The Eleventh North American Caribou Workshop,
Jasper, Alberta, Canada,
24-27 April, 2006.

Caribou nursery site habitat characteristics in two northern Ontario parks

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Abstract: To prevent further range recession, habitat features essential to the life-history requisites of woodland caribou (*Rangifer tarandus caribou*) such as calving and nursery sites need to be protected for the persistence of the species. Woodland caribou may minimize predation risk during calving by either spacing out or spacing away from predators in the forest to calve on islands, wetlands, or shorelines. Our objective was to determine the characteristics of shoreline habitats used as calving and nursery sites by female woodland caribou in northern Ontario. Detailed vegetation and other site characteristics were measured at nursery sites used by cow-calf pairs in Wabakimi and Woodland Caribou Provincial Parks for comparison with shoreline sites that were not used by caribou within each park. Differences in habitat variables selected by female caribou in the two study areas reflect broad ecoregional differences in vegetation and topography. In Wabakimi Provincial Park, understorey tree density and ground detection distance played key roles in distinguishing nursery sites from sites that were not used. In Woodland Caribou Provincial Park, groundcover vegetation and shrub density were important in the selection of nursery sites by female caribou. Generally, female caribou in both parks selected nursery sites with greater slope, lower shrub density but thicker groundcover vegetation, including greater lichen abundance, and higher densities of mature trees than shoreline sites that were not used. The identification of these important features for caribou nursery sites provides a basis for improving their protection in future management policies and legislation.

Key words: calving sites, forest-dwelling woodland caribou, nursery sites, predator avoidance, protected areas, *Rangifer tarandus caribou*, resource selection, Wabakimi Provincial Park, Woodland Caribou Provincial Park.

Rangifer, Special Issue No. 17: 167-179

Introduction

In Ontario, woodland caribou (*Rangifer tarandus caribou*) range of continuous occupancy has receded further north since the late 1800s (Racey & Armstrong, 2000). This recession is mainly attributed to habitat loss through anthropogenic disturbance and Schaefer (2003) estimates that, at the current rate, forest-dwelling woodland caribou will be extirpated from Ontario in 90 years. Increased predation, especially on calves, may result from habitat alteration and corridor development (e.g., roads, seismic lines) that facilitate ingress and movements of predators and alternative prey (James & Stuart-Smith, 2000). Caribou have evolved space-use strategies to avoid predation (Bergerud *et al.*, 1990; Rettie and Messier, 2001), which is considered the main proximate factor of population limitation of woodland caribou across North America (Bergerud, 1974; Seip, 1992; Ouellet *et al.*, 1996; Stuart-Smith *et al.*, 1997; Rettie & Messier, 1998). When forest disturbance (i.e., timber harvest) takes place, it reduces the available space for caribou, thereby increasing caribou densities elsewhere and forfeiting the advantage of space (Bergerud, 1985; Bergerud & Page, 1987). Predators can kill more than 50% of young ungulates in free-ranging populations (Bergerud, 1971). Ungulates appear to be particularly vulnerable when they are old enough to flush from hiding, but are still too young to outrun predators (Fitzgibbon, 1990). Studies of caribou report that calves are most vulnerable to wolf (*Canis lupus*) (Bergerud & Page, 1987) and black bear (*Ursus americanus*) (Ballard, 1994) predation in their initial weeks of life.

Female woodland caribou have distinct summer and winter ranges (Edmonds, 1988) and exhibit selectivity and fidelity for specific calving and summer ranges (Brown *et al.*, 1986). If islands and shorelines are available, female caribou scatter to these relatively safe habitats to calve (Bergerud, 1985). Woodland caribou may spatially separate themselves from other ungulates that provide prey for wolves and bears, such as moose, by using lakeshores and islands (Bergerud, 1985; Cumming & Beange, 1987) or bog complexes (Valkenburg *et al.*, 1996; Stuart-Smith *et al.*, 1997) to calve in the spring.

Ferguson & Elkie (2004) suggest that fine-scale attributes of preferred caribou calving and nursery sites, such as those found along shorelines, need to be examined further in Ontario. Disturbances caused by landscape exploitation surrounding parks and protected areas (e.g., forestry activities) and human recreational activities (e.g., outpost camps, shore lunch areas, camping) both outside and within protected area boundaries, may prevent female caribou from returning to previously used calving sites on shorelines or in bog complexes. As a result, female caribou may be forced to use less suitable habitats, which can lead to greater predation and reduced population viability. To ensure caribou persistence across northern Ontario and impede further range recession, it is critical to identify potential nursery sites and ensure that adequate protection is given to these sites (Morrill *et al.*, 2005).

We describe fine-scale habitat characteristics of caribou nursery sites in two protected areas, not directly disturbed by forestry activity, to provide baseline information that may be used to predict locations of potential caribou nursery sites both outside and within protected area boundaries across northern Ontario. Vegetation and topographic characteristics were measured at nursery sites along shorelines used by cow-calf pairs in Wabakimi and Woodland Caribou Provincial Parks for comparison with shoreline sites that were not used by caribou within each park. These surveys focused on lakes, rather than bog complexes, because of the high recreational use of these areas and the known importance of these types of areas to caribou cow-calf pairs (Bergerud, 1985; Cumming & Beange, 1987). Important characteristics were used to develop and evaluate Resource Selection Functions (Boyce *et al.*, 2002; Manly *et al.*, 2002) for calving woodland caribou in northern Ontario. Critical habitat characteristics selected at nursery sites were hypothesized to reflect predator avoidance strategies and thus their protection in future management policies and legislation would have the greatest impact on population persistence.

Study areas

Wabakimi Provincial Park

This park is located in northern Ontario about 200 km north of Thunder Bay (Fig. 1). In 1983, Wabakimi Provincial Park was established at 155 000 ha in size and in 1997, the park was expanded to roughly 892 000 ha (Duinker *et al.*, 1996). The average July temperature in Wabakimi Provincial Park is 16 °C, while the average January temperature is -17 to -20 °C (Chapman & Thomas, 1968). Total annual precipitation is approximately 750 mm, which is considered moderate relative to other parts of the province, with approximately two-thirds falling from May to September (Chapman & Thomas, 1968). Tree species (Harris & Foster, 2005) include white spruce (*Picea glauca*), black spruce (*Picea mariana)*, jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), white pine (*Pinus strobus*), and red pine (*Pinus resinosa*). Mosses are a conspicuous cover over much of the forest floor, while patches of ground lichen (*Cladina* spp.) are common on jack pine-dominated sand flats and under open spruce stands on bedrock (Harris & Foster, 2005). The fire regime of this ecoregion is characterized by numerous small fires (<1040 ha) and few large fires (>5000 ha), but most of the total area burned is in large, intense fires (Beverly, 1998). Beverly (1998) found that the total area burned in the park decreased steadily from the 1930s to the 1960s but increased in the 1990s. The estimated fire cycle range for Wabakimi Provincial Park is 65-250 years (Ride *et al.*, 2004).

Woodland Caribou Provincial Park

Woodland Caribou Provincial Park is 450 000 ha in size and is located between Red Lake and the Manitoba border in northwestern Ontario, about 500 km northwest of Thunder Bay (Fig. 1). The average July temperature in Woodland Caribou Provincial Park is 18.4 °C while the average January temperature is -20.4 °C (OMNR, 2004). Average annual precipitation is approximately 609 mm; the second lowest in Ontario (Brunton, 1986). Approximately two-thirds of the total precipitation falls from May to September (OMNR, 2004). Vegetation of the area consists of typical boreal tree species such as jack pine, black spruce, balsam fir, and trembling aspen dominating

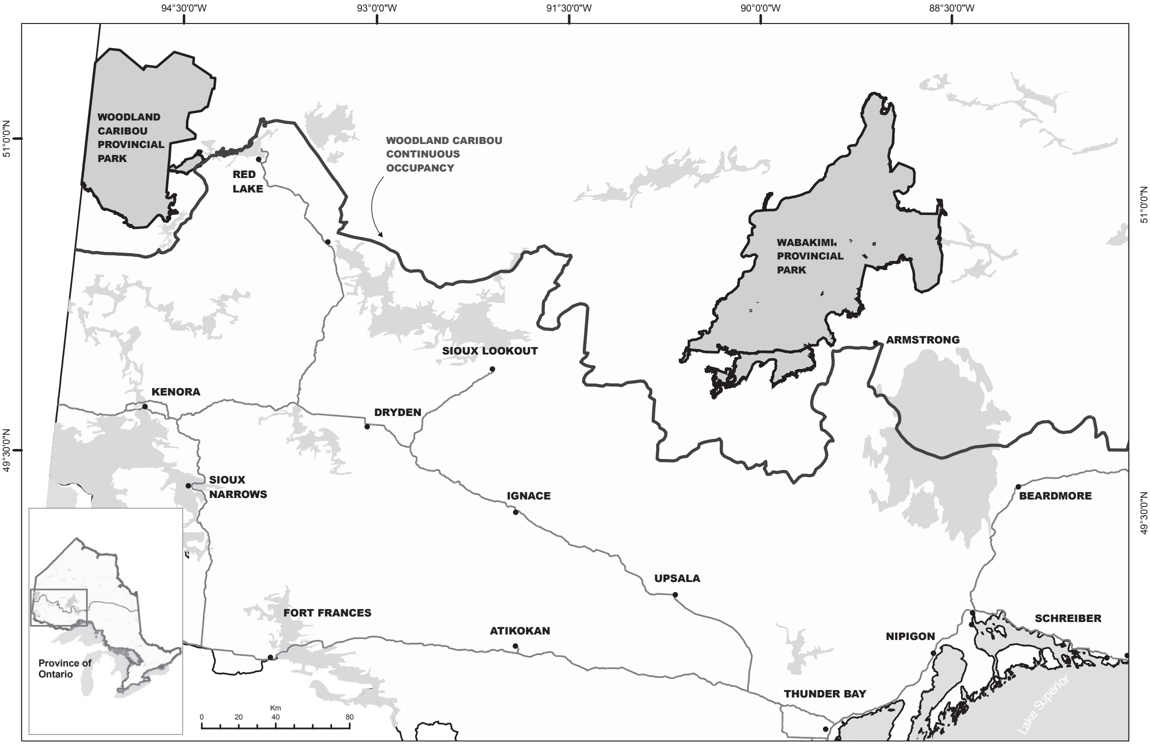

Fig. 1. Locations of Wabakimi and Woodland Caribou Provincial Parks in relation to the southern limit of continuous range occupancy of woodland caribou (*Rangifer tarandus caribou*) in northern Ontario.

upland sites, with black spruce and larch (*Larix laricina*) characterizing the wet, organic deposits commonly found in bedrock depressions (OMNR, 2004). The park is situated on a relatively flat plateau and soils are thin when present at all (Brunton, 1986). The slightly elevated position of the park area has resulted in a greater than normal incidence of dry upland forest, so jack pine is more dominant than black spruce (Brunton, 1986). Ground lichen is dominant in older jack pine forests and a dense ground cover of feather moss is common in black spruce forests (Brunton, 1986). This park is significantly affected by its proximity to the Prairie Provinces, resulting in a dry, hot growing season creating "boreal prairie" forests that experience a greater frequency of naturally occurring forest fires, in contrast with the more moist boreal forests further east (OMNR, 2004). The wilderness landscapes of this park have been strongly influenced by wildfire (Harris *et al.*, 2001). Brunton (1986) noted that most of the park had been burned between 1956 and 1986 and frequent and repeated burns appear to be representative of the area's natural cycle of burning since deglaciation. The estimated fire cycle range for Woodland Caribou Provincial Park is 40-110 years (Ride *et al.*, 2004).

Methods

Study sites

Caribou calves are generally born between the last week of May and first week of June in northern Ontario (Bergerud, 1975; Ferguson & Elkie, 2004). Based on systematic surveys (Timmermann, 1998) and anecdotal observations of caribou cow-calf activity in late May and early June in previous years, lakes ranging in size from 127 ha to 11 420 ha were selected for detailed study within each park; 4 lakes in Wabakimi Provincial Park (mean size 6 828 ha) and 10 lakes in Woodland Caribou Provincial Park (mean size 1193 ha). Systematic transect surveys for physical evidence (i.e., calf beds, pellets or tracks) of use (Timmermann, 1998) were then applied to identify nursery and "absence" sites associated with these lakes.

Calving sites are generally taken to be locations at which parturition occurs, whereas nursery sites are areas occupied by cow-calf pairs during the postpartum period (Lent, 1974; Addison *et al.*, 1990; Schaefer *et al.*, 2000). Calving and nursery sites cannot be readily distinguished from one another by physical evidence in transect surveys, and direct observations of parturition or cow-calf pairs were not made in this study. Therefore, all cow-calf sites identified in this study were classified as nursery sites, even

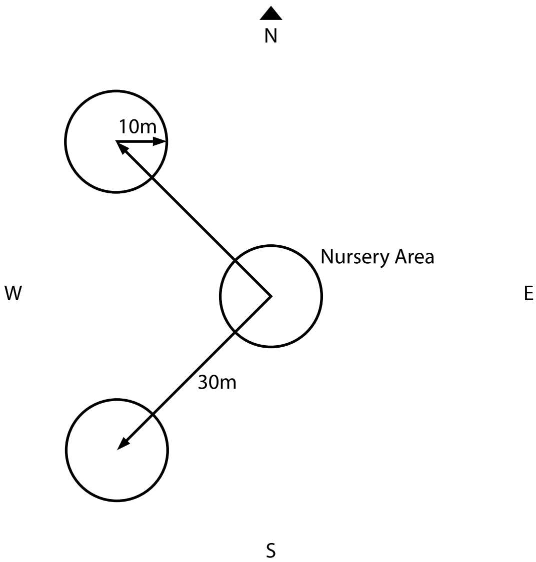

Fig. 2. Schematic of the three 10 m-radius sampling plots used to collect detailed vegetation data and other site characteristics at caribou nursery sites and randomly chosen absence sites on lakes in Wabakimi and Woodland Caribou Provincial Parks, northern Ontario.

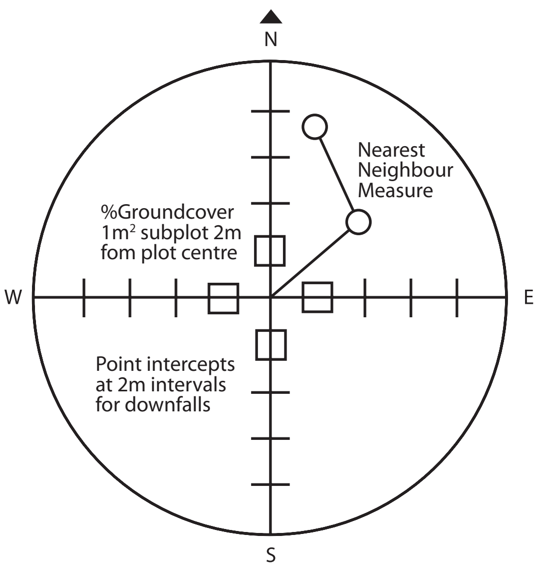

Fig. 3. Schematic of detailed vegetation measurements made within 10 m-radius sampling plots at caribou nursery sites and randomly chosen absence sites on lakes in Wabakimi and Woodland Caribou Provincial Parks, northern Ontario.

though birthing activity may have taken place as well. Absence sites were defined as areas with no physical evidence of use by caribou.

To limit the potential effects of human disturbance on the behaviour of calving caribou or physical disruption of nursery sites (e.g., by walking systematic transects, using motorboats, canoeing), surveys started in the middle of June each year (2001-2003) and most finished by the end of July. Along the shorelines of lakes and islands larger than 500 m in width or length, 100 m transects perpendicular to the shoreline were set every 1-2 km and surveyed for physical evidence of use (Timmermann, 1998). Islands less than 500 m in width or length were surveyed for nursery sites by walking transects, set perpendicular to the shoreline at 1 km intervals, across the entire island. Island and mainland transects were re-surveyed in subsequent years to determine whether or not nursery sites were used in the second and third year of the study. Absence sites were then identified as transects that were surveyed in at least two consecutive years without finding any physical evidence of caribou activity.

The transect surveys resulted in the identification of numerous nursery and absence sites from which 15 nursery sites in each park were selected for site measurements on the basis of accessibility. Fifteen absence sites in each park, on the same lakes as the nursery sites, were selected at random for comparisons.

Site measurements

Detailed vegetation data and other site characteristics were collected at three 10 m-radius plots established at each nursery site and each randomly chosen absence site (Fig. 2). Table 1 provides a list of the interval scale variables measured at each site (Leptich and Gilbert, 1986; Addison *et al*., 1990; Langley & Pletscher, 1994; Welch, 2000).

At nursery sites, the centre point of the first plot was established along the original transect where the most evidence of cow-calf activity was found. At absence sites, the centre of the first plot was established at the midpoint of the transect that had been walked at least twice without finding physical evidence of caribou activity. The geographic coordinates and elevation of the centre point of the first plot were determined with a handheld GPS unit (Garmin eTrex, Olathe, Kansas, USA). The slope was recorded using a clinometer and the direction of "downhill" (i.e., aspect) was also noted in 45-degree intervals (i.e., N, NE, etc.) relative to the evidence of cow-calf activity. Two additional 10 m-radius plots were established 30 m from the centre point of the first plot, both at a random compass direction, as long as there was no open water and no overlap between plots. Measurements from the three plots were averaged to obtain overall values for a site (Langley & Pletscher, 1994).

Measurements in each 10 m-radius plot

In each 10 m-radius plot, overstorey and understorey canopy cover were estimated occularly at plot centre and at points 30 m from plot centre in each of the four cardinal compass directions. These five cover estimates were later averaged to obtain a single percent cover estimate for each plot (Welch, 2000).

Ground detection distances were used as a means of quantifying the horizontal density of vegetation surrounding the centre of each plot. The minimum distance at which a red card measuring 0.5 m wide and 1 m high was completely hidden from view to an observer moving away from plot centre along each of the four cardinal compass directions was recorded (Welch, 2000). The observer used a 1 m-high pole to standardize the heights at which the card was viewed. This procedure was repeated with the bottom edge of the card on the ground. An average of the four measurements was used as an index of ground detection distances for 0-1 m and 1-2 m high views through the vegetation surrounding the site (adapted from Addison *et al*., 1990).

The total number of standing dead trees (>1 m in height, ≥5 cm dbh, and >30 degrees up from the plane of the ground) and the number of stumps (<1 m in height) in each 10 m-radius plot were recorded (Rodgers *et al*., 1997).

Each 10 m-radius plot was subdivided into four quadrants to measure tree density and species composition (Fig. 3). The dominant species of overstorey (woody vegetation ≥5 m in height and ≥5 cm dbh) and understorey (woody vegetation >2 m and <5 m in height and <5 cm dbh) trees (Rodgers *et al*., 1997) within each quadrant were recorded, and a T-square nearest neighbour method was used to estimate density (Hays *et al*., 1981). Two trees in each category were selected for density measurements in each quadrant. The first overstorey or understorey tree selected was the tree nearest to plot centre in each quadrant and the second tree was the nearest neighbour from the first tree within a 180° arc perpendicular to the line from plot centre to the first tree. Distances from plot centre to the base of the first tree and from the base of the first to the base of the second tree were used to estimate density of overstorey and understorey trees in each quadrant. Diameter at breast height was also recorded for overstorey trees used in density estimates and these measurements were averaged to determine the mean dbh of overstorey trees on each 10 m-radius plot.

One 20 m transect line, bisecting the centre of each plot (north-south), was used to determine the density and species of shrubs, consisting of woody vegetation >0.4 m and <2 m in height (Rodgers *et al*., 1997). A 1 m ruler was centred over the transect line (protruding 0.5 m on each side) and the number of shrubs contacting the ruler (counting only the base not the branches) by walking with it along the length of the line was recorded (Rodgers *et al*., 1997).

Line intercept methods (Hays *et al*., 1981) were also used to quantify downfalls and browse (herbaceous and woody shrubs). At 2 m intervals along the intersecting (diameter) transect lines (Fig. 3), the number of downfalls and stumps crossing the line were recorded, along with their height from the ground and their diameter. Downfalls were distinguished as logs/trees ≥1 m in length and ≥5 cm in diameter (Rodgers *et al*., 1997), lying horizontally along the ground or at an angle of ≤30 degrees up from the plane of the ground. The diameter of the log was determined at its maximum along its length. Total height from the ground was measured as the distance from the ground surface to the top of the fallen log or logs, if there were several overlying layers, and the number of layers was recorded.

One 30 m transect was walked that started at the centre of each plot and ran in the direction that had the most uniform ground distribution of lichens. At every one meter, at the tip of the right toe (2 cm spot), presence or absence of lichens was recorded (Lance & Eastland, 2000).

Square-metre sub-plots

Quadrats of 1 square metre were placed 2 m from the centre point of each 10 m-radius plot, along each of the four cardinal compass directions (Fig. 3). The dominant (most abundant) herbaceous species and woody plant species (<0.4 m in height) were recorded (Rodgers *et al*., 1997) along with an estimate of their percent cover in each of the square metre plots. Percent ground cover, consisting of bare rock, gravel, soil/litter, wood, grass, rushes, sedges, herbs, shrubs, ferns/allies, fungi, moss/liverworts, and lichen were estimated within each quadrat. The percent ground cover data from the 4 quadrats were averaged for each of the 10 m-radius plots.

Statistical analyses

Prior to statistical analyses and model development, we examined the variance and normality of all interval scale variables and determined that the groundcover percent coverage variables were highly variant, in spite of transformations, relative to the other variables. Since caribou eat opportunistically and quite broadly with regard to vegetation types in the summer months (Ahti & Hepburn, 1967), groundcover variables were grouped into open (i.e., bare rock, gravel, soil/litter, and wood) or vegetation (i.e., grass, rushes, sedges, herbs, shrubs, ferns/allies, fungi, moss/liverworts,

Table 1. Means ± standard errors of interval scale variables measured in sample plots at caribou nursery sites and randomly chosen absence sites on lakes in Wabakimi (W.P.P.) and Woodland Caribou Provincial Parks (W.C.P.P.), northern Ontario. Variables that showed significant differences in the MANOVA, individual park DFA results used to identify and determine variables most important in distinguishing nursery sites from absence sites, and variables used in the development and evaluation of Resource Selection Functions for calving caribou in each park are indicated by superscripts.

Measurement	W.C.P.P. Absence sites (n=15)	W.C.P.P. Nursery sites (n=15)	W.P.P. Absence sites (n=15)	W.P.P. Nursery sites (n=15)
Slope[2 3] (degrees)	13.4 ± 2.5	18.0 ± 1.2	6.4 ± 1.7	10.6 ± 2.7
Elevation[1 2] (m)	364.9 ± 94.2	364.8 ± 94.2	364.5 ± 94.1	360.9 ± 93.2
# Standing Dead Trees[3]	6.7 ± 1.7	6.9 ± 1.8	4.5 ± 1.2	4.0 ± 1.0
# Stumps	3.1 ± 0.8	3.6 ± 0.9	3.0 ± 0.78	2.7 ± 0.70
Ground Detection Distance1 2 3 5 (0-1 m)	19.5 ± 5.0	21.7 ± 5.6	28.0 ± 7.2	23.5 ± 6.1
Ground Detection Distance (1-2 m)	23.5 ± 6.1	25.9 ± 6.7	30.8 ± 8.0	26.1 ± 6.7
Shrub Density[1 2 5] (stems/m^2)	0.39 ± 0.10	0.25 ± 0.07	0.39 ± 0.10	0.22 ± 0.06
Lichen Transect Occurrence[1 2 3 6] (%)	31.1 ± 8.0	38.9 ± 10.0	9.6 ± 2.5	20.0 ± 5.2
Open Groundcover[1 4 6] (Rock, Wood, Soil/Litter) (%)	37.01 ± 9.6	18 ± 4.7	38.9 ± 10.0	22.7 ± 5.9
Vegetation Groundcover[2 4] (Moss, Lichen, Herbs, Shrubs, Fungi, Ferns) (%)	75.5 ± 19.5	93.6 ± 24.2	77.9 ± 20.1	83.0 ± 21.4
# Downed Trees[3]	0.75 ± 0.19	0.71 ± 0.18	0.13 ± 0.03	0.13 ± 0.03
Maximum Height of Downfall (cm)	30.0 ± 7.8	27.8 ± 7.18	34.2 ± 8.8	32.2 ± 8.3
Diameter of Downfall[1 2 6] (cm)	10.6 ± 2.8	11.2 ± 2.9	10.8 ± 2.8	12.3 ± 3.2
Overstorey Cover[1 2] (%)	19.9 ± 5.1	24.9 ± 6.4	14.3 ± 3.7	22.0 ± 5.7
Understorey Cover[1] (%)	7.5 ± 1.9	5.1 ± 1.3	3.0 ± 0.78	5.3 ± 1.4
Dbh (cm)	14.6 ± 3.8	13.8 ± 3.6	14.3 ± 3.7	13.5 ± 3.5
Overstorey Woody Vegetation Density[1] (stems/m^2)	0.58 ± 0.15	0.73 ± 0.19	0.68 ± 0.18	1.1 ± 0.28
Understorey Woody Vegetation Density[2 4 5] (stems/m^2)	0.87 ± 0.23	0.66 ± 0.17	0.41 ± 0.11	0.63 ± 0.16

[1] Variables included in Woodland Caribou Provincial Park models.
[2] Variables included in Wabakimi Provincial Park models.
[3] Variables that had significant differences between the two parks (MANOVA).
[4] Variables that had significant differences between nursery and absence sites (MANOVA).
[5] Variables marked as important from DFA standardized canonical discriminant functions in Wabakimi Provincial Park.
[6] Variables marked as important from DFA standardized canonical discriminant functions in Woodland Caribou Provincial Park.

and lichen) groundcover categories, leaving a total of 18 interval scale variables for analysis (Table 1). Subsequent statistical tests were completed using the Statistical Package for the Social Sciences (Version 14.0, SPSS Inc., Chicago, Illinois).

We tested for differences in aspect between nursery and absence sites within each park using a chi-square test but did not find any statistically significant differences in either Wabakimi Provincial Park (χ^2 = 5.717, d.f. = 4, P = 0.221) or Woodland Caribou Provincial Park (χ^2 = 7.671, d.f. = 4, P = 0.104), so this categorical variable was removed from further consideration.

To determine if the measured interval scale variables differed between the two parks, and between caribou nursery and absence sites, we used multivariate analysis of variance (MANOVA). Following the MANOVA, Discriminant Function Analysis (DFA) was used to determine how well the variables were able to distinguish among nursery and absence sites in both Wabakimi and Woodland Caribou Provincial Parks.

The variables for ground detection distance at the 0-1 m and 1-2 m level were highly correlated, as might be expected. An individual DFA for each park demonstrated the importance of the 0-1 m ground detection distance variable in distinguishing between nursery sites and unused absence sites in Wabakimi Provincial Park, but not in Woodland Caribou Provincial Park. Thus, we removed the 1-2 m ground detection distance variable from both models and used the remaining 17 variables for further DFA analyses.

The results of both the MANOVA and DFA suggested there were greater differences between the two parks than between nursery and absence sites within each, so we developed separate Resource Selection Functions (Boyce *et al.*, 2002) for each park following the model selection procedure suggested by Shtatland *et al.* (2003). This procedure maximizes variable selection strengths of stepwise regression in predictive and exploratory studies (Menard, 1995) while avoiding arbitrary alpha values by using an information-theoretic approach (Burnham & Anderson, 1998; Vander Wal, 2004). Models were evaluated using a combination of Akaike Information Criteria (AIC; Burnham & Anderson, 2002), Receiver Operating Curves (ROCs; Pearce and Ferrier, 2000) and k-fold cross-validation (Fielding & Bell, 1997).

Variable reduction

Because of potential statistical biases caused by the large number of independent variables (18) we measured relative to the sample sizes (15 nursery sites and 15 absence sites) in each park (Peduzzi *et al.*, 1996), we sought to reduce the number of variables used for model development. Initially, data for all 18 variables were combined for nursery and absence sites within each park and included in multivariate linear regressions. We followed this with a series of steps (Shtatland *et al.*, 2003) to remove variables that demonstrated multicollinearity with other independent predictors by examination of variance inflation factors (VIFs) in linear regression analysis, average linkages in hierarchical cluster analysis, and condition numbers in principal components analysis (PCA).

VIFs were obtained from multivariate linear regressions of all 18 variables in each park and were subsequently related by dendrograms in hierarchical cluster analyses. To remove potential multicollinearity, variables with VIFs > 2.5 (Allison, 1999) that were strongly linked in dendrograms were removed from further analyses. This procedure left 9 different potential variables in each park for further model development and evaluation. To validate the non-multicollinearity assumption in the VIF approach, condition numbers (k) were calculated using a PCA (Williams, 2005). As all condition numbers for the 9 remaining variables in each park were less than 15, multicollinearity among variables was apparently removed by the VIF approach (Williams, 2005) and no further variables were removed prior to model development and evaluation. The 9 different variables used for each park in predictive model development are identified in Table 1.

Model development and evaluation

Predictive model development using forward conditional logistic regression and automatic selection procedures were applied following variable reduction (Menard, 1995; Simonoff, 2000; Shtatland *et al.*, 2003). The data set was randomly subdivided into a model building subset and a model validation subset for Woodland Caribou and Wabakimi Provincial Parks. Two-thirds (n=20 sites) of the data from each park were dedicated to model development and the remaining one third (n=10 sites) were used to evaluate the resulting models for each park.

Stepwise logistic regression of the 9 variables associated with two-thirds of the caribou nursery and absence sites in each park was used to produce subsets of models with different combinations of predictor variables. Akaike's Information Criterion for small sample size (AIC_c) and associated evidence ratios were used to select the "best" and most parsimonious model from among the models with statistically significant coefficients produced by stepwise logistic regression (Burnham & Anderson, 1998; 2002). Candidate models were then evaluated using ROC curves. These curves allow evaluation of the predictive power of the logistic regression models and reflect how accurately and robustly models classify the data (Pearce & Ferrier, 2000; Boyce *et al.*, 2002). Validation data, representing the remaining one-third of the caribou nursery and absence sites in each park, were substituted into their respective models and tested by examining the predictive probabilities of each model (i.e., proportions of sites correctly or incorrectly classified as nursery or absence sites).

Results

The MANOVA indicated there were overall significant differences both between Wabakimi and Woodland Caribou Provincial Parks (F=14.23, d.f.= 18, 39, P = 0.000) and between caribou nursery and absence sites (F=2.04, d.f.= 18, 39, P = 0.031) in relation to some of the variables measured (Table 1). These overall differences suggested development and evaluation of separate Resource Selection Functions for calving caribou in each park.

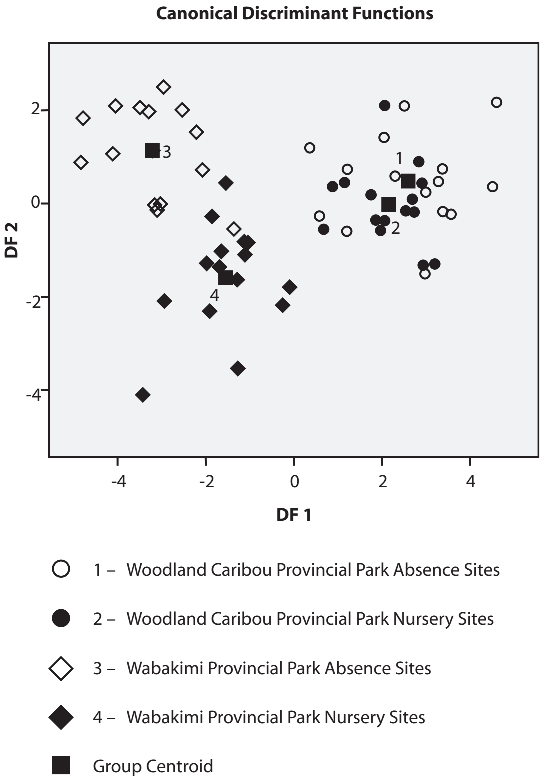

Fig. 4. Canonical Discriminant Functions of 17 variables measured at 30 caribou nursery sites and 30 randomly chosen absence sites on lakes in Wabakimi and Woodland Caribou Provincial Parks, northern Ontario. The *x*-axis (DF 1) indicates differences between the parks and the y-axis (DF 2) indicates differences between caribou nursery and unused absence sites.

The DFA results including all 4 groups indicated overall successful classification results of 87% (Fig. 4). Both the DF1 and DF2 tests were significant. DF1 explained 81.2% of the total model variance based on park differences and DF2 explained 13.7% of the total model variance in nursery versus absence sites. The variables important in differentiating between parks were primarily the number of downed trees and density of understorey woody vegetation. The variable most important in differentiating nursery from absence sites was groundcover vegetation.

Stepwise logistic regression of the 9 variables associated with caribou nursery and absence sites (Table 1) resulted in 3 candidate models with statistically significant coefficients ($P < 0.01$) for each park (Table 2). In Wabakimi Provincial Park, density of understorey woody vegetation, ground detection distance at 0-1 m, and vegetation groundcover were included in the models, whereas open groundcover, shrub density, and overstorey canopy cover were included in models for Woodland Caribou Provincial Park. Evidence ratios, based on AIC_c weights, indicated that the most parsimonious model for each park included all 3 of their respective variables. Further evaluation using ROC curves also indicated that the 3-variable model for each park had the highest predictive power in each case. However, examination of the predictive probabilities of candidate models, using the remaining one-third of the nursery and absence site data from each park, suggested the 3-variable models did not perform as well as the 2-variable models (Table 3).

The 2-variable Resource Selection Function model for calving caribou in Wabakimi Provincial Park, based on density of understorey woody vegetation and ground detection distance at 0-1 m, successfully classified caribou nursery and absence sites for 80% of the test data, while the 3-variable model, which also included vegetation groundcover, had a 60% success rate (Table 3). Although the 3-variable model performed better than the 2-variable model based on the logistic regressions, AIC_C, and ROC values using two-thirds (n=20) of the nursery and absence site data (Table 2), the 2-variable model had an R^2 of 0.74, a 90% correct classification rate, and an area under the ROC curve of 0.96. Given the small sample size relative to the number of variables in the models, the 3-variable model may overparameterize the data, leading to perfect separation as indicated by an area of 1.0 under the ROC curve (Pearce & Ferrier, 2000; Boyce *et al.*, 2002). Thus, we suggest the 2-variable model may better represent the Resource Selection Functions of calving caribou in Wabakimi Provincial Park.

The 2-variable Resource Selection Function model for calving caribou in Woodland Caribou Provincial Park, based on open groundcover and shrub density, successfully classified caribou nursery and absence sites for 80% of the test data, while the 3-variable model, which also included overstorey canopy cover, had a 60% success rate (Table 3). Similar to the Wabakimi Provincial Park models, the 3-variable model for calving caribou in Woodland Caribou Provincial Park performed better than the 2-variable model based on the logistic regressions, AIC_C, and ROC values using two-thirds (n=20) of the nursery and absence site data (Table 2), but the 2-variable model also provided good results; an R^2 of 0.85, an 85% correct classification rate, and an area under the ROC curve of 0.98. As before, given the small sample size relative to the number of variables in the models, the 3-variable model may overparameterize the data and the 2-variable model may also better represent the Resource Selection Functions of calving caribou in Woodland Caribou Provincial Park.

Table 2. Candidate Resource Selection Function models resulting from stepwise logistic regression of 9 variables associated with two-thirds (n=20) of the caribou nursery and randomly chosen absence sites sampled in Wabakimi Provincial Park and two-thirds (n=20) of the caribou nursery and randomly chosen absence sites sampled in Woodland Caribou Provincial Park, along with their evaluations by Akaike Information Criterion for small sample size (AIC_c) and Receiver Operating Characteristic curves (ROCs).

Park	Variables in Model	-2log likelihood	Nagelkerke R Square	% Correct	AIC_c	AIC_c Evidence Ratio	Area Under ROC Curve
Wabakimi Provincial Park	Understorey Woody Vegetation Density	20.777	0.39	75	49.055	>10	0.80
	Understorey Woody Vegetation Density, Ground Detection Distance (0-1m)	11.389	0.74	90	33.444	>10	0.96
	Understorey Woody Vegetation Density, Ground Detection Distance (0-1m), Vegetation Groundcover	1.52E-06	1.00	100	14.286	1	1.00
Woodland Caribou Provincial Park	Open Groundcover	16.878	0.56	65	41.256	>10	0.85
	Open Groundcover, Shrub Density	7.597	0.85	85	25.861	>10	0.98
	Open Groundcover, Shrub Density, Overstorey Cover	2.45E-06	1.00	100	14.286	1	1.00

Table 3. Predictive probabilities (i.e., proportions of sites correctly or incorrectly classified) of candidate Resource Selection Function models (Table 2) based on one-third (n=10) of the data from caribou nursery and randomly chosen absence sites sampled in Wabakimi Provincial Park and one-third (n=10) of the data from caribou nursery and randomly chosen absence sites sampled in Woodland Caribou Provincial Park.

Park	Variables in Model	Absence Sites		Nursery Sites	
		% Correctly Predicted	% False Positives	% Correctly Predicted	% False Positives
Wabakimi Provincial Park	Understorey Woody Vegetation Density	60	40	60	40
	Understorey Woody Vegetation Density, Ground Detection Distance (0-1m)	80	20	80	20
	Understorey Woody Vegetation Density, Ground Detection Distance (0-1m), Vegetation Groundcover	60	40	60	40
Woodland Caribou Provincial Park	Open Groundcover	80	20	80	20
	Open Groundcover, Shrub Density	80	20	80	20
	Open Groundcover, Shrub Density, Overstorey Cover	60	40	60	40

Discussion

In Woodland Caribou Provincial Park the slope, lichen occurrence, and number of standing and downed trees were higher, while ground detection distances at 0-1 m were lower, than at sites in Wabakimi Provincial Park. These small-scale differences between the parks are likely the result of large-scale geographic variation in weather, topography, soil productivity, and dominant vegetation across the two different ecoregions in which they are situated (Hills, 1959; Crins & Uhlig, 2000). Woodland Caribou Provincial Park falls in more of a "boreal prairie" area, being on the east Manitoba border, whereas Wabakimi Provincial Park falls in more of a "true boreal" region in north-central Ontario. Although not statistically different, the density of overstorey trees and canopy cover were higher at nursery sites than unused absence sites in both Woodland Caribou and Wabakimi Provincial Parks, suggesting selection of nursery sites in older-growth forests of both ecoregions.

Many of the characteristics associated with caribou nursery sites in Wabakimi and Woodland Caribou Provincial Parks, particularly those identified for inclusion in 2-variable Resource Selection Functions (Tables 1 and 2), were related to forage abundance and predator avoidance strategies. Female caribou in Woodland Caribou Provincial Park used nursery sites with less open groundcover, and thus more vegetative groundcover including higher lichen abundance, and lower shrub density than randomly chosen absence sites (Table 1). In Wabakimi Provincial Park, density of understorey woody vegetation and ground detection distance at 0-1 m were the two most important variables differentiating nursery sites from absence sites. The density of understorey woody vegetation was higher at nursery sites than absence sites (Table 1), although unused absence sites were generally in shrub-rich areas while nursery sites were in old-growth areas of spruce. Deciduous tree species such as white birch and trembling aspen were noted more often at absence sites than nursery sites. Due to differences in deciduous versus coniferous growth forms, particularly foliage density, ground detection distances at 0-1 m were higher at absence sites than nursery sites in Wabakimi Provincial Park. In both parks, nursery sites had higher densities of mature trees and lower shrub densities than unused absence sites (Table 1), providing concealment for calves and potentially greater sensory detection of approaching predators. As well, higher vegetative groundcover, including greater lichen abundance, was found at nursery sites compared to absence sites in the two parks (Table 1). All of these characteristics suggest female caribou in both parks were selecting nursery sites that may reduce predation risk while providing abundant forage.

Lent (1974) described the "hiding" and "following" responses of ungulate neonates as anti-predator strategies and Fitzgibbon (1990) described the tactics used by woodland caribou to be those of a "follower". In dense vegetation, a caribou calf may drop down out of sight and take a prone position, keeping the head low to the ground and remaining motionless if spotted by a predator (Fitzgibbon, 1990). Upon closer approach by a predator, the cow may take flight and the calf follows closely, rather than attempting to remain hidden in the vegetation as is the typical hiding behaviour of other ungulates such as white-tailed deer (*Odocoileus virginianus*: Lesage *et al.*, 2002). Caribou nursery site selection and response to predators is thus more similar to that of moose (*Alces alces*). Bowyer *et al.* (1999) identified greater forage abundance, a south-easterly aspect and better visibility as being the key variables at Alaskan moose birth sites. Although we did not find any relationship between aspect and nursery site selection, greater forage abundance and visibility were also important to female caribou nursery site selection in our study. In a manipulative habitat study, Bowyer *et al.* (2001) found that female moose were willing to trade off better foraging opportunities by choosing sites with more concealment cover. Food in the summer months for caribou consists of forbs, shrubs, fungi, grasses and sedges (Darby and Pruitt, 1984) but lichens, even though they have lower nutritional value, may also comprise a high proportion of their diet (Ahti & Hepburn, 1967). As vegetative ground cover, including greater lichen abundance, was found at nursery sites compared to absence sites in the two parks we studied, it does not appear that caribou necessarily trade off forage availability for greater concealment cover but they may be willing to accept lower forage quality (i.e., lichens rather than other summer foods) in exchange for a reduction in predation risk.

Protective cover inhibits prey detection, facilitates escape, and reduces the capture efficiency of visually oriented predators (White & Berger, 2001). There are variations in these findings and predators can use lateral cover to avoid being detected by prey (Moreno *et al.*, 1996). This same lateral cover may also obstruct the flight escape of prey (Lima, 1992). Bergerud (1985) and Ferguson *et al.* (1988) suggested woodland caribou maternal cows should take actions to reduce the success rates of wolves and bears in encountering, detecting and capturing calves by reducing movement and using shorelines with slopes, especially on islands, such as those in Pukaskwa National Park and Neys Provincial Park. Although not statistically different, the higher slopes at caribou nursery sites than absence sites that we found in both parks are consistent with this strategy. Similarly, Wilton & Garner (1991) found that moose calving sites were most often situated at high points, and on knolls, on islands, and Addison *et al.* (1990) determined these were usually within 200 m of water. A higher slope at nursery sites may help caribou detect oncoming predators more easily and facilitate escape. These locations may minimize encounters with mobile predators that will need to use more energy to get to islands and slopes will further increase their searching time for caribou with calves (Bergerud, 1985).

In Ontario, forest management guidelines for the conservation of woodland caribou, give special consideration to calving areas by providing a 1,000 m buffer around sites (Racey *et al.*, 1999). Given the potential for disturbance from attempting to directly observe parturition in calving caribou and the difficulties in distinguishing calving sites from postpartum nursery sites, protection should be extended to nursery sites in general. Moreover, as forestry activities generally increase the number of roads around parks and protected areas, allowing easy access for predators, roads need to be limited in number and use. The impact of recreational use on calving caribou within parks and protected areas also needs to be minimized. Travel and recreational use of lakes or areas of lakes, particularly near nursery sites that are reused by female caribou, should be restricted at least during the calving and nursery periods.

This study provides a preliminary basis for identifying caribou nursery sites both outside and within protected area boundaries across northern Ontario. Although logistically challenging, future studies should attempt to identify a larger number of nursery sites for assessment, but we do not suggest that all variables we initially collected be measured. Rather, the 12 variables we used for development of models (Table 1), particularly those related to overstorey and understorey cover and woody vegetation density, groundcover, especially lichen abundance, shrub density, slope, and ground detection distance at 0-1 m, may provide a more suitable starting point. As remote sensing information improves, it may be possible to correlate some of these variables with spectral data to decrease the logistic/financial problems associated with the identification of caribou nursery sites in remote locations, thereby improving their protection in future management policies and legislation. Ultimately, future studies need to relate caribou fitness to nursery site selection.

Acknowledgements

We thank the many individuals involved in this work, particularly Dr. Geoff Lipsett-Moore, Steve Kingston, Dr. Heidi Schraft, and Dr. Murray Lankester. We acknowledge Dr. Rob MacKereth, Scott Parker, and Eric Vander Wal for advice on the statistical analyses. We are grateful to Bill Thompson for his extensive botany skills in completing the vegetation plots in the summer of 2003. We thank Doug Lowman for the study area map. We also thank the staff of Ontario Parks for their flexibility which allowed us to complete this project. We appreciate the constructive comments and meticulous review of the manuscript provided by two anonymous reviewers. The majority of the funding for this study was provided by the Species At Risk program, Ontario Ministry of Natural Resources.

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