

## Use of Lake Areas in Winter by Woodland Caribou

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**Abstract** - Understanding space-use patterns of highly mobile animals, such as woodland caribou (*Rangifer tarandus caribou* Gmelin), is required for ecosystem conservation. We consider the use of lakes in winter as important habitat for woodland caribou both to reduce predation risk and acquire food. To test scale differences relative to caribou use of ice-covered lakes in winter, we compare the use of ice-covered lakes within a regional study area and within sub-regional landscapes at two spatial levels: (1) seasonal selection of winter ranges and (2) daily locations. We used 100% minimum convex polygons with a 500-m buffer for winter ranges, and 500-m radius buffer around individual radio telemetry locations of 27 caribou from 1995 to 2000 as spatial measures of use of lakes of various dimensions by caribou. In the winter-range analysis, caribou used areas with more lakes in the 5–100-ha size class, including lakes with more perimeter, larger area, and higher fractal dimensions as compared with the relative distribution of available lakes. These patterns were confirmed at the regional level (Manitoba border in the west to the Hudson Bay lowlands to the east) and at the sub-regional level. At the finest level of resolution of daily locations, caribou selected lakes with greater area and perimeter in the west but not in the east. Our findings should be considered when developing local plans for forest management and designing landscapes where the conservation of woodland caribou is a goal.

### Introduction

To conserve animals, we need an understanding of space-use patterns relative to the hierarchy of limiting factors that affect individual fitness (Allen and Starr 1982, McLoughlin and Ferguson 2000). Habitats can be arranged hierarchically within any given region, and studies of habitat-specific responses of animals require use of multi-scale approaches to provide ecologically relevant conclusions (Elkie and Rempel 2001, Johnson et al. 2002a, Kie et al. 2002, Morris 1987, Orrock et al. 2000). Habitat selection is expected to differ between coarse and fine scales (Holling 1992), reflecting the hierarchy of factors potentially limiting individual fitness (Rettie and Messier 2000). Scales of habitat selection are particularly important for ungulates, such as migratory species (e.g., wildebeest, *Connochaetes taurinus* Burchell, and woodland caribou, *Rangifer tarandus* Gmelin) that have evolved space-use strategies to minimize predation as a major limiting factor (Bergerud et

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al. 1984, Caughley and Gunn 1993, Fryxell 1998, Sinclair and Arcese 1995). In particular, the response of woodland caribou to managed habitats varies among populations and across spatial and temporal scales (Apps et al. 2001, Poole et al. 2000, Smith et al. 2000, Stevenson et al. 1991, Stuart-Smith et al. 1997, Terry et al. 2000), suggesting that habitat selection at any scale is not well understood.

Woodland caribou across North America are considered limited by predation as the proximate factor (Bergerud 1974, Bergerud and Elliot 1986, Ferguson et al. 1988, Ouellet et al. 1996, Rettie and Messier 1998, Seip 1992, Stuart-Smith et al. 1997), with the exception of a herd that lives primarily on the taiga and behaves as a barren-ground caribou herd (Messier et al. 1988). Therefore, knowledge of use of landscapes to avoid predators is important in addressing conservation issues related to the threatened status of woodland caribou (COSEWIC 2000). During spring, female caribou select safe calving refugia from wolves (*Canis lupus* L.) and bears (*Ursus* spp.) that include islands (Bergerud 1985, Cumming and Beange 1987), high elevation sites (Barten et al. 2001, Bergerud et al. 1984), and bog complexes (Stuart-Smith et al. 1997, Valkenburg et al. 1996). Less is known about the selection of safe habitat to reduce predation of adults and juveniles by wolves during winter.

During winter, we hypothesize that caribou use landscapes consisting of lakes of particular size and shape to reduce the risk of wolf predation. Particular spatial arrangements of lakes and lake-size distribution may favor prey escape during pursuit by wolf packs in winter. Predators may use forest stands as cover when approaching prey (Moreno et al. 1996, Underwood 1982). The same forest cover may obstruct the flight of prey (Lima 1992, Schooley et al. 1996). Differences in sensor perception by predators and prey can be used to modify risk. For example, the sense of vision is likely better developed in wolves than in their ungulate prey (Mech 1966), and therefore caribou may avoid large lake areas that provide a wide visual perspective. Conversely, caribou may select lakes with greater edge to reduce visual detection, while positioning themselves downwind to the forest edge allowing early detection of predators approaching through the forest along the lake edge (Carruthers et al. 1986). Two features of ice-covered lakes that benefit caribou in winter by lowering risk of predation are open areas (predator detection) and packed snow (successful escape due to ease of movement) (Mysterud and Østbye 1999).

Here, we study the effect of landscapes using patterns of ice-covered lakes as an indicator of winter habitat for woodland caribou. Specifically, we predict that caribou will select winter lakes more strongly at a coarse scale of winter ranges and this selection of lakes will be less strong at a finer scale of selection (i.e., daily locations).

We base this assumption on the selective advantage of caribou being located in areas of lakes that provide escape terrain while affording feeding opportunities in close proximity to lakes. Thus, caribou may not be located on lakes more than their availability but they may select areas with greater overall lake cover, thereby keeping escape habitat close by. Our operational definition of “strength of selection” is the sum of significant tests to determine whether frequency distributions of used lakes differed from distributions of available lakes. We used telemetry information from 27 caribou captured across a 160,000 km<sup>2</sup> area in northwestern Ontario. Two levels of selection, (1) winter range and (2) daily locations, were compared for both a regional study area and two sub-regional landscapes that were delineated within the larger study area. We used an objective method (cluster analysis) to subdivide the region based on groupings of caribou locations. We tested whether caribou from different regions responded to differences in available areas of winter lakes with different use of lakes. We tested the null hypothesis that woodland caribou select frozen lake areas equally at both scales and that an examination of selection at each resolution will be equally effective in predicting space-use.

## Materials and Methods

### Study area

The study area lies between approximately 49°30'N and 53°00'N and 87°00'W to 95°30'W and is largely within the Boreal Ecoregion of Ontario, Canada (Fig. 1). The area consists of jack pine (*Pinus banksiana* Lamb.) dominated forests with mixtures of black spruce (*Picea mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), white birch (*Betula papyrifera* Marsh.), white spruce (*P. glauca* (Moench) Voss), and trembling aspen (*Populus tremuloides* Michx.) on rolling rocky uplands with coarse well-drained soils (Rowe 1972). The natural wildfire cycle in the area is between 80–200 years (Li et al. 1996).

The climate is humid continental with a mean minimum January temperature of -25 °C and a mean maximum daily temperature for July of 23 °C (Baldwin et al. 2000). Mean annual precipitation is between 650–800 cm, including a mean January snowfall of 55 cm (Baldwin et al. 2000).

Other ungulates in the region include moose (*Alces alces* Gray) and white-tailed deer (*Odocoileus virginianus* Boddaert) (Dobbyn 1994). In addition to wolves (*Canis lupus*), large carnivores in the area include coyotes (*Canis latrans* Say), black bears (*Ursus americanus* Pallas), wolverines (*Gulo gulo* L.), and lynx (*Lynx canadensis* L.) (Dobbyn 1994).

### Capture and radio-collaring

Woodland caribou were captured across northwestern Ontario over four years resulting in 33 radio collars (19 in winter and 14 in spring) deployed on 27 female and six male caribou. Throughout the tracking period, five collars were redeployed. Caribou were captured using net guns and equipped with both satellite and VHF transmitters (Telonics, Inc., Mesa, AZ). Animal capture and handling procedures followed the approved protocol of the Ontario Provincial Animal Care Committee (#01-27).

### Locations

Radio-collared caribou transmitted UHF signals from 5 March 1995 to 24 April 2000 providing information for 5 winters. Of the original 11,354 locations, 5201 were of good quality (location quality > 0, indicating accuracy < 1 km) with only one location/day, and 1329 occurred during winter. Winter was defined as 15 December to

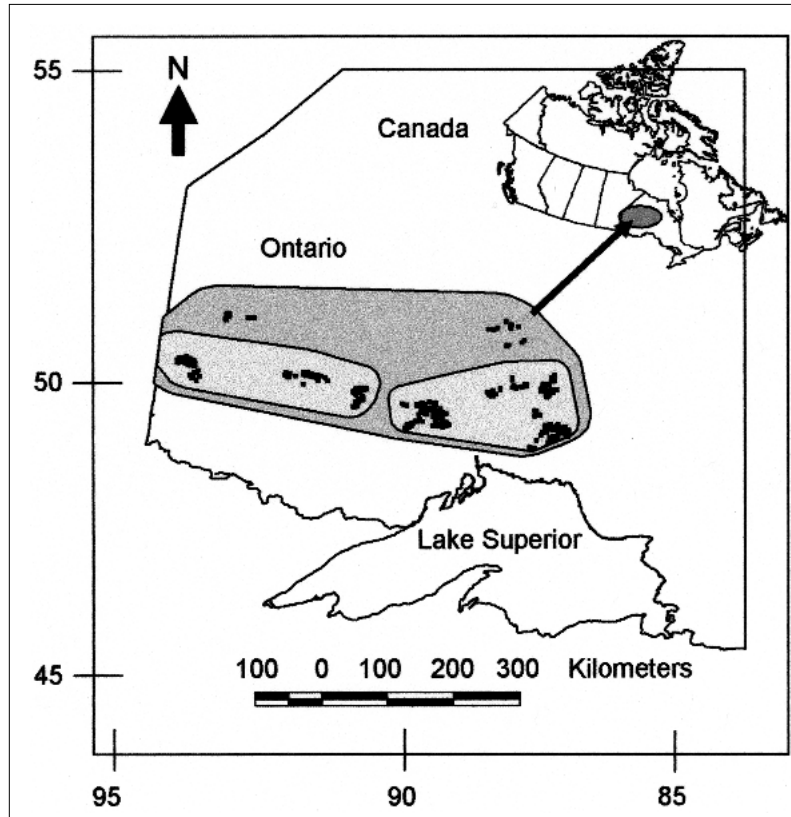


Figure 1. Location of regional study area and winter caribou locations including east and west landscapes within northwestern Ontario, 1995–2000.

15 March. We used 15 December because lakes in the region are usually frozen by December and snow accumulation is generally deep enough to make lake travel more favorable than forest travel (interviews with Regional and District Biologists). We chose 15 March as the end for winter because our initial viewing of the location data within our geographic information system (GIS) indicated that many of the caribou were making considerable movements after 15 March (i.e., spring migration to calving sites).

Animal locations were obtained from satellite transmitters that were programmed to transmit for 8-hour periods every 6<sup>th</sup> day from 1 January to 31 March and every 2<sup>nd</sup> day from 1 September to 31 December. Only caribou with almost continual observations were used (> 9 winter locations). We used one location for each transmission period and only used locations with a quality location 1 or better (Keating et al. 1991, Rettie and Messier 1998, Service Argos 1988). We examined locations for outliers by calculating the  $\xi$  value described by Keating (1994) and then plotting the locations using Arcview<sup>®</sup> GIS (Ver 3.2, Environmental Systems Research Inc., Redland, CA). Keating's  $\xi$  value is calculated from consecutive movement vectors and identifies out-and-back movements indicative of erroneous locations:

$$\xi = (V1 + V2 / 2)(\min V1, V2 / \max V1, V2)(\cos b + 1) / 2$$

where, V1 is the distance from point A to point B, and V2 is distance from point B to point C; b (beta) is the angle for ABC; MinV1, V2 is whichever V1 or V2 is smaller; and maxV1, V2 is whichever distance is larger. Locations with  $\xi < 5$  km were retained and when  $\xi > 5$  km, the location was deleted if it was contradicted by the other locations obtained during the same transmission period. When  $\xi > 10$  km, we deleted the location unless it was confirmed by a second location during the same transmission period. Deleted locations were replaced by the next best location from the transmission period (when available), subject to the same selection and outlier screening criteria. Twenty-three locations were replaced and 31 were deleted without replacement, yielding 739 locations of 27 radio-tracked animals.

#### **Winter range size**

Our focus was on coarse-scale movements by caribou in winter relative to lake patterns, and not on accuracy and precision of home range estimation. We used the 100% utilization distribution of the minimum convex polygon (MCP) method (Jennrich and Turner 1969, Mohr 1947) because this method has the fewest assumptions related to how the area was used by animals. Twenty-seven caribou were used over 5 winters, which resulted in 45 estimates of winter range. All calculated winter ranges used comparable numbers of locations—between 10 and 15—to estimate MCP. We considered the duplicate

measures of winter ranges by the same caribou ( $n = 18$ ) to be independent because in all cases caribou used a different winter range area (data on file). Also, animals had the capacity to traverse their seasonal ranges in two days (Ferguson and Elkie 2004a) and locations were estimated at different times of the day.

### **Delineation of sub-regional landscapes**

Previous researchers have suggested that caribou behave differently in the eastern and western regions of northwestern Ontario, due in part to habitat differences (Racey et al. 1991). Therefore, we delineated possible sub-regional landscapes using cluster analysis of  $x$ ,  $y$  coordinates for centroids (mean  $X$  and  $Y$  coordinates) of caribou  $MCP_{wr}$  (minimum convex polygon of winter range). Cluster analysis determined the groupings of winter-range centroids for caribou according to geographic locations. Classification of caribou winter ranges into groups was conducted by the average-linkage clustering method using a Euclidean distance similarity index (Romesburg 1984). All variables were standardized between 0 and 1. Change in linkage distance helped identify an appropriate number of clusters ( $n = 2$ ). We generated a  $MCP_{sr}$  for both sub-regional landscapes (east = 3788 km<sup>2</sup> and west = 2758 km<sup>2</sup>) and created a 25-km buffer around each which together (east + west + buffer) represented the extent of the regional  $MCP_r$ . We used a 25-km buffer to incorporate all available lakes that intersected the east and west  $MCP_{sr}$ . This allowed us to consider all lakes that were within at least  $\pm 2$  days travel, which equates to the potential movement that could have occurred without detection between transmission periods.

### **Winter range selection**

We examined use and availability of lakes at two spatial scales using both  $MCP_{wr}$  winter ranges and individual buffered locations; therefore, we had to ensure that our study area included lakes that were on the perimeter of the  $MCP_r$ . We delineated and identified the regional study area (15,897 km<sup>2</sup>) by generating a 100%  $MCP_r$  around all 739 winter points and then generating the 25-km buffer around the  $MCP_r$ .  $MCP_{wr}$  were generated for each animal for each winter season within the regional study area. We then intersected the  $MCP_{wr}$  with lake data to calculate the number of lakes, the area of each lake (surface area excluding islands), and the perimeter of each lake (including island shorelines). The area and perimeter of lakes were tallied for each lake intersecting  $MCP_{wr}$  regardless of whether part or most of that lake occurred outside of the  $MCP_{wr}$ . Fractal dimension was calculated as the slope of the log-linear relationship between area and perimeter (Lovejoy 1982) and is expected to provide a unique measure of landscape relative to animal movement behavior (Ferguson et al. 1998). We excluded Lake

Nipigon (455,424 ha) and Lac Seul (180,316 ha) due to their exceptionally large size (results did not differ qualitatively with or without their inclusion). We derived lake data from the Ontario Ministry of Natural Resource's 1996 provincial landcover. The provincial landcover is a raster based (25-m resolution) thematic image derived from Landsat TM satellite imagery.

Next we generated circles with areas equal to the mean size of  $MCP_{wr}$  and the center lying at a random point, taken from a uniform distribution within the study area (Rondinini and Boitani 2002). We chose to compare random circles with available  $MCP_{wr}$  as this affords direct statistical comparisons of used versus available with matched sample sizes. These hypothetical ranges were generated for the regional study area  $MCP_r$  and for the two sub-regional landscapes ( $MCP_{sr}$ ) (entire study area = 234.6 km<sup>2</sup>, east = 241.7 km<sup>2</sup>, and west = 175.3 km<sup>2</sup>). The number of randomly located hypothetical ranges was equal to the number of caribou  $MCP_{wr}$  at each scale. Generally, the number of simulated data samples should equal the sample size of actual data to produce similar statistical variability for comparison (Blasius and Stone 2000). Similar to the  $MCP_{wr}$  lake data collection, we intersected the randomly located circles with the lakes layer and counted the number of lakes, the area of each lake, and the perimeter of each lake. We define the lakes from the  $MCP_{wr}$  analyses as used and the lakes from the randomly located hypothetical range circle analyses as available.

### Daily selection

We generated a 500-m buffer around each winter location point and intersected the buffer layer with the lakes layer. We used 500 m because that distance approximated the potential location error of all locations (Ferguson and Elkie 2004a). In some instances, > 1 lake was within 500 m of locations. Similar to the  $MCP_{wr}$  technique, we intersected the buffered locations with the lakes layer and counted the number of lakes, the area of each lake, and the perimeter of each lake. We included all points in our analysis even if no lakes were within 500 m. We generated 739 random points (equal to the number of actual winter points; east = 475, west = 217 and 47 outside of sub-regional polygons) and generated a 500-m buffer around each random point. Again we intersected the random point buffer layer with the lakes layer and counted the number of lakes, the area of each lake, and the perimeter of each lake that intersected the random buffered locations. Buffered locations represent used lakes and the randomly located buffered points represent available lakes.

At the level of individual point locations, we compared available and used area of lakes, distance to lakes, perimeter of lakes, and whether caribou were within 500 m of lakes. We compared lake use relative to available by comparing whether individual locations were within 500 m

of a lake or not. We calculated the distance to lakes for actual locations and available random points to compare the distribution of distances.

### Statistical analyses

Statistical analysis was constrained by the nonparametric distance data (lake area and perimeter) that did not conform to a normal distribution after logarithmic transformation. Consequently, we used parametric analysis of ranked data (Conover and Iman 1981). We tested for differences between used and available lake size and perimeter using analysis of variance of ranked data (i.e., nonparametric test). Nonparametric data (area, perimeter) are reported as 25, 50 (median), and 75 percentiles as well as mean  $\pm$  SE to allow for comparisons with published data. In contrast, parametric data (slope, intercept, coefficient of variation (CV)) are reported as mean  $\pm$  SE. Data were analyzed using SAS statistical software for microcomputers (SAS 1989).

The above analyses compare lake characteristics, but caribou may be selecting a distribution of lake characteristics described within the winter range. Therefore, to compare lake-size distributions, we described the dispersion of available lakes according to quartiles (10, 25, 50, 75, and 90% of observations) from available distributions. We then compared the frequency of occurrence for lake-size observations within those categories (i.e., 0–10, 10–25, 25–50, 50–75, 75–90, 90–100%) for both available and used. The resulting graphs allowed us to visually compare distributions of lakes according to categories of lake sizes. The x-axis showed the available percentiles in ha or km calculated from lake area or perimeter (e.g., 0–1.2 ha) whereas y-axis showed the percent occurrences. Kolmogorov-Smirnov (K-S) tests were used to compare the statistical differences in distributions between available and used lakes.

To test the relative contribution of used-lake characteristics relative to scale of resolution we used K-S tests to determine whether frequency distributions of used lakes differed from distributions of available lakes. K-S tests have two limitations when comparing sample and source pool distributions: the two distributions are not truly independent because they contain some of the same lakes, and the test has low power to detect patterns at small sample sizes (Bakker and Kelt 2000).

### Results

Collectively, we estimated 45 winter ranges: 10 in 1995, 8 in 1996, 14 in 1998, 11 in 1999, and 2 in 2000. Five male and 22 female caribou provided radio telemetry estimates of 7 male and 38 female winter ranges (12 animals provided multiple winter results). The size of winter ranges did not differ between sexes ( $F = 2.10$ ,  $P = 0.16$ ), year of range ( $F = 0.17$ ,  $P = 0.95$ ), or year of range by sex interaction ( $F = 0.10$ ,  $P = 0.96$ ).

Therefore, we pooled samples for subsequent analyses. Median 100% minimum convex polygon for winter range size was 13,735 ha and ranged from a minimum of 125 to a maximum of 130,300 ha (25% quartile = 5794, 75% quartile = 28,610) (Table 1). Perimeter of winter ranges did not differ between landscapes ( $F = 0.19$ ,  $P > 0.50$ ) and varied from 5.7 to 141.5 km with a median of 55.9 km (25% quartile = 31.9, 75% quartile = 75.8).

Cluster analysis of winter midpoint locations delineated two distinct spatial groupings of winter ranges and we considered these as east and west sub-regional landscapes (Fig. 1). Three caribou ranges were outside the clustered landscapes. We used these three  $MCP_{wr}$  in comparisons of the regional study area but not in the comparisons between the east and west landscapes. When comparing lakes within  $MCP_{wr}$  derived from locations against randomly located  $MCP_{wr}$ , the east landscape was characterized by more lakes ( $84.2 \pm 2.9$  versus  $54.8 \pm 2.9$ ;  $F = 50.4$ ,  $P = 0.001$ ), smaller median size (13.9 ha versus 48.4 ha;  $F = 146.2$ ,  $P = 0.001$ ), smaller median perimeter (1.95 km versus 4.23 km,  $F = 50.3$ ,  $P = 0.001$ ), and greater total area ( $36 \pm 3\%$  versus  $30 \pm 2\%$ ;  $F = 4.21$ ,  $P = 0.03$ ). No differences in range size occurred between caribou occupying east and west landscapes ( $F = 1.16$ ,  $P = 0.32$ ).

### Winter range selection

We defined the coarse level as the individual caribou winter ranges and we examined the lake characteristics within each of these ranges. Generally, caribou chose winter ranges with more lakes, although between landscapes this selection was only significant in the west (Table 2). Median lake sizes selected by caribou within their individual winter ranges were larger than those that were available (8.0 ha versus 5.6 ha) (Table 2). The strongest selection pattern was observed for lake perimeter, where caribou chose winter ranges characterized by lakes with greater perimeter (4.4 km used versus 1.1 km available) (Table 2). Selection of larger lakes with larger perimeters by caribou interrelated with the selection of greater fractal dimensions of lake patterns. Slope of perimeter-area log-log regression was 0.632 for used versus 0.608 for random available lakes (Table 2). A higher intercept was calculated for used winter ranges versus available random points (3.1 and 2.6, respectively) (Table 2).

Table 1. Summary statistics (mean  $\pm$  SE) for 100% minimum convex polygon winter ranges of 27 radio-collared caribou in northwest Ontario. Ranges include east and west landscapes and 3 minimum convex polygons grouped outside of clusters.

Landscape	<i>n</i>	Area (ha)	Perimeter (m)
East	29	24,165 $\pm$ 5001	61,102 $\pm$ 5851
West	13	17,528 $\pm$ 4123	53,142 $\pm$ 7085
Other	3	45,066 $\pm$ 42,629	63,403 $\pm$ 39,030
Total	45	23,641 $\pm$ 4248	59,956 $\pm$ 4788

Table 2. Lake features of used and available<sup>A</sup> within caribou winter ranges<sup>B</sup>. Comparisons include the regional study area, and west, and east landscapes within northwestern Ontario.

Lake or feature	Model		Available				Used					
	F	P	25%	50%	75%	Mean ± SE	n	2.5%	50%	75%	Mean ± SE	n
Regional study area:												
Number of lakes	13.6	<0.01	54	79	103		674	26	56	104		45
Median area <sup>C</sup>	15.7	<0.01	3.62	5.58	9.27		674	4.00	8.03	10.39		45
Median perimeter <sup>D</sup>	20.8	<0.01	0.92	1.14	1.43		674	3.16	4.41	5.52		45
Intercept	5901	<0.01				2.63 ± 0.002	667				3.13 ± 0.006	42
Slope	11.6	<0.01				0.608 ± 0.002	667				0.632 ± 0.007	42
CV <sup>E</sup> area	16.2	<0.01				512 ± 8.4	674				376 ± 32.5	45
CV perimeter	14.4	<0.01				420 ± 8.3	674				295 ± 31.9	45
East landscape:												
Number of lakes	2.52	0.11	61	88	109		155	36	56	98		29
Median area	5.53	0.02	3.09	4.46	6.72		155	3.42	6.68	8.48		29
Median perimeter	6.49	0.012	0.85	1.01	1.20		155	2.73	4.19	4.55		29
Intercept	4130	<0.01				2.64 ± 0.003	150				3.14 ± 0.007	27
Slope	1.77	0.18				0.615 ± 0.003	150				0.627 ± 0.011	27
CV area	5.57	0.019				520 ± 19.4	155				418 ± 35.8	29
CV perimeter	4.93	0.028				403 ± 23.1	155				320 ± 40.9	29
West landscape:												
Number of lakes	15.2	<0.01	27	42	77		157	17	51	229		13
Median area	5.08	0.025	4.45	7.74	10.06		157	8.46	9.81	11.84		13
Median perimeter	481	<0.01	1.01	1.27	1.59		157	5.09	5.52	6.12		13
Intercept	1784	<0.01				2.63 ± 0.003	151				3.12 ± 0.02	13
Slope	9.91	0.002				0.605 ± 0.003	151				0.644 ± 0.016	13
CV area	11.4	<0.01				418 ± 22.6	157				268 ± 27.4	13
CV perimeter	10.6	<0.01				348 ± 19.2	1570				209 ± 33.1	13

<sup>A</sup>used ranges derived from actual caribou locations whereas available ranges defined by spatial random sample.

<sup>B</sup>winter ranges defined by 100% minimum convex polygons.

<sup>C</sup>area in ha.

<sup>D</sup>perimeter in km.

<sup>E</sup>coefficient of variation among range.

A similar pattern at the landscape level emerged. Caribou from the east and west selected similar lake patterns within their winter ranges; number of lakes ( $F = 0.02$ ,  $P = 0.89$ ), median lake area ( $F = 0.42$ ,  $P = 0.52$ ), and median lake perimeter ( $F = 0.38$ ,  $P = 0.54$ ) did not differ between the east and west landscapes (Table 2). Caribou ranges in the east landscape did not differ in number of lakes (56 used versus 88 available), but the lake areas within their winter ranges were greater (6.7 ha used versus 4.5 ha available) and the lakes within their winter ranges were characterized by greater perimeter (4.2 km used versus 1.0 km available) (Table 2). In the west landscape, caribou selected winter ranges characterized by having more lakes (51 used versus 42 available), bigger lakes (9.8 ha used versus 7.7 ha available), and lakes with greater perimeters (5.5 km used versus 1.3 km available) (Table 2). In the east and west landscapes, caribou selected areas with a greater fractal relationship as indicated by the regression of greater slope and intercept (Table 2). The lower coefficient of variation in lake area and perimeter (used versus available) also provides evidence that caribou were selecting specific lakes (Table 2).

Caribou were not selecting winter ranges with greater lake area as available  $MCP_{wr}$  had greater total lake area ( $57 \pm 3\%$  versus  $36 \pm 7\%$ ), although not significant at  $\alpha = 0.05$  ( $F = 3.27$ ,  $P = 0.07$ ). Instead, caribou were using winter ranges characterized by more lakes in the 5–100-ha size class (51% of observations versus 46% available;  $\chi^2 = 38.3$ ,  $df = 2$ ,  $P = 0.001$ ) and lakes with greater perimeter. Within their winter range, caribou had fewer lakes with less than 1 km perimeter (3 versus 44% available), and more lakes with 1–10 km perimeter (75 versus 50% available) and > 10 km perimeter (22 versus 5% available;  $\chi^2 = 4082$ ,  $df = 2$ ,  $P = 0.001$ ).

#### Daily lake selection

The fine scale of resolution was defined by selection of lakes in proximity to each individual recorded location. The size of lakes ( $F = 0.20$ ,  $P = 0.65$ ) and lake perimeter ( $F = 0.33$ ,  $P = 0.56$ ) selected by caribou did not differ between the east and west landscapes. Caribou were located in proximity to lakes in the 5–50-ha size class with less use of larger lakes (Fig. 2a,b). Caribou selection of smaller lakes occurred in the west landscape, but not in the east (Fig. 2a,b). Similarly, caribou selected lakes with greater perimeter in the west, but not in the east (Fig. 2c,d).

A comparison of distance to the nearest lake revealed no difference at the level of the regional study area (Table 3). At the landscape level, caribou were farther from lakes than expected in the east landscape and showed no difference in the west (Table 3; Fig. 2e f).

In the regional study area, we observed no differences in the percentage of locations on or near lakes between caribou locations and the

random locations. Of the 739 caribou locations, 457 (62%) were on or near (< 0.5 km) lakes compared with 444 of 739 (60%) from the random sample. In contrast, within landscapes, the east showed no difference in use of lakes ( $267/475 = 56\%$  used versus  $250/425 = 59\%$  available),

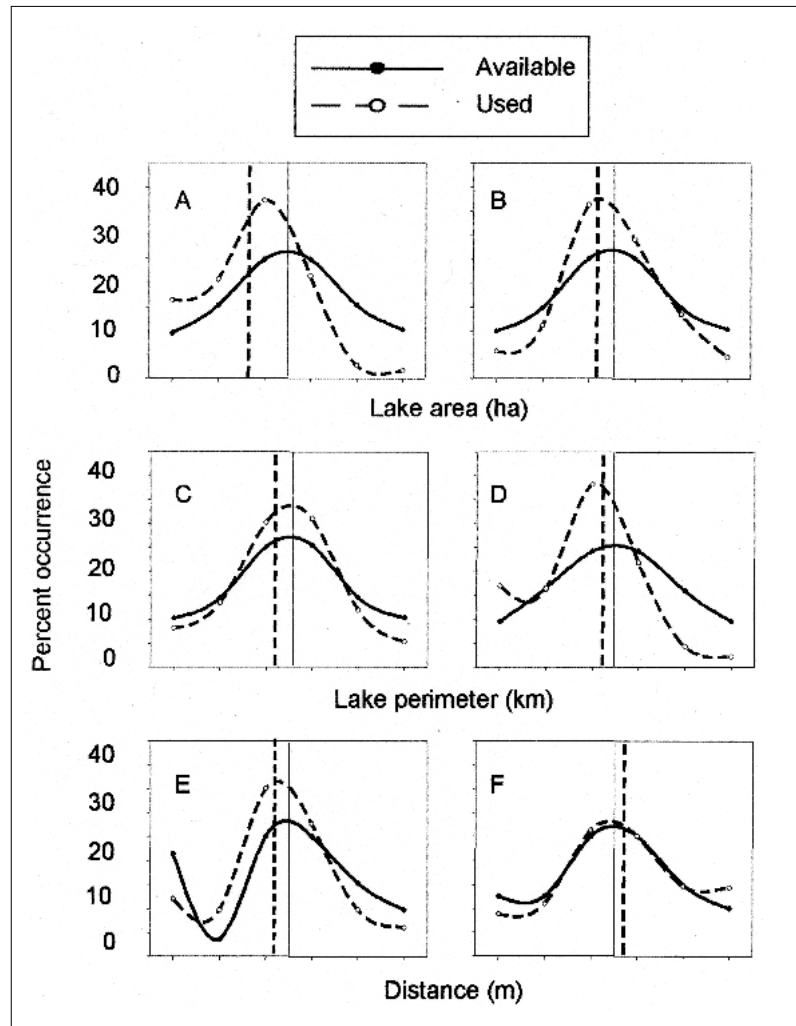


Figure 2. Characteristics of lakes that radio-tagged caribou were located on or near (within 0.5 km): A and B describe lake area used and available for west and east landscapes; C and D describe lake perimeter used and available for west and east landscapes; E and F describe distance to nearest lakes for all caribou locations compared to an available random set of points for west and east landscapes. Vertical lines for median values (solid line = available; dashed line = used). The y-axis is percent occurrence and x-axis categorized as 0–10, 10–25, 25–50, 50–75, 75–90, and 90–100% of occurrence.

Table 3. Lake features used and available<sup>A</sup> within 500 m of individual caribou locations. Comparisons include the regional study area, west landscape, and east landscape within northwestern Ontario.

Resolution	Lake or feature	Model		Available				Used			
		F	P	25%	50%	75%	n	25%	50%	75%	n
Regional study area:											
	Median area <sup>B</sup>	7.16	0.008	3.6	19.7	158.7	466	4.3	12.2	48.8	428
	Median perimeter <sup>C</sup>	5.76	0.017	0.92	2.52	11.44	466	0.98	1.90	5.05	428
	Fractal relationship <sup>D</sup>				$y = 0.722x + 2.53$				$y = 0.706x + 2.56$		
	CV <sup>E</sup> area				377				585		
	CV perimeter				355				446		
	Distance (m)	0.32	0.57	122.1	371.5	764.5	701	134.9	361.6	737.9	739
East landscape:											
	Median area	0.15	0.70	2.4	13.9	93.7	310	3.6	11.4	44.3	245
	Median perimeter	0.18	0.67	0.79	1.95	8.20	310	0.92	1.77	4.78	245
	Fractal relationship				$y = 0.688x + 2.60$				$y = 0.709x + 2.56$		
	CV area				391				566		
	CV perimeter				337				439		
	Distance (m)	8.03	0.001	107.0	367.0	764.1	423	158.8	414.2	863.5	475
West landscape:											
	Median area	21.9	<0.01	8.0	48.4	448.1	156	4.7	12.8	51.0	183
	Median perimeter	16.6	<0.01	1.33	4.23	21.72	156	1.06	2.01	5.49	183
	Fractal relationship				$y = 0.716x + 2.52$				$y = 0.703x + 2.56$		
	CV area				449				469		
	CV perimeter				413				366		
	Distance (m)	3.16	0.076	63.1	337.3	675.8	196	93.0	274.5	497.3	217

<sup>A</sup> used locations derived from actual caribou locations whereas available locations defined by random spatial sample.

<sup>B</sup> area in ha.

<sup>C</sup> perimeter in km.

<sup>D</sup> fractal relationship of log10 perimeter and log10 area of lakes used by caribou compared to a random selection of locations.

<sup>E</sup> coefficient of variation.

whereas the west differed in the percent of locations on or near lakes (163/217 = 75% used versus 137/217 = 63% random locations). Hence, caribou in the west were more likely to occur on or near lakes relative to available lakes.

### Comparison of scale for lake-size selection

To test whether differences in scale between winter range and individual locations affected choice of lakes by caribou, we compared distribution of lake sizes and lake perimeter using K-S tests. First, we compared the distribution of available and used lakes within winter ranges. For the regional study area, the distribution of lake sizes used by caribou did not differ from the available distribution (K-S test:  $P = 0.18$ ), although greater use of the 8–24-ha size class of lakes was observed (Table 2). Caribou in the west selected larger lakes relative to the available distribution (K-S test:  $P = 0.001$ ), with greater use of the 7–23-ha size class (Fig. 2a). In the east, the distribution of lakes used by caribou differed from available lake sizes (K-S test:  $P = 0.001$ ). Caribou used larger lakes (5–14 ha) than the median group available (2–5 ha) (Fig. 2b).

We also compared the distributions of used and available lake sizes based on individual daily caribou locations (Table 3). Over the regional study area, caribou used smaller lakes than available (K-S test:  $P = 0.001$ ). This pattern was particularly evident in the west, where caribou used smaller lakes as compared to the median lake size group available (K-S test:  $P = 0.001$ ) (Fig. 2). In contrast, caribou used lakes available in the east according to their distribution (K-S test:  $P = 0.34$ ) with greater use of the 2–15-ha size class (Fig. 2). In summary, caribou showed a stronger selection of lake sizes within winter ranges relative to selection of daily locations.

### Comparison of scale of lake-perimeter selection

First, we compared distributions of lake perimeter at the winter-range level. A strong pattern of selection occurred at this level with caribou selecting areas of considerably larger median lake perimeters relative to available in the regional study level ( $KS_a = 14.7$ ,  $P = 0.001$ ), the east ( $KS_a = 15.7$ ,  $P = 0.001$ ), and the west ( $KS_a = 14.8$ ,  $P = 0.001$ ).

Second, we compared distribution of lake perimeters at the individual daily location level. Within the regional study area, caribou selected different distributions of lake perimeters ( $KS_a = 2.60$ ,  $P = 0.001$ ) with a greater selection of the 1–3-km class. Comparing east and west, caribou selection of available lakes did not differ for the west ( $KS_a = 1.60$ ,  $P = 0.40$ ), where caribou in the east selected more lakes in the 0.8–2.0-km class ( $KS_a = 3.71$ ,  $P = 0.001$ ). In summary, caribou selection of lake perimeter was stronger at the level of winter ranges than daily locations.

### Discussion

Our analysis of caribou use of winter lakes was performed in a hierarchical manner: (1) low resolution at the level of the entire study area was composed of lakes within winter ranges for the entire region and the divided east and west landscapes; and (2) high resolution of the study area was at the level of individual lakes. According to hierarchical selection, we predicted that broad habitat factors, such as groups of lakes of particular shape and size, to be more strongly selected by caribou than specific habitat factors, such as selection of individual lakes. Selection by caribou was marginally strongest at the level of winter ranges compared with selection of individual lakes as predicted. Coarse-scale lake patterns combined with patterns of forest cover may identify areas where caribou are present in winter, and we hypothesize that this is, at the least, partly a result of predator avoidance. However, previous research suggests that forage (Barten et al. 2001, Johnson et al. 2001) and perhaps water-borne minerals are selected at the scale of caribou locations adjacent to lake shores (Heard and Williams 1990, Storeheier et al. 2002).

Caribou chose winter ranges with more lakes than available both regionally and in the west sub-regional landscape, but not in the east. The eastern landscape had more lakes available to caribou, and caribou selection of lakes was less strong indicating that more of the sub-region contained suitable lake patterns that met caribou needs. In contrast, the western landscape had fewer lakes and these were larger than in the east. Caribou in the west sub-region showed stronger selection for winter ranges that contained many smaller lakes, likely because suitable areas were less available relative to the east. For example, caribou selected areas with considerably larger lake perimeters at the regional study level and in the west landscape, but not in the east where larger perimeter lakes were more available. Similarly, caribou used smaller lakes than available at the regional level and in the west, but in the east, lakes were used in proportion to their availability suggesting that the east landscape provided areas with more preferred lakes.

Woodland caribou are wide-ranging and highly mobile mammals that repeat their movements annually (Johnson et al. 2002b, Schaefer et al. 2000). Some populations of caribou demonstrate large-scale inter-annual shifts in range, likely as a response to snow or perhaps forage-predation trade-offs (Johnson et al. 2002a). Seasonal range shifts imply that suitable habitat occurs annually within similar areas and may reflect habitat selection to reduce predation risk and locate predictable food patches. For example, differences in the movements and habitat selection between female caribou with and without calves suggest that females alter their movement patterns and shift winter ranges if they have

a calf to protect from predators (Ferguson et al. 1996, Ferguson and Elkie 2004b, Rettie and Messier 2001).

Anti-predator adaptations include predator avoidance mechanisms, which reduce the probability of successful predation when a prey animal is within the perceptual field of a predator (Brodie et al. 1991). For caribou, wolves are the predator species that causes substantial mortality (Bergerud and Elliot 1986, Edmonds 1988, Pimlott 1967, Seip 1992); therefore caribou anti-predator behavior will be related to wolf search and attack behavior. Caribou may select home ranges during winter that encompass a pattern of lakes that allows for early detection of approaching wolf packs. Caribou selected winter ranges consisting of medium sized lakes (5–100 ha) with considerable perimeter (3–6 km) relative to available lake features. While on lakes, caribou can see and smell approaching wolf packs and the wind-packed snow on the frozen lake surface may provide better escape opportunities by allowing caribou to outrun wolves. Moving within areas of numerous mid-sized lakes close together ensures that foraging caribou will have access to frozen lakes as escape terrain nearby. Therefore, during chases whereby wolves test caribou, caribou if forced into deeper softer snow under forests will have access to lakes within a reasonable distance. Too small a lake may not provide a long enough packed surface to allow caribou to outrun wolves and too large a lake may increase detection of caribou by wolves and increase the risk of predator-prey interactions. The irregular pattern, or higher fractal dimension, of lakes may reduce the likelihood of detection by wolves while providing proximate escape cover. Behaviors of ungulates often reflect the likelihood of encountering a predator in a particular habitat irrespective of whether the predator is present (Bleich 1999, Hirth 1997, Molvar and Bowyer 1994).

Ungulates, which form the principal prey of wolves (Keith 1974, 1983; Pimlott 1967), may respond to changes in predation risk associated with habitat. For example, woodland caribou may increase mobility as a response to wolf presence (Bergerud and Elliot 1998; Bergerud et al. 1984, 1990; Cumming et al. 1996). Wolves rely on surprise (as provided by stalking cover) to increase predation success (Kunkel and Pletscher 2001). Despite their efficiency, wolves are not perfect hunters. Only 8% of wolf pack attacks of moose on Isle Royal were successful (Mech 1966), and less than 10% of observations of wolves chasing deer and moose in Minnesota resulted in capture of the prey (Nelson and Mech 1981). In addition to unsuccessful attacks, cervids may use olfactory and visual cues to estimate the level or type of predation risk (Laundré et al. 2001), such as used by mustelids (Stoddart 1976). Therefore, prey evolve behaviors that seem to be adaptive for different predator situations such that animals

move about the physical landscape constantly adjusting their behavior in response to changing levels of predation risk. Caribou have likely evolved behavioral mechanisms that allow early detection of approaching wolf packs and choose landscapes that reduce detection by predators while favoring their escape.

In this study, we examined the scales that best predict caribou use of winter habitat. Determining the scales of importance can help managers find a landscape analysis with predictive power and thereby help to conserve populations (Wiens et al. 1993). Spatially explicit models that incorporate a hierarchy of landscape structure and habitat utilization are needed to predict population responses to landscape change (Turner et al. 1995). Predation by wolves seems to be the major cause of mortality in most woodland caribou populations and may drive habitat selection (Rettie and Messier 2000, Stuart-Smith et al. 1997). Unfortunately, little is known about wolf density in this region. Forest management with the aim of conserving woodland caribou should avoid disturbing areas of high densities of medium-sized lakes that may be selected by caribou to reduce predation risk. While our work has identified factors associated with caribou landscape selection, a profitable next step would be to follow cohorts of caribou within various habitats in manipulated landscapes to clarify the roles of wolf predation and landscape structure in affecting habitat selection by individual caribou. Is differential caribou survival associated with particular lake patterns? For example, fetch and orientation of lakes and presence of islands would be interesting variables to investigate sensory perception of predator and prey. Integration of predator-prey field data, satellite imagery, and GIS technology (e.g., Johnson et al. 2001, 2002a) provides management methods to determine fine-scale and coarse-scale population responses to forest management.

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