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Habitat use by woodland caribou in a managed boreal forest landscape

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HABITAT USE BY WOODLAND CARIBOU IN A MANAGED BOREAL FOREST LANDSCAPE

by

Terrence J. C. Honsberger

"The land! That is where our roots are. There is the basis of our physical life. The farther we get away from the land, the greater our insecurity. From the land comes everything that supports life, everything we use for the service of physical life. The land has not collapsed or shrunk in either extent or productivity. It is there waiting to honor all the labor we are willing to invest in it, and able to tide us across any local dislocation of economic conditions. No unemployment insurance can be compared to an alliance between man and a plot of land."

-Henry Ford

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ABSTRACT

Woodland caribou (*Rangifer tarandus caribou*) populations throughout much of the boreal forest have decreased as a result of changes to forest composition, including an increase in moose (*Alces alces*) and wolf (*Canis lupus*) density with increased predation on caribou. For this study, a multi-scalar analysis of Argos telemetry data from 18 radio-collared caribou during 2000-2009 in northwestern Ontario compared their use of habitat in a landscape with a longer history of logging (Lake Nipigon area) with their use of habitat in an adjacent, less exploited landscape, managed following caribou mosaic guidelines (Ogoki area). The objective was to determine whether differences in caribou habitat use occurred with varying availability of winter habitat patches and varying moose density for these two landscapes. A field investigation of the Lake Nipigon area was conducted to determine if increased use of the Lake Nipigon islands in winter was more likely based on avoiding predators or on finding higher forage availability. Caribou in the Lake Nipigon area had smaller home ranges, used smaller winter habitat patches, and used areas of lower moose density more than caribou in the Ogoki area. Fine-scale habitat selected in the Lake Nipigon area was for low moose densities on the mainland and on islands >500 ha. Islands <500 ha were shared by caribou and moose, probably because access to these islands was more difficult for predators. The Lake Nipigon islands had the same available forage as the mainland, also suggesting that the use of islands by caribou is to reduce predation risk. In the Ogoki area, where larger winter habitat patches occur, these areas were selected and likely serve as predator escape habitat. In all areas of escape habitat, use by caribou was in sites of higher tree basal area and arboreal lichen cover than randomly selected sites, suggesting that at this finer scale (plots of 150-m radius), caribou selected for higher food availability. Protecting caribou in the region depends on the conservation status of the Lake Nipigon islands and on the maintenance of large patches of winter habitat in areas further from these islands.

Keywords: boreal forest, caribou, habitat loss, predation, *Rangifer tarandus caribou*

CONTENTS

TABLES

FIGURES

LIST OF APPENDICES

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DEDICATIONS

To Edgar Allen Pett (1921-2009), distinguished veteran of WWII, professional engineer, environmentalist, artist, and musician. I am sorry I didn‟t get this thesis finished in time for you to read it, Papa, but you were, and will always be, an important part of everything I do. I miss you.

To my wife Emma, who has listened to me talk about caribou incessantly over the last few years and has tolerated my late nights and my absenteeism throughout this process. And to my children; Oliver, Jonah and Ruby, now that this chapter of my life is closing, I can‟t wait to spend more time with all of you.

I would also like to thank Dr. A. T. Bergerud. Most people involved in the world of caribou have an opinion regarding Dr. Bergerud, and no matter how one feels about him, one has to admire his dedication, passion and relentless efforts to prove the importance of predation. Thank you Dr. Bergerud, for your seemingly endless supply of stories, and continuous compliments regarding my ability to barbeque steaks. I have yet to visit the Bell Museum of Natural History, but I promise you that I will.

Context for this study

Woodland caribou (*Rangifer tarandus caribou* L.; hereafter, caribou) occur at low densities across most of their range in Canada (Schaefer 2003) and have been listed as a threatened species throughout mainland Canada (COSEWIC 2000). Management to maintain caribou habitat has long revolved around the paradigm that caribou need mature and old-growth conifer stands with low canopy closure and an abundance of lichens, especially in winter (Rettie and Messier 2000, Courtois et al. 2007, Schaefer and Mahoney 2007). As forestry operations expand across the boreal forest, caribou habitat of this description continues to be altered in favour of younger, managed forest (Schaefer 2003, Vors et al. 2007, Wittmer et al. 2007). An indirect consequence is functional habitat loss, when other ungulate species are attracted to the younger forests (Courtois et al. 2004, Wittmer et al. 2007), allowing an increase in predator populations (Rettie and Messier 1998, Kunkel and Pletcher 2001, McLoughlin et al. 2005, Briand et al. 2009). Cumming (1992) and Cumming and Beange (1987) suggested conservation strategies that protect areas already known to provide caribou habitat until they are no longer used by caribou; they also suggested increased hunting of alternate prey species, such as moose (*Alces alces* L.) and white-tailed deer (*Odocoileus virginianus* Zimm.), in and around these protected areas.

The management of caribou habitat has become a significant consideration in the preparation of Forest Management Plans (FMPs), because of progressive loss of caribou range and functional habitat throughout Canada over the last century (McLoughlin et al. 2003, Courtois et al. 2004, Vors et al. 2007). Identification and conservation of caribou habitat in the boreal forest of Ontario within the context of forest management planning has evolved from *Forest Management Guidelines for the Conservation of Woodland Caribou: A Landscape Approach* (Racey et al. 1999) to the *Forest Management Guide for Boreal Landscapes* (OMNR *in prep*), the *Ontario Woodland Caribou Conservation Plan* (OMNR 2009) and the *Forest Management Guide for Conserving Biodiversity at the Stand and Site Scale* (OMNR 2010).

The *Forest Management Guide for Boreal Landscapes* (OMNR *in prep.*) requires that the Ontario Landscape Tool (OLT) be used for all forest management plans written after 2010. The OLT was developed by the Ontario Ministry of Natural Resources (OMNR) as a modelling tool that allows members of a Forest Management Planning team to assess landscape habitat conditions for a number of species, including caribou. The *Ontario Woodland Caribou Conservation Plan*, which provides policy direction for caribou management, has proposed 12 “Caribou Population Ranges” in Ontario that form the management units by which caribou habitat will be managed. In 2005, OMNR biologists noted that Argos collar data from the Lake Nipigon area indicated a possible shift in the types of forest being used by caribou, from traditional upland, sparse pine stands to mature, birch-dominant, mixed stands, prompting the inception of this study. The resulting study area, centered on Lake Nipigon in northwestern Ontario, was determined by the boundaries of the Lake Nipigon Caribou Population Range (LNCPR) as presented in the *Ontario Woodland Caribou Conservation Plan* (OMNR 2009).

Introduction

Most animals are vulnerable to predation throughout their lives, but precocious, neonatal ungulates are particularly vulnerable to carnivores evolved to consuming largebodied prey. In order to reduce predation on their young (calves), female ungulates exhibit two general behavioural strategies: "hider" and "follower" (Hirth 1977). These strategies are not necessarily mutually exclusive. Caribou calves are followers for the most part, but are hiders for the first few days of life (Skogland 1989). Predation by wolves (*Canis lupus* L.) and black bears (*Ursus americanus* Pall.) is considered to be the proximate cause of caribou mortality, particularly on calves (Bergerud 1974, Seip 1992, Lambert et al. 2006), which is ulimately facilitated by habitat alteration (Briand et al. 2009). There are many gaps in understanding caribou habitat selection, ungulate habitat partitioning, and caribou population dynamics underlying the caribou-wolf dynamic (Armstrong 1996, Armstrong et al. 1998). The key habitat requirement of caribou is sufficient space to practice anti-predator tactics of spacing themselves into small aggregations and distancing themselves from alternative prey for wolves, such as moose, particularly when calves are young (Bergerud 2000). To reduce predation risk, caribou exhibit extreme dispersion across the landscape, thereby increasing the search time required of their predators and promoting prey-switching in wolves (Bergerud and Elliot 1986, Gustine et al. 2006).

In a comparison of two caribou populations in British Columbia, Seip (1992) found that the population that could reduce its contact with moose and wolves through spatial separation had lower mortality rates, whereas the population that had more contact with moose and wolves suffered higher rates of predation. High deer densities have also been shown to result in a numerical response in wolves and increase the incidental predation of caribou in Alberta (Latham et al. 2011). Habitat selection by caribou has been shown to occur at multiple scales with the most important limiting factors influencing habitat selection by individuals or populations at coarser scales (Rettie and Messier 2000). When caribou are faced with a managed forest, where suitable habitat patches are dispersed across the landscape and predation risk is high, caribou may be forced to select smaller habitat patches. The scales at which limiting factors influence habitat selection may consequently change.

The effect of scale on a population‟s response to its habitat has been shown to be dependent on its flexibility to use different habitats (Andren et al. 1997). Most studies of caribou habitat selection have focused on coarse-scale attributes (Mahoney and Virgil 2003, Ferguson and Elkie 2004). Most fine-scale investigations of caribou habitat (e.g., Rettie and Messier 2000, Ferguson and Elkie 2005) have focused on attributes derived from a Geographical Information System (GIS) rather than on field data, with some exceptions (e.g., Terry et al. 2000, Johnson et al. 2001, Mayor et al. 2007, 2009, Briand et al. 2009). A multi-scalar evaluation using field data may allow for the identification of ecological processes that contribute to the importance of habitats (Wheatley and Johnson 2009).

The area for this study was determined by the boundaries of the LNCPR and lies approximately between N50 44.550 and W90 01.072 to N49 57.119 and W87 15.959 (Fig. 1). It is found entirely within the boreal ecoregion of northwestern Ontario. This study investigated winter habitat use in two phases, with the first phase focusing on winter habitat use at two spatial scales: the study area and the home range. These scales of habitat use were investigated within two areas: the Lake Nipigon area and the Ogoki area (Fig. 1). The area boundaries were defined by creating 100% minimum convex polygons (MCPs) around all of the MCP home ranges used by Argos-collared caribou during 2000-2009, with one group of caribou staying <10 km from Lake Nipigon (Lake Nipigon area sample, n = 9) and a second group using home ranges ≥10 km from Lake Nipigon (Ogoki area sample, n = 9). The two areas overlapped, although the percentage of overlap was negligible. The premise governing the selection of the two areas was to compare winter habitat use in a landscape dominated by forestry activities (Lake Nipigon area) with winter habitat use in a landscape managed with the caribou mosaic framework (Ogoki area; Armstrong et al. 1989). Wolf densities were similar in the two areas, on average 7.5 wolves per 1,000 km^2 (Patterson 2008). This density is higher than the minimum proposed to negatively affect caribou populations (Bergerud 2007). If the amount and arrangement of winter habitat patches is not the same for the two areas, caribou are likely experiencing different predation risk or finding different escape habitats.

Caribou vary their habitat use strategies in response to disturbance across their range (Smith et al. 2000, Schaefer 2003, Courtois et al. 2007), including reducing their home range sizes and movement distances in highly managed mosaic landscapes in Alberta (Smith et al. 2000), and expanding home range sizes and traveling greater distances in more homogeneous landscapes in Quebec (Courtois et al. 2007). However, one common habitat use strategy is distancing themselves from recently disturbed areas, probably as a predator avoidance strategy (Chubbs et al. 1993). Previous work conducted in the Lake Nipigon area revealed that caribou used the islands of Lake Nipigon in summer to reduce predation risk during calving, then migrated to the Armstrong area for the winter (Bergerud and Butler 1975). Recent interpretation of Argos radio-collar data has suggested that at least some of the caribou in the Lake Nipigon area have altered their winter habitat selection behaviour and continue to use the Lake Nipigon islands in the winter.

This study investigates two landscapes with similar caribou densities, one that has been logged using traditional forest management (Lake Nipigon area) and one that has been logged using the caribou winter habitat protection guidelines (Ogoki area). The objectives for the phase one analysis in this study were to determine 1) whether different sizes of winter habitat patches, from 100 ha to >20,000 ha, were being used by caribou in each of the study areas, and 2) how caribou in both study areas were using the landscape during winter with respect to moose distribution. An assumption was that winter habitat patches represent ideal caribou habitat. The predictions for this phase of the study were that 1) because more restricted movement by caribou at the landscape scale will occur when preferred habitat patches are smaller and more dispersed (Smith 2000), the Lake Nipigon area will support smaller home ranges than the Ogoki area; 2) in order to escape predators, caribou will use smaller patches to maintain their low densities as part of their "spacing out antipredator strategy" (Bergerud and Elliot 1986); and, 3) the use of areas of low moose density as a means of avoiding wolf activity (Rettie and Messier 2000) will occur at the study area scale in both areas, but will also occur at smaller scales in the Lake Nipigon area. The objective of the second phase of this study involved determining whether caribou in the Lake Nipigon area use islands in winter to reduce predation risk or to find higher forage availability (terrestrial and/or arboreal lichen abundance). For this objective, a field survey was conducted on sites of approximately 10 ha. The predictions were that 1) if caribou are selecting sites based on food abundance (terrestrial or arboreal), then lichen abundance should be greater at sites of known caribou use compared to randomly selected sites within their home range; and 2) if caribou are selecting sites as a means to reduce predation risk, then these patches would have fewer moose fecal pellet groups than randomly selected sites.

Study Areas

The total area of the LNCPR is 22,304 km^2 including water bodies. The Lake Nipigon and Ogoki areas are 4,785 km^2 and 10,930 km^2 respectively. Dominant tree species are black spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.), with balsam fir (*Abies balsamea* (L.) Mill.), trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), and white spruce (*Picea glauca* (Moench) Voss) on coarse, well-drained soils on rocky rolling uplands (Rowe 1972). Mean January temperature is -26.4 °C with an average snowfall of 42.3 cm, as recorded at the Environment Canada weather station located at the Armstrong Airport.

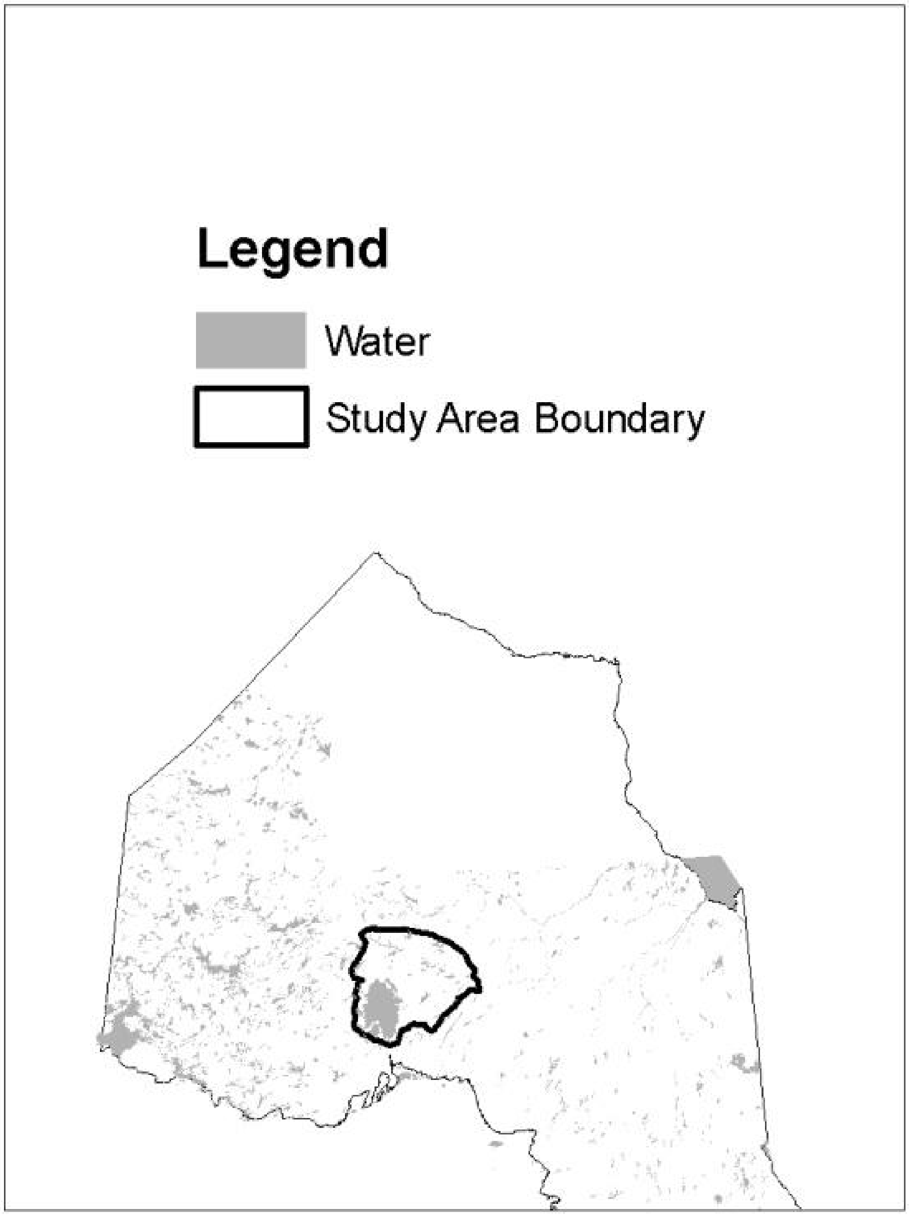

Fig. 1. Location of Lake Nipigon Caribou Population Range (LNCPR) within the province of Ontario.

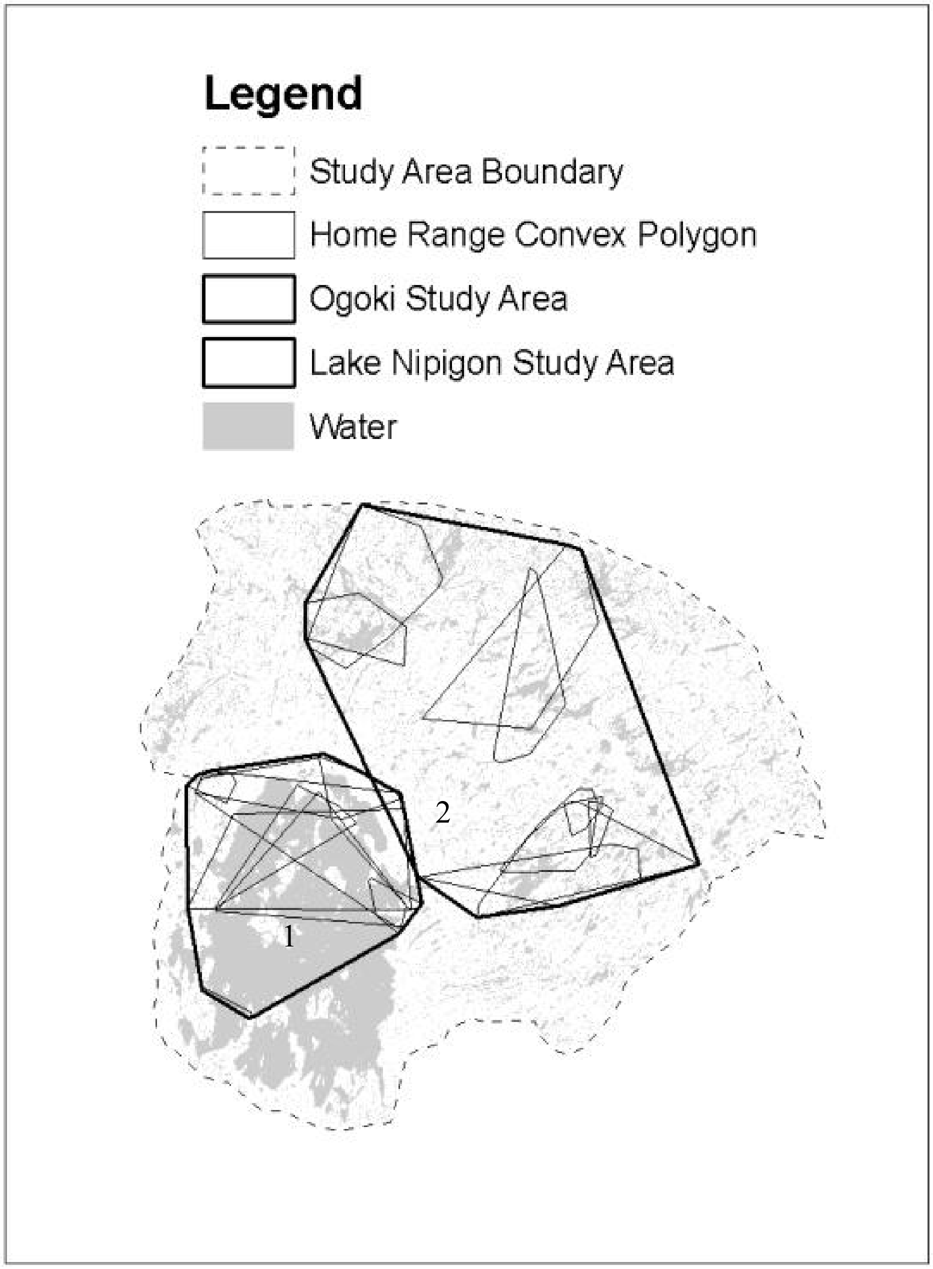

Fig. 2. Location of the Lake Nipigon study area (1) and Ogoki study area (2) within the LNCPR.

Methods

Small groups of caribou, comprised of both males and females have previously been observed together in the Lake Nipigon and Ogoki areas (Cumming and Beange 1987, personal observations). Eighteen adults (6 male and 12 female) among this group were captured between 2000 and 2009 and fitted with Argos satellite radiocollars. An initial comparison to determine differences in habitat use for females and males was attempted, but due to small sample sizes, the effort was abandoned. Restricting the combined dataset to collar records with ≥10 locations with an accuracy category of location classes 1, 2 or 3 (≤1,000 m, ≤350 m, and ≤150 m respectively) per winter resulted 1,718 locations (mean = 95, range = 10 to 309 per caribou). The winter period (November 15 to March 15) was defined by Ferguson and Elkie (2004), based on changes in the rates of movements of radio-collared caribou. For this study, collars transmitted data approximately every 7 days for an average of 1.7 winter seasons over 1 to 4 years.

One hundred percent minimum convex polygons (MCPs) were calculated using Hawth‟s Analysis Tools extension in ArcGIS 9.2 (Beyer 2004). The use of MCPs has been shown to have the potential to overestimate home range size (Burgman and Fox 2003), but to ensure sufficient sample sizes, the 100 % MCP was used in this study. If a caribou had data for multiple winters then all locations were combined for the creation of its MCP. All nine of the caribou on the Lake Nipigon study area used the islands of Lake Nipigon throughout the winter. A t-test was used to detect differences in caribou home range sizes between the two study areas.

In phase one of this study, habitat was modelled with the Ontario Landscape Tool. The OLT uses Landscape Scripting Language, which is a proprietary tool for Geographic Information Systems (GIS) developed by the OMNR (Elliot et al. 2010). Caribou winter habitat was estimated by accessing standard forest unit classifications found in Forest Resource Inventory (FRI) data and a caribou habitat model derived from earlier studies (Racey et al. 1999, Brown et al. 2007, and Ferguson and Elkie 2004). For this model, eligible caribou winter habitat consists of stands comprising 100 % black spruce, eastern white cedar (*Thuja occidentalis* L.) and American larch (*Larix laricina* [Du Roi] Koch) on sites considered to have low productive capacity due to drainage and soil types (site class 3 and 4), as well as stands with ≥70% black spruce and ≤20% trembling aspen and white birch on all other sites. Jack pine stands are also eligible according to the caribou habitat model, provided they comprise ≥70% jack pine and ≤20% trembling aspen and white birch, or the trembling aspen and white birch component of the stand was ≤20% and the jack pine component was larger than the combined black spruce and white spruce components. In the model, all stands constituting winter caribou habitat must be ≥60 years old.

To determine the spatial arrangement of winter caribou habitat, habitat „parcels" were derived from the intersection of a hexagonal grid overlain on an FRI shapefile (Elliot et al. 2010). The hexagon parcels became the basic layer from which broader scale analyses were based. Winter habitat patches were estimated at scales of 101-250 ha, 251-500 ha, 501-1,000 ha, 1,001-5,000 ha, 5,001-10,000 ha, 10,001-20,000 ha, and ≥ 20,000 ha. Winter habitat patches were located on the landscape by developing parcels and used the 50% rule, where 0.8-ha hexagons that contained ≥50% habitat were considered occupied. For a parcel to become part of a larger patch size, it had to be adjacent to another parcel comprised of hexagons containing ≥50% winter habitat patches. This approach explicitly identified habitat patches at a fine-grain, high-resolution scale, then combined adjacent hexagons to approximate the location of winter habitat at successively larger patches. This approach resulted in a representation of increasing connectivity of winter habitat on the forested landscape. Most winter habitat patches were distributed equally by size throughout the study areas, with the exception of the 5,001-10,000 ha size, for which there were only two patches, and the ≥20,000 ha size, for which only one patch occurred in the northeastern portion of the study area. Therefore, the 5,001-10,000 ha patch size was eliminated from the analysis, and the ≥20,000 ha patch size was only included in the analysis of the Ogoki area.

All delineated patch sizes of winter habitat were buffered at two increments of 1,000 m, which approximated the maximum estimated error associated with Argos collar locations (including Location class 1) (ARGOS 2004). These buffers resulted in three habitat categories for each scale: (1) within a core habitat patch as delineated from the OLT, (2) ≤1,000 m from a core habitat patch, and (3) >1,000 m from a core habitat patch (ARGOS 2004).

Predicted moose densities (PMDs), expressed as moose per km^2, were developed according to OLT rules, using the same 0.8-ha hexagonal grid. PMDs were derived from stand composition, stand age and climate variables, based on the moose habitat model created by Allen et al. (1991). In the OLT, stand composition and age from the FRI is used to estimate, at a scale of 50 ha, the proportions of 1) young forest, 2) mature conifer forest and 3) mature mixed conifer-deciduous forest. Each 0.8-ha hexagon that possessed

≥50 % of its area as pre-sapling or sapling seral stages is classified as young forest. The proportion of each forest type is determined at the 50-ha scale and then averaged over four 50-ha hexagon offsets. Spatial climate data is from Environment Canada and includes temperature for the warmest and the coldest three months of the year and precipitation for the coldest six months of the year (Colombo et al. 2006). To develop the model, all spatial data were merged with moose aerial survey data from 2000-2006 and the resulting regression model was tested with similar survey data from 1990-1999. The model performed with >90 % accuracy, with a slope for the regression line matching real moose densities from 1990-1999 to PMD of 1.00 ± 0.03 (standard error, S.E.), and an intercept of -0.019 ± 0.007 (Robert Rempel, personal communication). Three ranges of PMD were constructed for this study: (1) 0.00-0.12 per km^2, (2) 0.13-0.17 per km^2, and (3) ≥0.17 per km^2. These categories spanned the range of real moose densities found within the study area and divided relatively equally the area represented by each category.

Ranked availability of winter habitat patches and their buffers, and ranked available area occupied by each of the PMD categories were calculated separately within the study area and within the home range. Ranked use of all these defined areas by each caribou was calculated from the total area of each habitat category within the home ranges (for a study-area assessment), and from the relative number of locations with ≥50% of the buffered locations in each habitat category (for a home-range assessment). The differences between the ranked available area of a category and its ranked use were averaged across all caribou to provide a mean rank difference for all categories. The mean rank difference estimated relative habitat selection (Johnson 1980). Categories were ordered from least to most preferred habitat based on the magnitude of the mean difference. This method tested two hypotheses: J_1) the relative selection for all habitat categories was equal, and J_2) the relative selection for habitat *i* equalled that for habitat *j*. J_1 states that the rank orderings of habitat from least to most used is the same as the availability of habitats (least to most available). A significant difference in the rank order results in the rejection of J_1, and leads to the test for J_2. Hypothesis J_1 was tested using Hotelling"s T^2 statistic and was rejected if there was a substantial difference in the ranks (i.e., the multivariate normal vector of means was not equal to a vector of zeros). Hypothesis J_2 was tested using a Tukey"s multiple comparison test.

The interpretation of the field data obtained in phase two of this study followed a field sampling protocol that is appropriate when individual animals are identified and locations for each animal represent a set of used habitats; both available and used habitats are sampled randomly on the assumption that used habitats are a subset of all habitats (Thomas and Taylor 1990). Individual 100% MCPs were generated around location class 3 locations of five Argos-collared caribou. For each caribou, an equal number of used sites (Argos locations) and available sites (random locations) were selected with the help of a random points generator extension in ArcMap (Beyer 2004). Each used or available location point was buffered with a 150-m radius circle approximating the error associated with location class 3. Field plots actually visited were a subset of all points that fell within 2 km of a road or navigable waterway, for easy access by field crews. Plot selection was intentionally biased toward investigation of the Lake Nipigon islands when preliminary field investigations revealed that islands were being used in different proportions. Two to four of the used and available points were visited for each of the caribou totalling 21 used and 14 available sites sampled: 13 sites on islands <500 ha, 14 on islands ≥500 ha, and eight on the mainland. These size categories defined three hypothesized regions of winter escape habitat. Field sampling occurred between late May and August 2007.

The study plot structure at used and available sites within each of the escape habitats consisted of four transect lines, 150 m in length and 2 m in width, each originating on the site co-ordinates. Each transect line was oriented parallel to one of four cardinal directions (Fig. 3). Data collected continuously along each transect consisted of a count of moose pellet groups (as a surrogate of moose density at a finer scale than the PMD), stem counts of each tree species ≥2 cm diameter at breast height (dbh), and estimates of arboreal cover for each tree ≥2 cm dbh up to a height of 3 m. An estimate of lateral cover (horizontal visual obstruction) was made from the plot centre towards the end of each transect to the maximum visible distance for a 21.6 cm x 28.0 cm reflector held at breast height. Cover of terrestrial lichen was estimated to the nearest 5% on 61 subplots of 1 m x 2 m, whose placement consisted of 15 subplots each 10 m apart along each of the four transects and one subplot located on the study plot centre. Data collected at the study plot centre and at the end of each transect included diameter class for each encountered tree, basal area by species, stems per ha, number of tree species present, an ocular estimate of canopy closure to the nearest 5%, and age of one randomly selected representative tree from a core obtained by trunk increment borer (Table 1). All individual measurements were calculated as averages for each variable for each study plot. Terrestrial lichen frequency was determined by dividing the number of sub-plots containing lichen by the number of sub-plots within each study plot. Arboreal lichen frequency was determined by dividing the number of trees with arboreal lichen by the number of trees counted along each transect on each study plot. A binary variable was created that assigned plot locations to Lake Nipigon islands or to the mainland.

A Shapiro-Wilk (*W*) test for normality was conducted on all continuous variables and histograms constructed for assessment of normality for these variables. Data were considered normally distributed when $p \geq 0.1$ for the test statistic *W*; all continuous variables met this criterion. Differences were tested between plot types (used and available) and among escape habitats (mainland, large island and small island), in a two-factor multivariate analysis of variance (MANOVA). Multiple comparisons used a Bonferroni adjustment. Moose pellet group counts were transformed into a binomial categorical variable with plots possessing <10 pellet groups separated from plots with ≥10 pellet groups. This threshold was chosen as a natural break between plots containing generally <5 or >10 pellet groups. Data exploration continued by entering all variables, including the binary variables associated with moose pellets and with identifying the escape habitat, into a stepwise logistic regression analysis. Continuous variables were first screened in a Pearson‟s product moment pairwise correlation matrix to identify collinearity. The logistic regression model was fit without an intercept, as is the normal procedure for use and availability designs (Boyce et al. 2002). A significance level of 0.1 was used to include more variables and more differences in a fuller exploration of habitat use at all scales. Diagnostic index scatter plots of DFBeta residuals were conducted for any continuous variables entering the best-fit model to find influential observations. Leverage and Cooks plots were also drawn to determine outlying observations (Sall

1990, O‟Hara Hines and Hines 1995). All analyses were conducted with SPSS 16.0 (SPSS Chicago, IL) and DataDesk (Data Description Inc. 1996).

Table 1. Description of habitat variables used to determine fine-scale winter habitat selection of caribou in the Lake Nipigon area.

Variable	Definition
Stem density	Total number of tree stems per hectare
Number of tree species	Average number of tree species per plot
Average lichen	Average percent cover of terrestrial lichen cover per plot
Lichen frequency	Average percentage of lichen plots containing terrestrial lichens
Average arboreal lichen	Average percent cover of trees with arboreal lichen per plot
Arboreal frequency	Average percentage of trees with arboreal lichen per plot
Age	Average age of trees per plot
Canopy closure	Average percent canopy closure per plot
Visibility	Average distance of visibility per plot
Land size	Binomial category of plot location (mainland and large island vs smaller island)
Island (Y/N)	Binomial category of plot location (island or mainland)
Moose pellet	Average number of moose pellet groups per plot

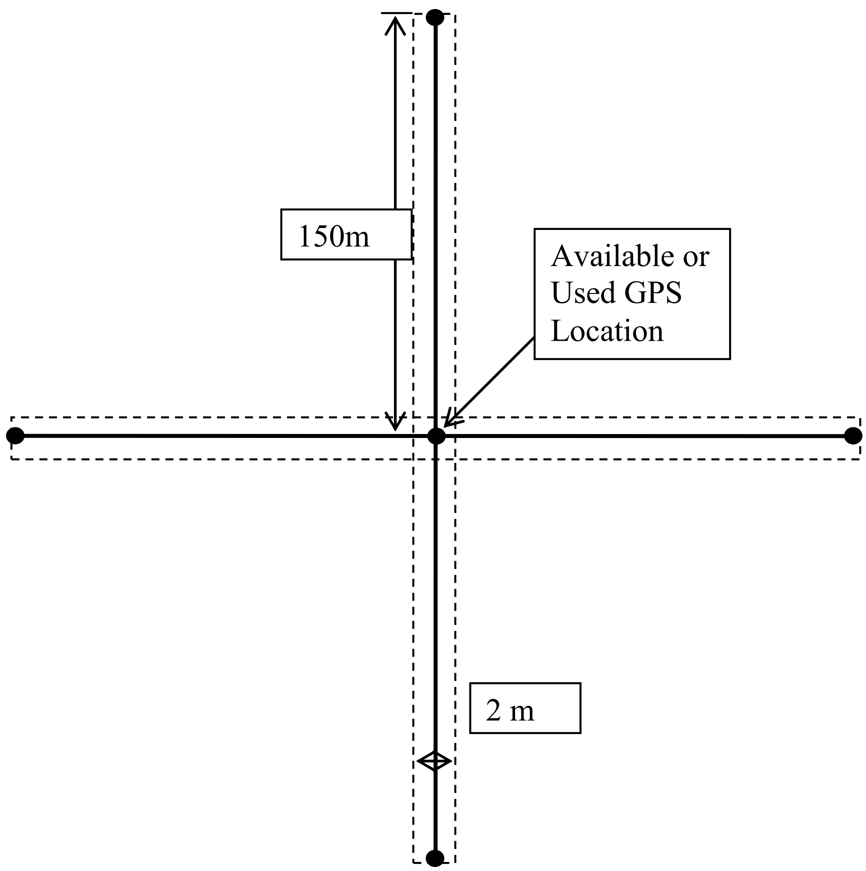

Fig. 3. Plot structure for fine-scale winter caribou habitat data collection in the Lake Nipigon area, consisting of four transects originating on a point used by caribou or a random point.

Results

Home range sizes differed for the two study areas (t = 1.87, df = 16, $p = 0.08$), with the smaller home range sizes belonging to Lake Nipigon area caribou. They had an average home range size of 312 km^2 (6 km^2 to 958 km^2), while caribou in the Ogoki area had an average home range size of 551 ha (65 km^2 to 1,238 km^2). Winter habitat in the Lake Nipigon area was more often in patch sizes <20,000 ha. In the Ogoki area, 37% of the landscape was comprised of winter habitat patches of ≥20,000 ha (Table 2, Fig. 4). In the Lake Nipigon area, the frequency of caribou locations was greater than expected in core winter habitat patches calculated at the 251-500 ha and the 1,001-5,000 ha scales

(Table 3). Caribou in the Ogoki area had greater than expected frequency of locations outside the 1,000 m buffer around core winter habitat patches (i.e., in random habitat) at the 101-250 ha scale, but greater than expected frequency of location within core winter habitat patches calculated at the 1,001-5,000 ha and 10,001-20,000 ha scales. In the home-range analysis, the frequency of caribou locations was not significantly different than expected in the Lake Nipigon area for any winter habitat patch scales. Caribou locations occurred more often than expected in the Ogoki area within core habitat and areas >1,000 m of winter habitat patches calculated at the >20,000 ha scale (Table 4). Use of winter habitat by caribou occurred over a wider range of patch sizes at the study-area scale than at the home-range scale. Smaller habitat patches were used in the Lake Nipigon area than the Ogoki area at the study-area scale (Table 5).

In the Lake Nipigon area, caribou locations occurred more frequently than expected in areas with lowest PMD (0-0.12 per km^2). In the Ogoki area, caribou locations were found more often than expected in areas with intermediate and high PMD (0.13-0.17 per km^2 and ≥0.18 per km^2). At the home-range scale, caribou were found more often than expected in areas with PMD of 0-0.12 per km^2 in the Lake Nipigon area, but were not affected by PMD in the Ogoki area. The southern extent of caribou home ranges occurred at the northern extent of continuous high PMD (≥0.17 per km^2) throughout the Lake Nipigon area.

Table 2. Total area and percent of study area in winter habitat at various patch sizes for the Lake Nipigon and Ogoki areas.

Scale	Habitat category	Nipigon		Ogoki	
		Area (ha)	Percent area	Area (ha)	Percent area
101-250 ha	Core habitat	7,850	4.6	41,717	4.7
	≤ 1,000 m	10,982	6.4	469,984	53.2
	> 1,000 m	152,600	89.0	371,333	42.1
251-500 ha	Core habitat	3,760	2.2	10,080	1.1
	≤ 1,000 m	10,982	6.4	41,065	4.7
	> 1,000 m	156,690	91.4	831,888	94.2
501-1,000 ha	Core habitat	0	0.0	0	0.0
	≤ 1,000 m	0	0.0	0	0.0
	> 1,000 m	0	0.0	0	0.0
1,001-5,000 ha	Core habitat	15,783	9.2	10,080	1.1
	≤ 1,000 m	18,957	11.1	41,065	4.7
	> 1,000 m	136,692	79.7	831,888	94.2
10,001-20,000 ha	Core habitat	17,806	10.4	55,532	6.3
	≤ 1,000 m	24,692	14.4	68,250	7.7
	> 1,000 m	128,933	75.2	759,251	86.0
> 20,000 ha	Core habitat	0	0.0	329,677	37.3
	≤ 1,000 m	0	0.0	289,189	32.7
	> 1,000 m	0	0.0	264,168	29.9

Table 3. Results of test for preference (Johnson 1980) for winter habitat patches at study area scale for the Lake Nipigon and Ogoki areas. Significant results are highlighted in grey, where differences occur for different superscripted letters.

Scale	Habitat category	Lake Nipigon		Ogoki	
		F	Tukey's LSD	F	Tukey's LSD
101-250 ha	Core habitat	2.61	0.000	5.12	0.000[a]
	≤ 1,000 m		-0.556		0.778[b]
	>1,000 m		0.556		-0.778[c]
251-500 ha	Core habitat	4.24	-0.333[a]	0.94	-0.333
	≤ 1,000 m		0.222[b]		0.000
	>1,000 m		0.000[b]		0.000
501-1,000 ha	Core habitat	0	0.000	N/A	N/A
	≤ 1,000 m		0.000		N/A
	>1,000 m		0.000		N/A
1,001-5,000 ha	Core habitat	6.78	-0.444[a]	29.65	-0.778[a]
	≤ 1,000 m		0.333[b]		0.222[b]
	>1,000 m		0.000[b]		0.000[b]
10,001-20,000 ha	Core habitat	0.94	-0.333	29.65	-0.778[a]
	≤ 1,000 m		0.000		0.333[b]
	>1,000 m		0.000		0.000[b]
> 20,000 ha	Core habitat	N/A	N/A	2.42	0.333
	≤ 1,000 m		N/A		0.111
	>1,000 m		N/A		-0.444

Table 4. Results of test for preference (Johnson 1980) of winter habitat patches at the home range scale for the Lake Nipigon and Ogoki areas. Significant results are highlighted in grey, where differences occur for different superscripted letters.

Scale	Habitat category	Lake Nipigon		Ogoki	
		F	Tukey's LSD	F	Tukey's LSD
101-250 ha	Core habitat	0.53	-0.111	0.05	0.000
	≤ 1,000 m		-0.056		-0.111
	>1,000 m		0.167		0.111
251-500 ha	Core habitat	0.00	-0.278	0.00	-0.167
	≤ 1,000 m		0.278		0.167
	>1,000 m		0.000		0.000
501-1,000 ha	Core habitat	0.00	-0.056	0.00	-0.167
	≤ 1,000 m		0.056		0.167
	>1,000 m		0.000		0.000
1,001-5,000 ha	Core habitat	1.42	-0.444	1.66	0.000
	≤ 1,000 m		0.333		-0.222
	>1,000 m		0.111		0.000
10,001-20,000 ha	Core habitat	0.05	0.111	2.63	0.111
	≤ 1,000 m		0.000		-0.333
	>1,000 m		0.222		0.000
> 20,000 ha	Core habitat	N/A	N/A	7.88	-0.111[a]
	≤ 1,000 m		N/A		0.667[b]
	>1,000 m		N/A		-0.556[a]

Regions were selected differently based on PMD at the study area scale for the Nipigon area and the Ogoki area (F = 2.70, df = 2, 15, p = 0.10) and at the home-range scale for the Nipigon area (F = 3.46, df = 2, 6, p = 0.10). Lake Nipigon area caribou selected low moose density (0-0.12 per km^2) at the study-area and home-range scales, while Ogoki area caribou selected intermediate moose densities (0.13-0.17 per km^2) at the study-area scale. Within the Lake Nipigon area, the probability of a plot being used by caribou in winter increased where fewer tree species, a higher frequency of arboreal lichen, and older stand ages occurred ; avoidance of areas of high moose density on the mainland and on islands ≥500 ha was the most significant factor (the interaction term including land size and moose pellets) predicting probability of use by caribou (Table 5). The two-factor MANOVA suggested differences between used and available winter locations (F = 2.28, df = 1, 29, p = 0.06), among the three escape habitats (F = 2.36, df = 2, 29, p = 0.02), and in the interaction between these two independent variables (F = 7.19, df = 2, 29, p = 0.07). Pairwise comparisons (Table 6) showed that used sites had greater overall basal area (F = 4.77, df = 1, 29, p = 0.04 and percent arboreal lichen (F = 5.19, df = 1, 29, p = 0.03) compared to available (randomly chosen) sites. Areas on the mainland supported lower stem densities than small islands (F =7.70, df = 2, 29, p = 0.002) and greater visibility than large and small islands (F = 11.77, df = 2, 29, p = <0.001 and F =8.77, df = 2, 29, p = 0.001 respectively). Basal area, stem density, and percent arboreal lichen were all significantly higher in used mainland (21.6, 1,001, 12.2 respectively) sites compared to available mainland sites (9.5, 630, 3.9 respectively). Visibility was significantly greater in used mainland sites compared to available large and small island sites (29.5, 12.6, 16.5 respectively), and significantly greater in available mainland sites compared to used small island sites (25.5, 12.9 respectively).

Table 5. Final fine-scale caribou winter habitat use for the Lake Nipigon area by best-fit logistic regression ($X^2 \geq 9.24$, df = 5, α=0.1). Significant variables entering the stepwise regression are listed with their coefficients (β), standard errors of the coefficients (S.E.) and X^2 statistics.

Variables	β	S.E.	X^2	df	*p*
Land size x moose pellets	-3.867	1.56	6.145	1	0.013
Number of tree species	-1.546	0.666	5.393	1	0.02
Stand age (years)	0.5	0.027	2.828	1	0.068

Table 6. Two-factor MANOVA comparing characteristics of used and available plots among mainland, large-island (>500 ha) and small-island escape habitats. Significant differences among means (± S.E.) are highlighted in grey, but do not occur where superscripted letters are the same.

Variable	**Units**	**F**	***p***	**Plot type**		**Escape habitats**		
				Used	**Available**	**Mainland**	**Large island**	**Small island**
Basal area	m^2	2.6	0.0	19.6±1.3	15.2±1.5	15.6±2.0	16.8±1.6	19.9±1.6
Stem density	stems/ha	3	0	2,291±344	1,811±380	815^{a}±513	$2{,}009^{b}$±405	$3{,}327^{b}$±404
Percent arboreal lichen	%	2.7	0.0	8.0±0.8	5.2±0.9	8.1±1.2	6.0±1.0	5.7±1.0
Arboreal lichen frequency	%	1	0	31±4	26±4	21±5	29±4	35±4
Age	years	1	1	85±6	82±6	78±8	90±6	83±6
Canopy closure	%	1	0	51±4	58±5	44±6	61±5	58±5
Visibility	m	5.1	0.0	19.2±1.6	18.2±1.8	27.5^{a}±2.4	13.9^{b} ±1.9	14.7^{b}±1.9

Discussion

The Lake Nipigon area comprises less available winter caribou habitat, measured as total area, proportion of the landscape, or fraction of larger winter habitat patches, relative to the Ogoki area. As a result, winter locations for caribou in the Nipigon area were more restricted than in the Ogoki area. Clear-cut logging has been increasing the amount of younger forest in the Lake Nipigon area over the past four decades, resulting in a heterogeneous landscape of small stands of varying ages. As documented by Smith et al. (2000) for caribou in Alberta, it is likely that smaller home ranges are a result of clear-cut logging in the Lake Nipigon area. Forced to use smaller patches, caribou in the Lake Nipigon area are dispersed at landscape-scale densities low enough to reduce predation risk, so long as they also find escape habitat in small islands in Lake Nipigon. Caribou in the Lake Nipigon area also appeared to avoid moose more than in the Ogoki area. Likely, the Ogoki area caribou reduced the threat of predation at the landscape scale as a result of the caribou mosaic management framework, while the Lake Nipigon caribou were required to actively avoid wolves at smaller scales.

At a finer scale, features selected by caribou differ among mainland and large and small islands. Especially on the mainland, used sites likely provided the best foraging opportunities with trees of larger basal area and greater amounts of arboreal lichen. Mainland sites also had greater visibility than the island sites, likely because escape from predators is more important on the mainland, even in winter habitat patches. The islands supported higher stem densities likely due to different growing conditions than mainland sites such as colder temperatures and reduced fire cycles, which result in multi-cohort stands (Bergeron 2000). Despite the fact that the islands do not offer the same foraging opportunities as the mainland, their value lies in their ability to provide reduced predation risk due to low moose densities.

Previous habitat use studies have supported the paradigm that non-migratory caribou select large, lichen rich, shrub poor, patches of mature habitat as an anti-predator strategy that diminishes the risk of predation, while at the same time fulfilling forage requirements (Briand et al. 2009, Latham et al. 2011). If the availability of ideal winter habitat patches is reduced, caribou must adopt a strategy that still allows them to disperse and maintain low densities. Large, lichen-abundant stands in the Lake Nipigon area may be less important as caribou habitat than in the past. Cumming and Beange (1987) found 22 wintering locations during their four-year study of caribou in the Lake Nipigon area, with only a single wintering location identified on a Lake Nipigon island; the remaining 21 wintering sites were located in large, mature, low-density conifer sites with abundant terrestrial lichen. It appears that during the last 20 years, caribou with home ranges near the shores of Lake Nipigon have increased their use of islands during the winter. The terrestrial lichen cover and frequency in used sites on the islands were lower than the mainland, with very few of the used sites on islands containing any terrestrial lichen.

Bergerud (2000) believed that caribou do not have specific food or habitat requirements when they winter in the northern extent of their boreal forest range, and that their primary habitat requirement is enough space to allow for anti-predator tactics. Historical reports of the previous southern distribution of caribou illustrate that they were found inhabiting landscapes that did not support lichen rich conifer stands in Maine, Vermont, New Hampshire, Michigan, Wisconsin, and Minnesota (Cringan 1956). In the Lake Nipigon area, caribou have adjusted their winter patch size use in the face of increasing habitat loss to incorporate patches smaller than 10,000 ha. These same caribou have begun using sites that are not „typical" caribou winter habitat (i.e. not large contiguous conifer dominated stands, high in terrestrial lichen). The ability of caribou to alter their winter habitat use indicates that caribou may be more plastic in their habitat preference than previously thought; whether fitness consequences might lead to eventual extirpation from the Lake Nipigon area remains to be seen.

Management implications

The OLT uses FRI and geo-climatic data to infer areas of caribou winter habitat over a range of scales from 1 ha to > 30,000 ha. If the OLT modelled winter habitat correctly, it would stand to reason that areas delineated as winter habitat should be used in higher proportion than expected if stands were chosen at random. This was an important finding for this study. Because caribou locations were found disproportionately within winter caribou habitat patches as delineated by the OLT, it would seem that the OLT correctly identified habitat.

Due to the higher degree of anthropogenic influence in the Lake Nipigon area, the threat of predation is greater for Lake Nipigon caribou relative to caribou in the Ogoki area and other less disturbed regions. Disturbed areas have higher predation risk for caribou, as mature forest is converted to younger forest favourable to alternative prey (Rettie and Messier 1998, Latham et al 2011). The amount and arrangement of critical winter habitat within managed forests can have a dramatic effect on the overall distribution of a population (Rempel et al. 1997, Lindenmayer and Franklin 2002). When caribou managers are planning for caribou habitat provisions during FMP exercises, consideration should be given to multiple factors, including silvicultural considerations that can maintain low moose densities by reducing the amount of stands that are converted from conifer to mixed deciduous stands.

This study illustrates the importance both of the caribou mosaic management approach to protect larger patches of winter habitat and of the Lake Nipigon islands as escape habitat for caribou. It is likely that persistent use of islands year-round has been assisted by the creation of the Lake Nipigon Conservation Reserve, which includes the islands of Lake Nipigon and its shoreline up to 1000 m on the mainland. This reserve prohibits any development or resource extraction activities to occur within its boundaries. The importance of predation in limiting caribou populations has been well established in the literature. Numerous studies have been initiated to investigate habitat selection throughout the range of caribou in Canada (e.g., Seip 1992, Hins et al. 2009, Briand et al. 2009, Mayor et al. 2009, Faille et al. 2010). In the interest of caribou conservation, more research programs should focus on the mechanisms that drive bear and wolf predation and prey-switching, and more specifically, on what role various elements of forest disturbance play with regard to increased wolf and bear predation on caribou.

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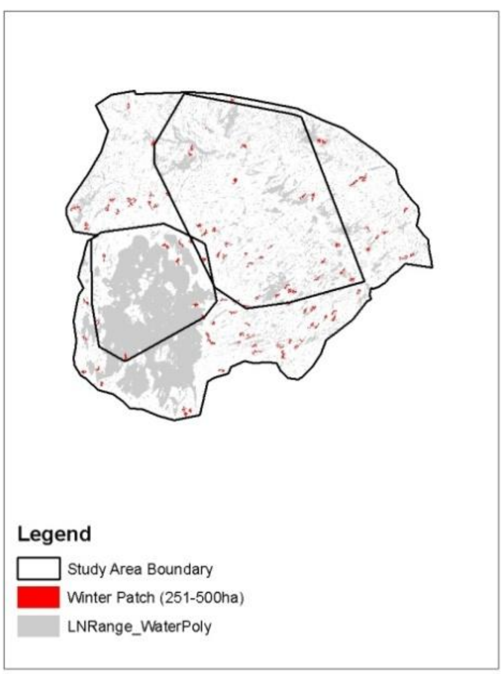
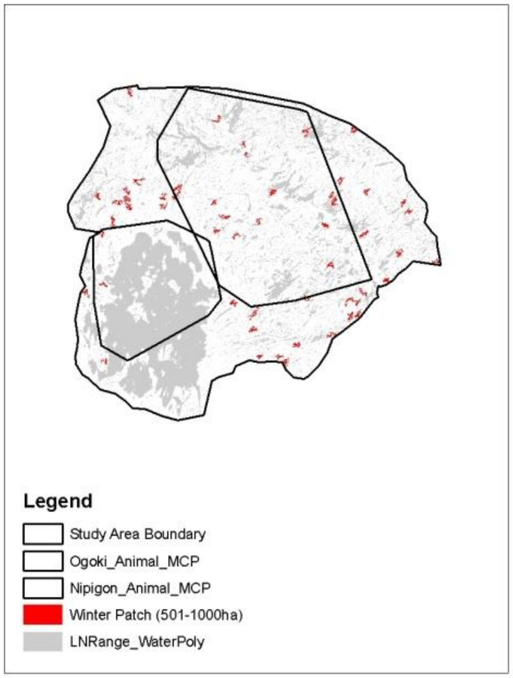
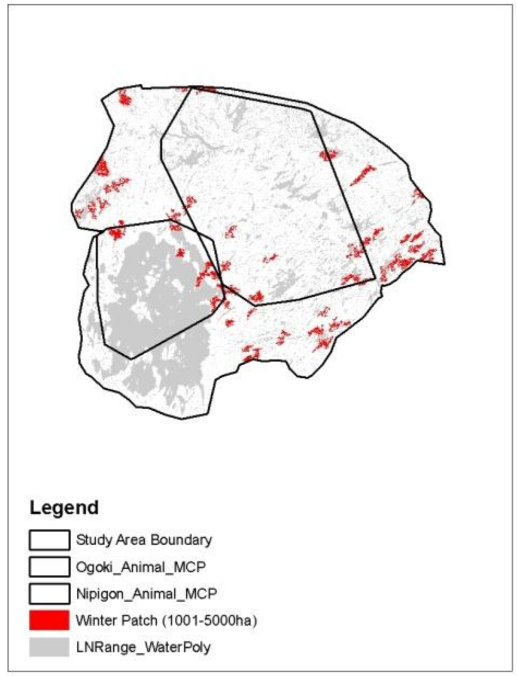
APPENDIX 1.

Winter habitat patch sizes as delineated by the OLT



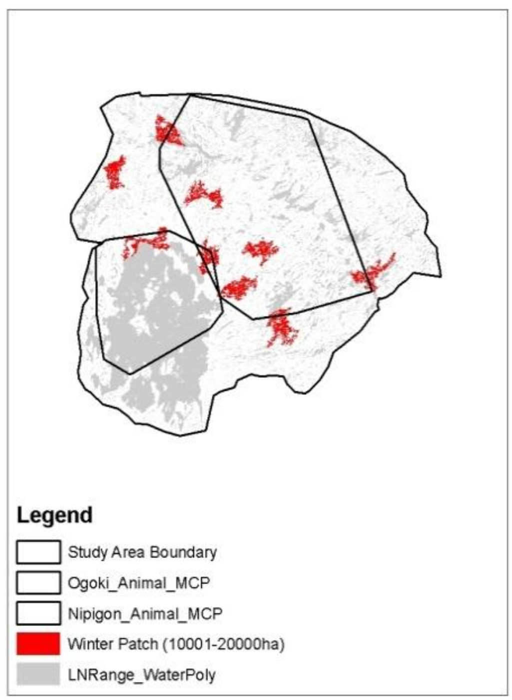
a) b)


Legend
Study Area Boundary
Ogoki_Animal_MCP
Nipigon_Animal_MCP
Winter Patch (501-1000ha)
LNRange_WaterPoly


Legend
Study Area Boundary
Ogoki_Animal_MCP
Nipigon_Animal_MCP
Winter Patch (1001-5000ha)
LNRange_WaterPoly

c)

d)


Legend
Study Area Boundary
Ogoki_Animal_MCP
Nipigon_Animal_MCP
Winter Patch (10001-20000ha)
LNRange_WaterPoly

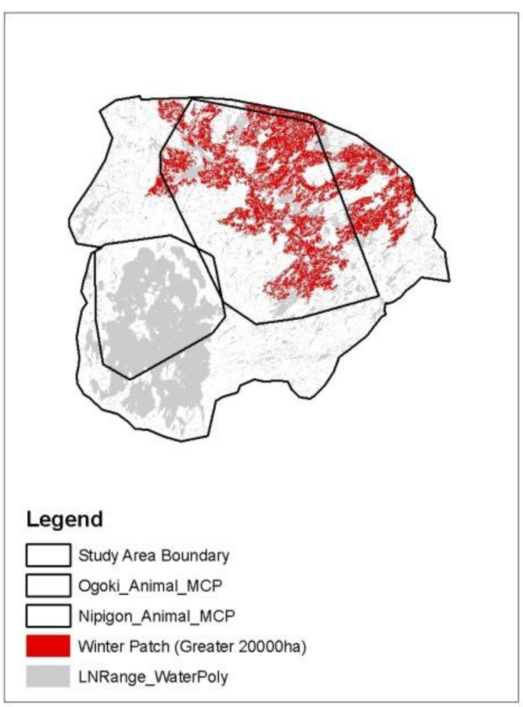
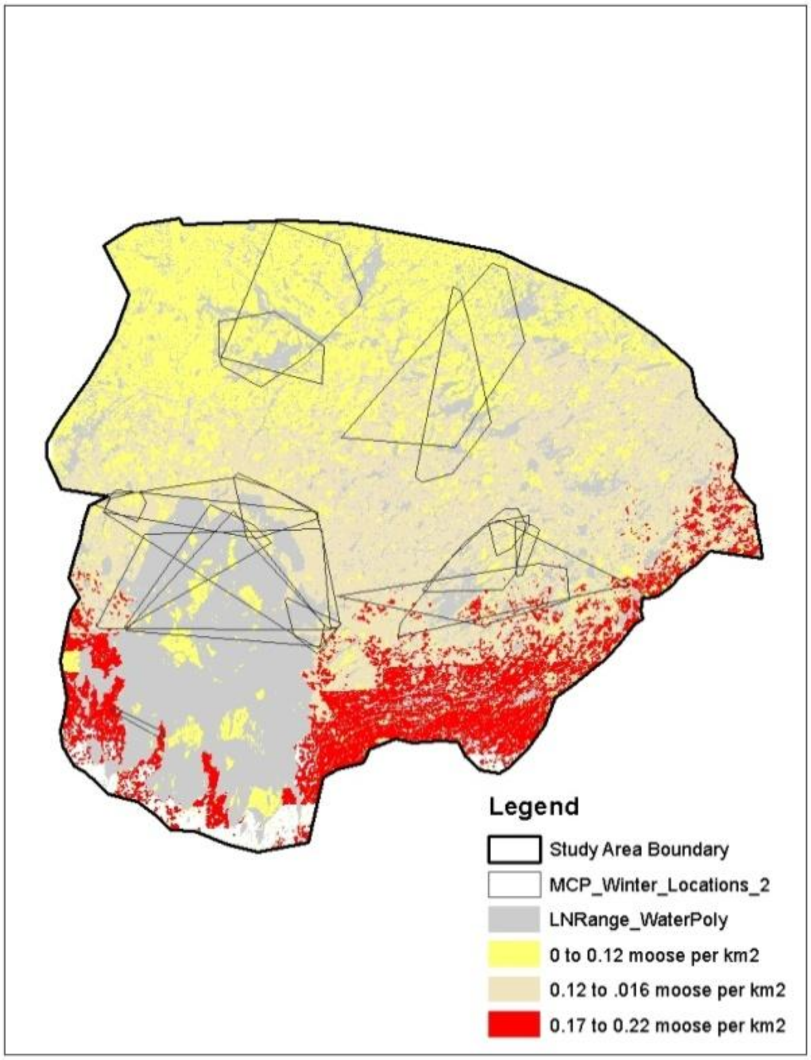

Legend
Study Area Boundary
Ogoki_Animal_MCP
Nipigon_Animal_MCP
Winter Patch (Greater 20000ha)
LNRange_WaterPoly

Fig. 4. Location and distribution of winter habitat patches in the Lake Nipigon and Ogoki study areas at seven scales: a) 1–250 ha, b) 251–500 ha, c) 501–1,000 ha, d) 1,001–5,000 ha, e) 5,001–10,000 ha, f) 10,001–20,000 ha, and g) >20,000 ha.

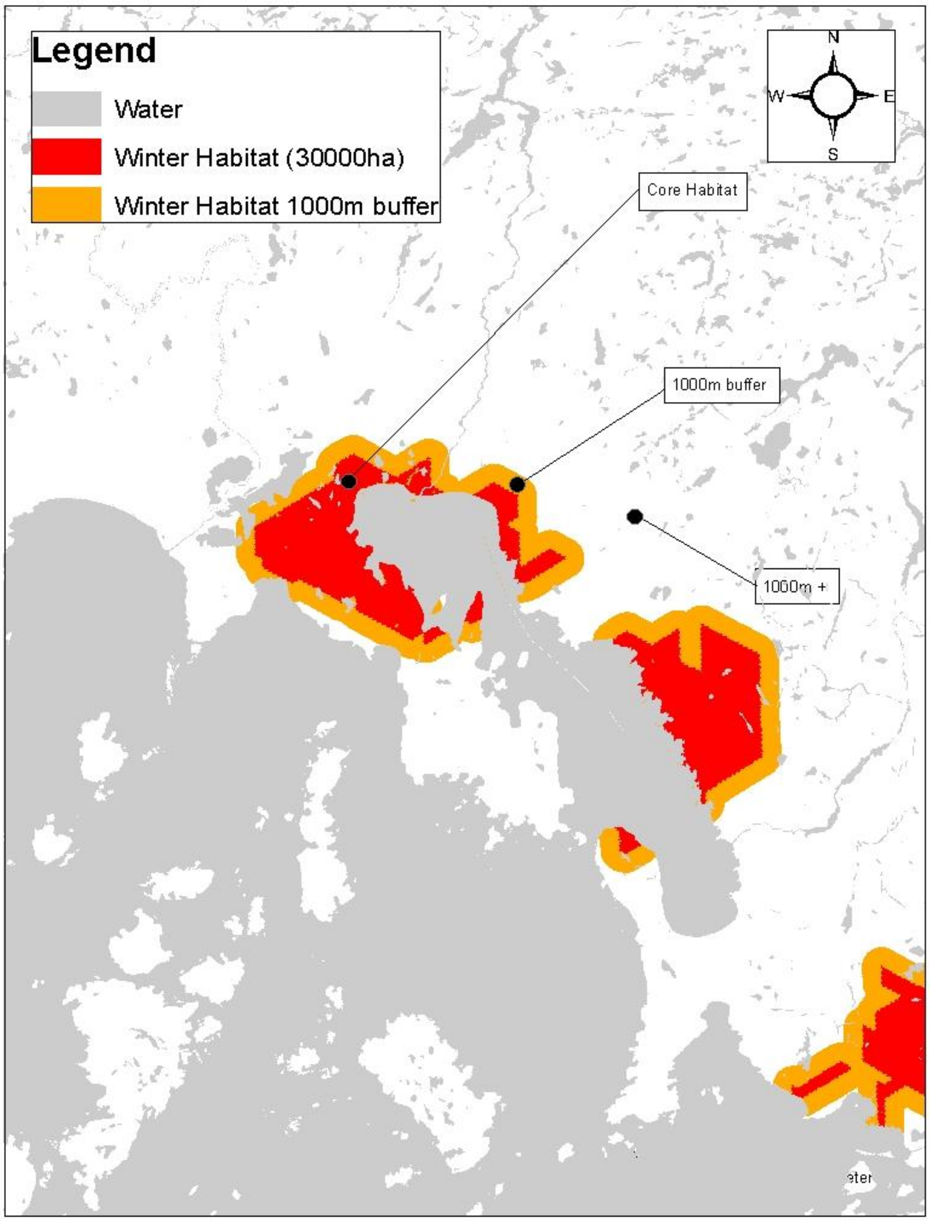
APPENDIX 2

Predicted moose densities as delineated by the OLT


Legend
Study Area Boundary
MCP_Winter_Locations_2
LNRange_WaterPoly
0 to 0.12 moose per km2
0.12 to .016 moose per km2
0.17 to 0.22 moose per km2

APPENDIX 3.

Example of three categories of winter habitat


Legend
Water
Winter Habitat (30000ha)
Winter Habitat 1000m buffer
N
W
E
S
Core Habitat
1000m buffer
1000m +