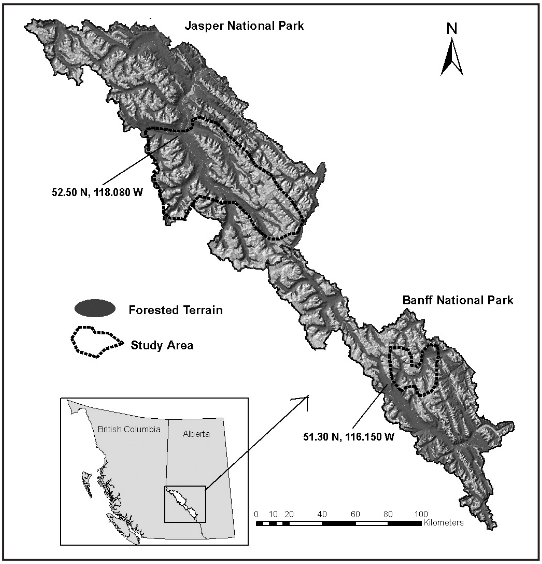

**Fig. 2.** Early winter locations of caribou (2002 to 2006), by herd, showing lack of spatial overlap during this season for woodland caribou in central British Columbia.

### *Spatial scales*

Our coarse scale corresponded to stand level selection, and was chosen to reflect the scale at which fires tend to occur on the JNP and BNP landscape (Tande, 1979; Rogeau, 1996). Fine scale corresponded to foraging level selection, consistent with other studies (Johnson *et al.*, 2001; Szkorupa, 2002; Saher, 2005). At the coarse scale, available habitat was delimited by height of land and main valley-bottom rivers beyond the furthest caribou observations from 2001-2004 GPS collar data, earlier radio-telemetry locations from the area (Brown *et al.*, 1994; Thomas & Armbruster, 1996), and recorded historical caribou observations dating back to 1978 (Parks Canada, unpublished data; see Fig. 1). At the fine scale, we defined available habitat as treed areas within valleys containing GPS telemetry caribou use locations from 2001-2003. Valleys were delimited by surrounding mountain ranges and defined as the continuous forest cover on either side of a single main valley-bottom river or stream. Topography is a physically-limiting factor for caribou travel in this mountainous terrain, and thus arguably more biologically relevant than average daily distance traveled (e.g., Joly *et al.*, 2003; Johnson *et al.*, 2004). Fine scale sampling was further limited to include only those locations south of a major highway transecting JNP (Highway 16); north of which we had no caribou location data.

*Coarse-scale resource selection*

We used a Generalized Linear Modeling approach (GLM), applying logistic regression to compare used (caribou "use" location) and available (random) sites for a set of candidate models derived from a suite of land cover and topographic data, and conducted model training and validation using partitioned data to evaluate model performance. Locations from 2 caribou collared in 2001/2002, and 9 caribou collared in 2002/2003 were used for model training (a total of 4288 "use"; 9798 "available" locations), and validation was undertaken using two independent data sets: JNP's 2003/2004 telemetry data (8 caribou - 3048 "use"; 11 292 "available" locations) and BNP's 2003/2004 data (1 caribou - 783 "use" locations; 783 "available"). Available locations were randomly generated separately for each of the training and validation sets, from coordinates constrained to the park boundary for JNP (sample of 15 000), and subsequently restricted to the study region (i.e. the treed portion of the park), and constrained from the outset to create a number of available locations for the treed portion of BNP equal to the total number of "use" locations we had for BNP. This procedure resulted in some variation in the ratio of "use" to "available" locations in the different data sets, but we do not feel it unduly influenced our results.

Digital ecological land classification maps for JNP and BNP (Holland & Coen, 1983) identify the following vegetation types: lodgepole pine, Douglas-fir, white spruce, poplar, aspen, closed Engelmann spruce/subalpine fir, Engelmann spruce/subalpine fir/whitebark pine, shrub, meadows, or alpine. From these, we assigned each use or available location to either open forest (meadow, alpine, poplar, or aspen [which was leafless during the winter sampling period]), or closed conifer (all other categories). We used 75-year stand origin categories ("Fire.cat"), based on related research reporting development of preferred lichen forage at 70-80 years post-fire (Thomas & Armbruster, 1996; Thomas *et al.*, 1996a; Szkorupa, 2002), and created a binary variable, "fire.old", to compare old stands (>150 years) to younger stands (<150 years). Aspect categories correspond to the eight cardinal and semi-cardinal compass directions. All elevation, stand origin date, slope, and aspect data were obtained from the parks digital elevation models (20m resolution) and stand origin maps (Tande, 1979; Rogeau, 1996; Parks Canada, unpublished data). Table 1 summarizes all variables evaluated in the coarse scale models.

Candidate coarse scale models contained combinations of stand origin, structure, and topographic variables (Table 2). We included linear and non-linear forms of stand origin variables as well as stand origin interactions with topography to determine whether these influenced caribou selection (beta coefficients significant at $\alpha < 0.05$). We compared our suite of candidate models using the Akaike Information Criterion (AIC; Burnham & Anderson, 1998), including only significant predictor variables (beta coefficients with $\alpha <0.05$), as AIC calculations for large sample sizes tend to favor over-parameterization of models (Link & Barker, 2006). To determine the relative significances of "levels" within categorical variables, we used the Sidak post-hoc multiple comparison test (Venables & Ripley, 1999) to rank levels based on beta coefficients. Ranking of selection preference is recommended by Keating & Cherry (2004) for use/availability RSF studies. We summed the number of times each level was selected over another (given a 95% confidence interval) to determine an overall category ranking. Those with highest ranks were considered preferred by caribou.

Model performance was evaluated using Spearman rank correlation to compare relative probability values from the validation data sets, which were divided into 9 bins of 0.0-0.10, 0.11-.20, 0.21-0.30, 0.31-0.40, 0.41-0.50, 0.51-0.60, 0.61-0.70, 0.71-0.80, and 0.81-1.00, with interpolated values from the training model (see Boyce *et al.*, 2002). The 10th bin (0.91-1.00) was grouped with the 9th because only 3 predicted probabilities were greater than 0.90.

*Fine-scale resource selection*

Our fine scale selection analysis included a large number of biologically plausible variables related to stand age, forest structure and topography, and it was necessary to reduce this set to generate candidate RSF models for analysis. We first used univariate logistic regression to identify variables that accounted for deviance of at least one. We further reduced this list of potential predictors using a stepwise approach to create three groups of candidate models: 1) lichen based, 2) forest age and structure based, and 3) lichen and forest age and structure combined. The use of frequentist techniques can bias parameter estimation and model selection when mixed with an information-theoretic approach (Burnham & Anderson, 1998; Whittingham *et al.* 2006). We have employed it recognizing these limitations, and acknowledge the exploratory nature of our analyses.

In order to populate fine scale models, we sampled 38 field plots in 2003 ("use" locations), and 154 field plots in 2004 (90 "use"; 64 "available"). The 2003 use sites were selected from a random draw of filtered locations from the two caribou collared in 2001/02 (see Animal Location Data and Spatial Scales), whereas in 2004, we randomly selected 10 use sites from each of 9 animals. Year was evaluated as a variable within our set of candidate models, to assess the potential influence of differences in sample design. We sampled 64 randomly located sites (available sites) within valleys containing caribou use locations, while excluding areas within 300 m of a use location; 300m is one order of magnitude larger than the reported error for a study on uncorrected GPS collar accuracy in mountainous terrain (D'Eon *et al*., 2002). Since GPS caribou location data from BNP were not available during the 2004 sampling season, fine scale selection analysis used JNP sample data only.

At each sample location, we used 2 diagonally-adjacent 10m by 10m quadrats laid out on a north-south by east-west grid to delineate the plot area, and recorded local slope and aspect in degrees. For each tree (≥ 5 cm diameter at 130 cm above ground (DBH)), we recorded species, DBH, and arboreal lichen abundance by categories (<0.1g: *class 0*, 0.1-5 g: *class 1*, 5.1-50 g: *class 2*, 50.1-250 g: *class 3* as per Stevenson *et al*., 1998). To quantify arboreal lichen abundance, we used counts of numbers of trees per plot in each of the different lichen abundance classes (Stevenson *et al*., 1998) and also evaluated a binary variable that coded plots as having at least one Class 3 tree (estimated > 50 grams of lichen) or not. To quantify terrestrial lichens we estimated percent

**Table 1.** Definitions of independent variables used in the coarse scale selection models. The description of the "Fire Category" (stand age categories) variable also includes percent of study area for each category.

| Variable | Data type | Description |
|---|---|---|
| fire | continuous | stand origin date based on park stand origin map |
| fire.cat | categorical | six stand origin categories of 75-year intervals; <75 yrs old (9% of study area), 75-150 yrs (43%), 151-225 yrs (16%), 226-300 yrs (20%), 301-375 yrs (7%), >375 yrs (4%)* |
| fire.old | binary | stand origin date of either <150 yrs ago or >150 yrs ago |
| elev | continuous | elevation in meters above sea level from a digital elevation model (DEM) |
| slope | continuous | slope in degrees from the park DEM |
| aspect.cat | categorical | eight aspect categories of 45 degree intervals: north*, northeast, east, southeast, south, southwest, west, and northwest |
| aspect.cat1 | binary | south and southwest aspect (157.6-247.5 degrees azimuth) versus any other aspect |
| closure | binary | closed forest versus open based on Holland & Coen (1983); open stands include meadow, shrub, alpine and deciduous coded sites |

*reference categories for each categorical variable.

**Table 2.** Definitions of independent variables that were included in the top 10 fine scale selection models.

| Variable | Data type | Description |
|---|---|---|
| cladonia.cov | continuous | average percent *Cladonia* cover (from 5 quadrats per sample location) |
| #saplings | count | number of saplings (in one 2m x 2m plot) |
| all.lichen.cov | continuous | average percent cover of lichens (from 5 quadrats per sample location) |
| #logs | count | number of logs from line intersect count |
| %notPl.Se.Fa | continuous | percent of trees in plot that are not pine, spruce or fir |
| max.core | continuous | highest tree age (ring count from increment core) in plot |
| litter&moss | continuous | average depth in cm of litter and moss (5 measures per sample location) |
| #class1trees | count | number of arboreal lichen class 1 trees in a plot |
| basal.area | continuous | basal area of all trees in a plot calculated from dbh measurements from each tree |
| SorSW.aspect | binomial | south and southwest aspect (157.6-247.5 degrees azimuth) versus any other aspect |
| %fir | continuous | percent of trees in plot that were subalpine fir |

cover (to genus) to the nearest 1% in five, 240 $cm^2$ subplots in fixed corner locations of the plot. We also estimated cover of feathermoss (*Pleurozium* spp. or *Ptilium* spp.) and other moss genera (all other moss genera). In each subplot we also recorded moss and litter depth and depth from litter or moss surface to mineral soil. For the cover and depth estimates, we averaged the five subplot values to provide overall estimates for each sampling location. From the dominant canopy layer we selected three trees and took cores (at DBH) for aging. We used the highest ring count, as determined from these cores, as a conservative measure of minimum number of years since stand replacing fire at each site. We used the 20 m east-west line delineating the sides of the two quadrats as for line intercept sampling of the number of pieces of downed logs and had a 2 m by 2 m plot off the intersect point of the two quadrats in which we recorded the number and species of saplings (<5 cm diameter at 130 m height above ground). These variables and the model abbreviations are listed in Table 2.

We reduced the initial set of 49 habitat variables to 25 using univariate regression. Twenty candidate models derived from these 25 variables were constructed using data from all 192 field plots. We used AIC corrected for small sample sizes (AICc; Burnham & Anderson, 1998) to identify the most parsimonious model, and evaluated the top performing model using the Spearman rank, K-fold cross validation technique (Boyce *et al.*, 2002). We used a series of 10 random draws of 80% (154 plots) of our data for model training and the remaining 20% (38 plots) for validation. To ensure sufficient use locations per bin, with only 38 plots in our testing set, we used only 6 probability bins for the Spearman rank correlation test, and scaled the bins to correspond roughly with occurrence frequency (Boyce *et al.*, 2002), resulting in the following ranges: 0.00-0.25, 0.26-0.50, 0.51-0.70, 0.71-0.85, 0.85-0.95, and 0.96-1.00.

## Results

### *Coarse-scale resource selection*

The best coarse-scale model, in which all variables were significant, was the one incorporating all variables (Table 3). This model included: the linear form of slope in degrees (negative coefficient), elevation in meters (positive coefficient), the six (75-year) stand origin categories, the eight cardinal and semi-cardinal aspect categories, and a positive association for stands categorized as "closed conifer". Among predictor variables, elevation was most influential, explaining 74% of the variation, and forest closure the least (2%; Table 3). The model performed quite well, with significant and high Spearman Rank correlations (JNP: 0.950, BNP: 0.983; two tailed probability < 0.001).

At a landscape scale during winter, within the forested portion of BNP and JNP, caribou preferred higher elevations, less steep slopes, and closed conifer forest (*vs.* deciduous or open forest) (Table 3). Apparent preference for closed conifer forests supports our earlier assertion that accounting for habitat-induced bias was not necessary. Based on multiple comparison analysis of the six different fire categories, caribou preferred relatively older forest, showing the greatest preference for stands that were 226-300 years old and 75-150 years old. Caribou were least likely to select the youngest stands (<75 years old), but also avoided some older stands (151-225 years old and 301-375 years old) (Table 3). Multiple comparison analysis of aspect categories revealed that south and southwest aspects were avoided. "Fire" (stand origin date) was not a significant predictor for the training data set, while "fire.old" was not a consistent predictor variable between the training and testing data sets. "aspect.cat" with eight categories explained significantly more variation than "aspect.cat1" (south & southwest *vs.* all other aspects).

### *Fine-scale resource selection*

At a fine scale, the best performing model included variables related to lichen abundance, along with several stand-structure variables. The model indicated a preference for locations with high terrestrial lichen cover (especially *Cladonia* spp.), that had older trees and more saplings (of which 75% were subalpine fir), with avoidance of areas with deeper litter and moss, more downed logs, more trees with low arboreal lichen abundance, and sites with Douglas-fir or deciduous trees as part of the canopy (see Table 4).

Validation runs of this model yielded average Spearman's rho values of 0.921 ($0.02<P<0.05$). Two of the 10 runs were not significant at $\alpha = 0.05$ (both were $0.10<P<0.20$); this is likely due to the relatively small sample size ($n=192$) that was partitioned for testing. There was only a slight decrease in AICc with the addition of either the binary aspect category (negative association with south or southwest aspects), or basal area (negative). All coefficients in our top model were significant (at $\alpha = 0.05$).

## Discussion

### *Coarse-scale resource selection*

At a coarse scale, caribou in BNP and JNP avoid areas with younger forest, preferring forest that was at least 75 years old. Research in Alaska (Joly *et al.*, 2003), the Northwest Territories (Thomas *et al.*, 1998) and west-central Alberta (Szkorupa, 2002;

Saher, 2005) has similarly shown that caribou avoid younger forest. Preference for older forest is most likely related to lichen forage availability (Rominger & Oldemeyer, 1989; Thomas *et al.*, 1996a). Shepherd (2006) found that *Cladonia* spp. cover in forest younger than 75 years was insufficient to attract caribou; other researchers report similar thresholds (Thomas & Armbruster, 1996; Thomas *et al.*, 1996a; Szkorupa, 2002). Caribou avoidance of 151-225 year old forest, while strongly selecting for 226-300 year old forest, was unexpected. The avoidance could be attributed to a decline in terrestrial lichen cover as forest floor mosses increase, which has been observed in forests older than 150 years (Coxson & Marsh

**Table 3.** Coefficients and 95% confidence intervals for variables included in the coarse scale model '*full1*'. The reference category for "firecat" (stand origin categories) was 1300 -1625 and the reference category for "aspectcat" (Aspect categories) was North (337.6°-22.5° azimuth). Beta coefficients and 95% confidence intervals are from a combined data set of all 3 years of caribou data (2001-2004). The percent of variation explained by each parameter is included.

| Variable | $\beta$ | CI upper | CI lower | *t* value | % of model variation explained |
|---|---|---|---|---|---|
| elev | 0.007 | 0.0072 | 0.0068 | 55.49 | 74% |
| slope | -0.054 | -0.049 | -0.0590 | -21.82 | 11% |
| closure | 0.375 | 0.4690 | 0.2810 | 7.99 | 2% |
| fire.cat2 301-375yrs | -0.195 | -0.0888 | -0.3012 | -4.72 | |
| fire.cat3 226-300yrs | 0.148 | 0.1922 | 0.1038 | 8.65 | |
| fire.cat4 151-225yrs | -0.052 | 0.0030 | -0.1070 | -2.58 | |
| fire.cat5 75-150yrs | 0.052 | 0.0788 | 0.0252 | 5.57 | |
| fire.cat6 < 75 yrs | -0.071 | -0.0044 | -0.1376 | -2.49 | Total= 4% |
| aspect.catNE | 0.009 | 0.0786 | -0.0606 | 0.24 | |
| aspect.catE | 0.001 | 0.0402 | -0.0382 | 0.07 | |
| aspect.catSE | -0.086 | -0.0534 | -0.1186 | -5.28 | |
| aspect.catS | -0.235 | -0.2002 | -0.2698 | -13.5 | |
| aspect.catSW | -0.067 | -0.0484 | -0.0856 | -7.27 | |
| aspect.catW | 0.055 | 0.0706 | 0.0394 | 7.09 | Total= 8% |
| aspect.catNW | 0.029 | 0.0436 | 0.0144 | 4.00 | |

**Table 4.** Coefficients and 95% confidence intervals of variables included in the best fine scale model (*comb6*). Data were from all 192 plots sampled.

| Variable | $\beta$ | CI upper | CI lower | *t* value | % of model variation explained |
|---|---|---|---|---|---|
| all.lichen.cov | 0.054 | 0.103 | 0.005 | 2.22 | 29% |
| cladonia.cov | 0.129 | 0.226 | 0.032 | 2.65 | 14% |
| litter&moss | -0.226 | -0.034 | -0.418 | -2.36 | 9% |
| #saplings | 0.118 | 0.227 | 0.009 | 2.18 | 19% |
| #class1trees | -0.037 | -0.010 | -0.064 | -2.72 | 9% |
| #logs | -0.147 | -0.028 | -0.266 | -2.46 | 7% |
| max.core | 0.008 | 0.014 | 0.002 | 2.42 | 6% |
| %not.Pl.Se.Fa | -4.392 | -0.321 | -8.463 | -2.16 | 8% |

2001). The selection for stands older than 225 years may reflect stand transition from lodgepole pine to Engelmann spruce and Subalpine fir, which begins to occur 150 years post-fire in JNP and BNP (La Roi & Hnatiuk, 1980). Caribou may be avoiding less mature, mixed Engelmann spruce/Subalpine fir/lodgepole pine stands (151-225 years) but selecting for the more mature spruce/fir stands (226-300 years) which tend to have greater amounts of arboreal lichen (Edwards *et al.*, 1960; Stevenson & Enns, 1992; Terry *et al.*, 2000). This corresponds to the observed selection for closed-conifer stands. The selection for higher elevation and avoidance of south and south-west aspects could also reflect effects of time-since-fire. High elevations tend to have older forest, while south-west aspects tend to have more frequent fire occurrence (Tande, 1979; Rogeau, 1996).

There are alternative explanations for the observed caribou habitat selection preferences. Preference for higher elevations and avoidance of southwest aspects would be likely to promote separation from predators, as research in JNP found wolves generally preferred low elevation and southwest aspects (Whittington *et al.*, 2005). Predator avoidance may also explain the preference for less steep slopes and for closed canopied forest over open areas. Flatter slopes may provide easier escape, while closed conifer forests likely offer greater hiding cover and at the same time confer a foraging benefit since snow interception by the canopy would reduce the cratering depth necessary to access terrestrial lichens (Terry *et al.*, 2000). Predator avoidance can deter selection of preferred forage (Bergerud & Luttich, 2003). The combined influence of predators, other prey, and fire on caribou habitat selection requires further investigation.

### *Fine-scale resource selection*

Our fine scale model agrees with other fine-scale caribou selection research in suggesting preference for sites with greater lichen cover and older-forest characteristics (Johnson *et al.*, 2000; Szkorupa, 2002; Saher, 2005; Saher & Schmiegelow, 2005). Due to our initial frequentist approach, however, the fine scale model results should be viewed as suggestive rather than statistically definitive (Burnham & Anderson, 1998; Whittingham *et al.* 2006). At a fine scale, caribou preferred sites with high terrestrial lichen cover. Of the individual lichen genera examined, cover of *Cladonia* spp. was the strongest predictor of caribou use, and indeed was the strongest single predictor in univariate analyses. Interestingly, *Cladonia* spp. are not generally recorded as the primary terrestrial forage genus for caribou, with the possible exception of *Cladonia uncialis* or *C. arbuscula* (Szkorupa, 2002; Dunford, 2003; Saher, 2005; Saher & Schmiegelow, 2005). One study in northeastern British Columbia evaluated *C. uncialis* vs. *Cladonia* spp. and found only the latter to be a significant predictor of caribou habitat selection (Johnson *et al.*, 2000). In JNP, *Cladonia* spp. is the most abundant genera among the terrestrial forage lichens (Thomas & Armbruster, 1996; Shepherd, 2006), but overall, terrestrial lichen is relatively scarce in JNP and BNP as compared to northern Alberta, Alaska, or eastern Canada (Thomas *et al.*, 1996a, Arsenault *et al.*, 1997; Dunford, 2003, Joly *et al.*, 2003). Poole *et al.* (2000) and Johnson *et al.* (2001) found that in northern British Columbia, caribou selected for the species of lichen that was most abundant. The selection for areas with high cover of *Cladonia* spp. in this "lichen-impoverished" environment thus may represent a local foraging strategy.

Surprisingly, the number of heavily laden arboreal lichen bearing trees (Class 3 trees) was not an important predictor of caribou selection at the fine scale. While arboreal lichen has been identified as an important forage resource for caribou in west-central Alberta (Thomas & Armbruster, 1996; Szkorupa, 2002; Saher, 2005; Saher & Schmiegelow, 2005), this was not apparent from our analysis. However, arboreal lichens have been found to comprise only ~1% of caribou diet in BNP and JNP (Thomas *et al.*, 1996b). If areas with high abundance of arboreal lichens are important only during a relatively brief period of the winter season, our analysis may not have detected this as we included all early and late winter foraging (mid-October to mid-April). It is also possible that the short duration of our study did not capture a season in which heavy or long-lasting snow conditions necessitated a greater reliance on, and therefore noticeable selection for, areas with abundant arboreal lichen (Thomas *et al.*, 1996b). As mentioned previously, it is possible caribou are selecting for areas that would tend to have a higher likelihood of abundant arboreal lichen at the stand or coarse-scale, rather than at a foraging level. This is supported by avoidance of sites with Douglas-fir or aspen forest, and by avoidance of sites that had greater numbers of trees with little arboreal lichen (Class 1 trees).

Several lines of evidence point to selection for older stands at a fine scale. The strong positive influence of maximum tree core age (fine scale variable) indicates preference for sites with older trees. This is complementary to avoidance of sites with high numbers of Class 1 trees (< 5 grams of lichen /tree); these likely being younger, denser stands (Sillet & Goslin, 1999; Dettki *et al.*, 2000). Stand density itself, however, was not a significant predictor of caribou habitat selection. The positive influence of sapling density in the model is also suggestive of a preference for older forest, since 75% of the saplings found in the sample plots were subalpine fir, a late-successional, shade-tolerant, climax species that dominates under mature forest canopies in the subalpine (Johnson & Fryer, 1989; Callaway *et al.*, 2000). Selection for shallower duff could indicate favourable conditions occur on sites that had experienced a more recent fire event but that still have older trees present. This would have to be a low severity fire event, which is not considered the historic norm for the higher elevation sites preferred by caribou (Tande, 1979; Rogeau, 1996). In these areas, fire has been characterized as infrequent, severe, and stand replacing (Bessie & Johnson, 1995; Veblen, 2003). Determining the extent of low intensity fires in JNP and BNP would be required to assess this further.

Basal area, which increases with stand age, was not included in our top model, but it was a strong (positive) predictor of caribou selection in other candidate models. No other studies of woodland caribou in Alberta have reported basal area to be a significant predictor of habitat selection, but two studies in British Columbia's Selkirk Mountains found mountain caribou selected for habitat with greater basal area (Rominger & Oldemeyer, 1989; Terry *et al.*, 2000).

Avoidance of sites with increased numbers of downed logs could also reflect avoidance of younger sites, which would contain an abundance of fire-derived downed wood. A simpler explanation, however, is that this avoidance is related to logs being a physical barrier to travel (Schaefer & Pruitt, 1991). Areas with an abundance of downed wood may have been avoided to conserve energy, or to allow easier escape from predators.

## Conclusions

Our selection models at both scales indicated a preference by caribou for older forest, or sites likely to have older forests. At a landscape scale, caribou selected older forest (75-150 yrs and 225-300 yrs), higher elevations and less steep slopes. Similarly, in the fine scale model there was selection for sites with older trees, and older forest characteristics. Terrestrial lichen abundance was a significant predictor of caribou habitat selection while arboreal lichen abundance was not. Nevertheless, harsher conditions than those encountered during the years of this study could increase the relative importance of arboreal lichens at a fine scale. It should also be emphasized that predator avoidance may be indirectly linked to several of the model variables. Information on the response of predators and their primary prey to stand age, as reflecting fire history, is critical for determining how to manage disturbances in caribou range. High disturbance levels in caribou ranges, with associated changes in habitat availability and distribution and shifts in predator and primary prey abundance and distribution, have been indentified as the ultimate cause of caribou decline throughout Alberta (Dzus, 2001; Alberta Woodland Caribou Recovery Team, 2005; Lessard *et al.*, 2005).

Our habitat selection models do not suggest that the lack of recent fire in JNP and BNP has been detrimental for caribou. Large prescribed burns within caribou habitat would create areas that caribou would be likely to avoid during the winter for up to 75 years. Caribou habitat would therefore benefit, at least in the short term, from exclusion of prescribed fires and wildfires from caribou range. Currently, only 9% of the study area includes stands in the <75 year category (Shepherd, unpublished data). While 9% is sufficient representation to ensure that caribou are not avoiding this age class due to scarcity, this proportion is negatively skewed from the expected negative exponential stand age distribution (Van Wagner *et al.*, 2006). To achieve fire management goals of restoring historic stand age distributions within the national parks, while avoiding negative impacts on caribou habitat, prescribed burning will need to be focused away from areas identified as critical caribou winter range.

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