# INVESTIGATION OF WINTER HABITAT SELECTION BY WOODLAND CARIBOU IN RELATION TO FORAGE ABUNDANCE AND SNOW ACCUMULATION

by

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# ABSTRACT

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Imprecision and misclassification of land cover types are two issues commonly encountered in habitat selection studies using satellite land cover classifications and telemetry data. Here, the utility of broad land cover types is explored in a study of habitat selection by woodland caribou (*Rangifer tarandus caribou*). Broad land cover types have potential to reduce the misclassification error associated with finer land cover types, while remaining relevant to the factors influencing habitat selection in the species of interest. Lichen abundance and snow accumulation are two factors important in explaining the selection of land cover types by woodland caribou in winter, and they are used here to predict the probability of occupation by caribou of land cover types in three regions of the boreal forest in Eastern Canada. Land cover types were initially categorized using Landsat EOSD land cover data, and field surveys were conducted to measure terrestrial and arboreal lichen abundance in each land cover type. The relative accumulation of snow was modeled for land cover types using documented patterns of snow distribution in the boreal forest as well as data collected in the Greater Gros Morne Ecosystem, Newfoundland, and the Côte-Nord region, Quebec. Subsequently, land cover types were collapsed into three (dense forest, sparse-open forest, and non forest) that reflected differences in lichen abundance and snow accumulation while reducing misclassification errors. Resource selection functions were estimated using logistic regression where GPS and Argos satellite telemetry data existed for caribou in the Greater Gros Morne Ecosystem and Middle Ridge regions of Newfoundland and the Côte-Nord region of Quebec. In all regions, telemetry-monitored caribou selected non-forested areas, where lichen abundance was high and snow accumulation was low, more than expected by chance. The similarities in selection of non-forested areas across regions despite variation in landscape composition indicates that there are congruencies both in the factors influencing winter habitat selection and in the relative value of land cover types on a given landscape. These findings support the argument that resource selection functions with parameters based on broadly defined land cover types are applicable among different regions of caribou occurrence and are therefore a valuable tool for understanding patterns of space use in caribou throughout the boreal forest.

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# INTRODUCTION

For declining or threatened populations of wildlife, the identification of important habitat and the knowledge of how and why animals use the habitat available to them are two key components to assisting their recovery. As for many species, successful recovery of woodland caribou (*Rangifer tarandus caribou*), a declining and threatened subspecies throughout most of Canada's boreal forest (Environment Canada 2012; Festa-Bianchet et al. 2011), depends on an understanding of *why* animals select a particular habitat or land cover type. This understanding facilitates the identification of important land cover types on a broader scale than is possible through sole examination of *how* animals select land cover types, which varies with local factors such as the availability and composition of land cover types on the landscape (Lesmerises et al. 2013; Osko et al. 2004). For the purpose of this thesis, "habitat" can be considered as a collective term referring to the sum of the "land cover types" that make up the landscape.

This thesis explores the simplification of land cover types as an approach to gaining meaningful and valuable insight into habitat selection in situations where available data are imperfect, as is often the case in studies of resource selection that rely on imprecise satellite telemetry data and land cover classifications (Boan et al. 2013; Aarts et al. 2008). Often, land classifications do not consist of land cover types relevant to the species of interest, and in addition there are often land cover types that have a higher chance of being incorrectly identified by remote sensing (Kerr and Ostrovsky 2003). By simplifying the factors influencing habitat selection to their fundamentals, it may be possible to reduce the number of land cover types that are investigated to a number that balances the accuracy of each land cover type with its potential relevancy to factors underlying habitat selection. In addition, the use of broad, land cover types may facilitate the comparability and understanding of habitat selection among multiple regions throughout the range of a species.

For the case of caribou in the absence of predators, two overarching factors are known to influence habitat selection during winter: forage abundance, and the relative distribution and accumulation of snow (Mayor et al. 2009; Brown and Theberge 1990; Bergerud 1972). Where caribou predators such as gray wolves (*Canis lupus*) occur, and where anthropogenic changes to the landscape are significant, these factors could also be considered in the choice of which land cover types to investigate as they have been shown to influence caribou behaviour (Latombe et al. 2013; Courbin et al. in press). However, this thesis treats the predator free case in two regions of Newfoundland that are protected from logging where caribou are assumed to select habitat based on the fitness benefits of the forage available to them in different land cover types. An ideal free distribution is assumed, because while there is evidence that individuals may compete for resources at the feeding site scale (Schaefer and Mahoney 2001; Barrette and Vandal 1986), it seems unlikely that they compete at the scale of the land cover type as they are frequently observed in groups occupying a single land cover type.

The broad scale applicability of a land cover classification that includes fewer, relevant land cover types can be assessed by comparing patterns of habitat selection in regions where the available proportions of land cover types on the landscape varies. By including a region in Québec where wolves are present, this thesis investigated whether predictions of habitat selection based on forage-related factors are still relevant to caribou in predated systems.

## Winter: a critical period for caribou

Winter is recognized as a nutrient-deficient season for northern ungulates, including all *Rangifer tarandus* subspecies (Post and Stenseth 1999; Skogland 1985; Telfer and Kelsall 1984). The importance of adequate winter forage for caribou is apparent through documented relationships between population viability and winter severity, winter diet quality, and reproductive success (Tveraa et al. 2003; Heggberget et al. 2002; Ferguson and Mahoney 1991; Skogland 1985; White 1983). Terrestrial and arboreal lichens are typically the primary winter forage items of caribou, and the easily-metabolized sugars and carbohydrates they contain allow caribou to offset the energetic costs of thermoregulation, locomotion, and foraging in deep snow (Klein 1990, Fancy and White 1987, Holleman et al. 1979).

## Snow and lichen: two factors influencing habitat selection

Snow is an implicit part of northern ecosystems in winter, and its accumulation and distribution is recognized as a factor affecting habitat selection by caribou (Roturier 2011; Tucker et al. 1991; Brown and Theberge 1990; Fancy and White 1987; Bergerud 1974; Pruitt 1959). Caribou typically select land cover types with shallow snow, where cratering for terrestrial lichens is less energy intensive; however, deep snow also creates opportunities to access arboreal lichens otherwise too high to reach (Mayor et al. 2007; Tucker et al. 1991; Antifeau 1987). Most studies of caribou behaviour in winter acknowledge the importance of snow conditions (Rettie and Messier 2000; Tucker et al. 1991; Brown and Theberge 1990; Rominger and Oldemeyer 1990), but general models of snow distribution relevant to habitat selection by caribou have been underutilized in the literature despite their predictive potential (Roturier and Roué 2009). Reindeer (*Rangifer tarandus*) herders in Sweden have been using patterns of snow distribution as a component of winter range evaluation for centuries. The Swedish experience suggests that a model that makes predictions on snow distribution might be useful in the identification of important land cover types for caribou (Roturier 2011; Roturier and Roué 2009). Courbin et al. (2009) measured the depth of snow throughout the winter in a number of land cover types in the Côte-Nord region of Québec to create an index of relative snow depth. This model provides a sound basis which could be easily extended to areas where data on snow depth is unavailable, as snow distributes predictably according to forest characteristics such as overstory canopy closure, stem density, and wind exposure, and for which data are available through remote sensing or forest resource inventories (Pomeroy and Gray 1995, Swanson 1988).

Just as the distribution of snow can be predicted using features of a boreal forest, the distribution of terrestrial and arboreal lichens can be generalized based on a few ecological factors important to their growth, such as light, moisture, and time to grow (Boan et al. 2011; Lesmerises et al. 2011; Ahti and Hepburn 1967). Brown and Theberge (1990) suggest that lichen should be distributed according to general landscape characteristics, as caribou are able to recognize areas of lichen occurrence based solely on above-snow habitat features in areas where mean snow depth reached almost 2 m. Perhaps the strongest predictor of lichen presence is overstory canopy closure: both terrestrial and arboreal lichens are photophilic and do not flourish under dense overstories (Ahti and Hepburn 1967). Trees in open and sparse forests are most likely to support arboreal lichen, especially on sun-exposed forest edges and in their crowns, and as overstory canopy closure decreases from sparse forest to non-forest areas, terrestrial lichens become more abundant. Another factor influencing lichen abundance is humidity; where atmospheric humidity is sufficiently high terrestrial lichens can occupy a wide variety of poor soils such as drained peatlands, sandy uplands, and barren or rocky areas (Ahti and Hepburn 1967, Ahti 1959).

### How important are lichen abundance and snow accumulation as factors driving habitat selection?

Caribou do not forage exclusively on lichens during the winter; they also forage on dead sedges, grasses, and deciduous shrubs (Bergerud 1972). However, this part of the diet is generally thought to supplement lichen, which they can consume at rates of up to 5 kg per day (Kumpula et al. 2000; Holleman et al. 1979). Terrestrial lichen species commonly consumed are *Cladonia mitis*, *C. rangerifera*, *C. alpestris*, and *Stereocaulon* spp., and are generally consumed in the proportion that they occur (Bergerud 1974; Ahti 1959). Arboreal lichen species commonly consumed include *Alectoria jubota* and *Bryoria* spp., although arboreal species are generally less nutritious and terrestrial lichens are thought to be preferred where both are available (Bergerud 1974; Ahti and Hepburn 1967; Ahti 1959). There probably exists a tradeoff between nutritional gain and ease of access where snow accumulation is extreme. For example, in deep snow cover, cratering for terrestrial lichen is very energy intensive, while in the same conditions, arboreal lichens become relatively closer to the ground (Antifeau 1987).

The relative importance of snow accumulation and forage abundance in habitat selection by caribou is not well explored. The question is further complicated by variance in snowfall regimes across the range of caribou, as the increased foraging cost related to deep snow probably depends on local weather patterns and is likely more prevalent in some regions than others. Some researchers have proposed threshold snow depths at which caribou stop cratering for terrestrial lichens and increase their intake of arboreal lichens (Brown and Theberge 1990; Pruitt 1959). These reported threshold snow depths range between 50 and 125 cm (Kumpula 2000; Farnell et al. 1996; Brown and Theberge 1990; Rominger and Oldemeyer 1990; Pruitt 1959), with the large variation suggesting that these thresholds might be dependent on local snow conditions as well as the overall abundance of terrestrial and arboreal lichens. For example, if terrestrial lichen resources are poor, caribou may switch to eating arboreal lichens even at low snow depths. Conversely, if arboreal lichens resources are poor, caribou may continue feeding on terrestrial lichens even when snow is very deep.

With regard to the relative importance of forage abundance and snow conditions in habitat selection by caribou, in the absence of predators it seems reasonable to expect that forage abundance is the primary factor driving the selection of land cover types as forage is the resource being sought after in decisions of which land cover types to occupy. Snow accumulation can be thought of as a cost to foraging that varies according to each land cover type, and as such plays a secondary role in driving habitat selection that may become increasingly important during periods of peak snow accumulation when costs of foraging negate the energy gained.

## Bridging the gap: The potential for inter-regional differences in landscape configuration to reveal common and important land cover types

Examining patterns of habitat selection in multiple regions has important implications for understanding how the composition or proportion of land cover types on the landscape influences their selection by animals. The configuration, or spatial occurrence, of land cover types on the landscape is known to influence movement patterns of caribou, as is seen in migrations between areas to make use of resources that are important or available seasonally (Wittmer et al. 2005; Schmelzer and Otto 2003; Mahoney and Schaefer 2002). Even in areas where caribou are considered sedentary some studies have identified seasonal movement patterns that indicate caribou alter their use of space seasonally to access different resources (Rudolph 2011; Ferguson and Elkie 2004).

While the composition and configuration of the landscape probably explains the variation in seasonal movement patterns among regions of caribou occurrence, there are likely similarities in the land cover types being utilized on a given landscape due to the ecological functions they serve. Following this logic, a multi-region comparison of the selection of land cover types where the availability and configuration of land cover types on the landscape differs should lead to a better understanding of the features being selected on a given winter range, and provide insight into land cover types commonly important to caribou throughout their range.

## In practice: Using resource selection functions to investigate habitat selection by animals

Resource selection functions have become a ubiquitous tool in ecological literature for studies of resource selection by animals (McLoughlin et al. 2010). In their most popular format, dubbed the use-availability design by Manly et al. (2002), resource selection functions compare resource units that were used by animals (typically telemetry locations) to resource units assumed to be available to animals but not known to be used or unused (typically randomly selected locations within the home range of an individual or population). An examination of the coefficients estimated by logistic regression for each resource type allows the researcher to interpret the relative selection of land cover types by the animals in the study sample.

While resource selection functions allow statistical insight into complex ecological systems, many issues have been raised about the nature of the data used in their estimation as well as the assumptions imposed by statistical design. Primarily, there are inherent assumptions of accuracy in satellite telemetry data, as well as the land cover data from which resource units are derived (Fieberg et al. 2010; Aarts et al. 2008). In addition, the statistical frameworks used to estimate the resource selection functions carry their own sets of assumptions such as independence of locations, which if violated may introduce uncertainty in the interpretation of the resulting coefficients (Beyer et al. 2010; Boyce et al. 2002).

The questions raised regarding the validity and reliability of resource selection functions given the potentially unrealistic assumptions underlying their statistical frameworks are typical of the growing pains associated with any developing technology.

As such, methodologies are constantly being developed and updated to address areas where uncertainties arise in resource selection analyses. For example, Gillies et al. (2006) propose that the inclusion of random effects can account for non-independence and unbalance in telemetry data, and Boyce (2006) presents a cross-validation method useful for evaluating the robustness of model coefficients. Other authors propose methods for dealing with autocorrelation in telemetry data, as well as guidelines for the construction of hierarchical regression models, and the interpretation of resulting model coefficients (Northrup et al. 2013; Wagner et al. 2011; Fieberg et al. 2010). As the toolbox for resource selection models becomes increasingly comprehensive, the ecological research community will undoubtedly benefit from increased statistical certainty and a greater ability to investigate and understand resource selection by animals.

An integral component to resource selection models that is often overlooked is the classification of land cover types to which telemetry locations are related (Aarts et al. 2008). In doing so, researchers must make decisions regarding how many land cover types to investigate and how they should be defined, as the most meaningful interpretations of habitat selection should reflect the choices perceived by animals with regard to what constitutes a land cover type as well as the relationship between fitness and occupation of a particular land cover type (Knight and Morris 1996). Unfortunately, finding appropriate land cover data that is relevant to the ecological questions posed by a study is challenging, especially when study animals are wide-ranging and occur in isolated areas, as is the case for caribou (McLaren and Mahoney 2001). In these instances, researchers are often forced to trade off biological relevance in land cover classification for availability of land cover data that matches the spatial occurrence of the species of interest, despite being developed for an unrelated purpose (Aarts et al. 2008).

Many studies of habitat selection in caribou investigate selection of between 5 and 12 land cover categories (Table 1). While potentially providing precision in a local area as to the importance of land cover types, the likelihood that land cover types will remain relevant in another area decreases as more types are considered. In addition, there is a potential to misinterpret the relative importance of selected land cover types through the inclusion of irrelevant ones, as resource selection coefficients depend on the definition of what is considered available to animals at any given time (Johnson 1980). Frequently, land cover types investigated in one area are defined such that they are not represented in other regions, making comparisons of resource selection studies difficult even among regions in close proximity to one another (Mosnier et al. 2003). In fact, the variation observed in the findings of habitat selection studies for caribou likely results as much from variation in the definition of the land cover types as from differences in ecological processes among regions. For example, classifications of forests by age, as in Hins et al. (2009), are not comparable to classifications by dominant species or timber volume, as in Terry et al. (2000), regardless of locality. The potential applicability of land cover types among regions thus depends largely on the decision of how to best distill land cover types into a few categories that are ecologically relevant and found throughout the boreal forest.

This study investigates just three cover types – dense forest, sparse-open forest, and non-forest – by identifying criteria known to influence choices of habitat selection for caribou (forage abundance and the accumulation and distribution of snow), and then

Table 1. Number of land cover categories examined in previous studies of resource selection by woodland caribou during winter. Also included are the study area and land cover types selected and avoided by caribou.

| Authors | Study area | Number of land cover types | Selected | Avoided |
|---|---|---|---|---|
| Moreau et al. 2012 | Côte-Nord, QC | 8 | Open conifer forest with lichen; closed canopy mature conifer forest | Lake; mixed or deciduous forest; regenerating clearcut; recent clearcut; road |
| Briand et al. 2009 | Saguenay, QC | 5 | Open lichen woodland; > 80 year-old spruce forest | 40-80 year-old spruce forest; > 40 year-old fir forest |
| Hins et al. 2009 | Saguenay, QC | 10 | Open lichen woodland | Road; water; regenerating forest; 0-5 year-old clearcut |
| Fauteux et al. 2009 | Saguenay, QC | 5 | Mature forest; barren | Road |
| O'Brien et al. 2006 | Owl Lake, MN and Kississing, MN | 9 | Jack pine dominated; sparsely treed rock; mature conifer upland | Young conifer wetland; water; recent burn or harvest |
| Mosnier et al. 2003 | Gaspésie, QC | 5 | Barren | Mature fir forest |
| Johnson et al. 2003 | Northern Rockies, BC | 13 | Alpine little vegetation; pine terrace | n/a |
| Terry et al. 2000 | Central Rockies, BC | 6 | Subalpine fir forest; low basal area | Cedar/hemlock/spruce forest |

measuring these criteria in parent land cover types which were then collapsed to reflect the greatest distinctions between them while attempting to mitigate misclassification errors associated with some land cover types. Landsat EOSD (Earth Observation for Sustainable Development of Forests; Wulder et al. 2003) was used to define land cover types because it was developed with overstory canopy closure as a criterion, and as such the base categories were conducive to combinations that had biological relevance to caribou. In addition, EOSD was developed nation-wide using a standard methodology that lent confidence in identification of similar land cover types in different landscapes, pixel size matched the scale of investigation, and the breakpoints for land cover types reflect soil regimes and gross forest characteristics that should be less susceptible to outdating due to forest succession than other commonly used land cover data such as forest resource inventories that are developed according to seral stages.

## Study Objectives

With the overarching goals of understanding winter habitat selection by caribou and assisting in their recovery, the objectives of this thesis are as follows:

(1) Characterize the boreal forest into land cover types that reflect broad differences in the abundance of terrestrial and arboreal lichen as well as the accumulation of snow that are relevant to woodland caribou. This will be accomplished by measuring lichen abundance and snow accumulation while groundtruthing parent land cover types from a Landsat land cover classification. Parent land cover types will be collapsed into fewer land cover types that reflect the greatest differences

in relative snow accumulation and lichen abundance while minimizing misclassification error. Predictions are as follows:

- i. Overstory canopy closure predicts the greatest distinction in lichen abundance and snow accumulation, and is the best available criterion for collapsing land cover types into three: Dense forest, sparse-open forest, and non-forest.
- ii. Terrestrial lichen occurs in highest abundance in non-forested areas, in lesser abundance in sparse-open forest, and in least abundance in dense forest.
- iii. Arboreal lichen occurs in highest abundance in sparse-open forest, in lesser abundance in dense forest, and in least abundance in non-forested areas.
- iv. Snow accumulates most in sparse-open forest, to a lesser degree in dense forest, and least in non-forested areas.

(2) Compare among three regions the relative selection of land cover types by caribou in their winter ranges. The selection of the three land cover types (dense forest, sparse-open forest, and non-forested areas) will be compared in resource selection functions based on satellite telemetry data for caribou occupying the Greater Gros Morne Ecosystem and Middle Ridge regions of Newfoundland, and the Côte-Nord region of Québec. Assuming that the three land cover types differ most to caribou in food supply, it is predicted that relative selection of each land cover type within the landscape of the winter range will be similar among regions.

(3) Associate the pattern of habitat selection in each region with the relative abundance of lichen and accumulation and distribution of snow among land cover types as determined in Objective 1. It is predicted that common factors will explain similar patterns in habitat selection among regions.

## STUDY AREA

The majority of the current range of boreal woodland caribou lies in the Boreal Shield ecozone, an area of 1.8 million km$^2$ extending from northern Alberta to Newfoundland (Environment Canada 2012; Urquizo et al. 2000). The Boreal Shield is characterized by long, cold winters and short cool summers, with an average of 60-100 frost-free d/y. Soils are thin and acidic as a result of repeated glaciations, and glacial till and exposed bedrock are common. Conifer forests make up roughly 85% of the ecozone, while the remainder is a mixture of non-forested areas consisting of bogs, fens, and marshes in lowland areas and heath barrens at higher elevations (Urquizo et al. 2000; Ecological Stratification Working Group 1996). Telemetry data for woodland caribou are increasingly collected across the ecozone as a result of research projects aimed at understanding habitat selection by caribou. Three regions were chosen within the Boreal Shield for their variation in landscape configuration and composition of land cover types with the aim of testing the applicability of broadly characterized land cover types for cross-region robustness in relation to factors driving habitat selection: the Greater Gros Morne Ecosystem in western Newfoundland, Middle Ridge in central Newfoundland, and the Côte-Nord region in northeastern Québec (Figure 1).

The average temperature, precipitation, and other abiotic characteristics of each region are summarized in Table 2, while Table 3 summarizes the land cover types found in the regions as their average occurrence in individual home range core areas (see Methods for details on home range core delineation) as well as the disturbance and predation regimes for each region. Details regarding landscape configuration and common plant species, caribou ecology, and telemetry history in each region are summarized below.

### Greater Gros Morne Ecosystem

The Greater Gros Morne Ecosystem is comprised of three prominent ecoregions that differ in elevation and maritime exposure in and around Gros Morne National Park (GMNP). The Coastal Plain is situated on the west coast of Newfoundland and is part of the larger Northern Peninsula ecoregion (Ecological Stratification Working Group 1996). Inland and adjacent to the Coastal Plain is the Long Range Mountains ecoregion, whose eastern slopes form the boundary to GMNP. Further inland still is the Humber River valley in the Central Newfoundland ecoregion, which forms the eastern limit of the Greater Gros Morne Ecosystem.

From 1993-1998, GMNP conducted a study of caribou in the Greater Gros Morne Ecosystem (Mahoney et al. 2001). The study revealed an annual migration from summer range in the Long Range mountains to two winter ranges: ~80% of collared animals wintered on the Coastal Plain, while ~20% wintered 50 km inland in the Humber River valley. The study took place at a time when caribou populations were at a peak and were

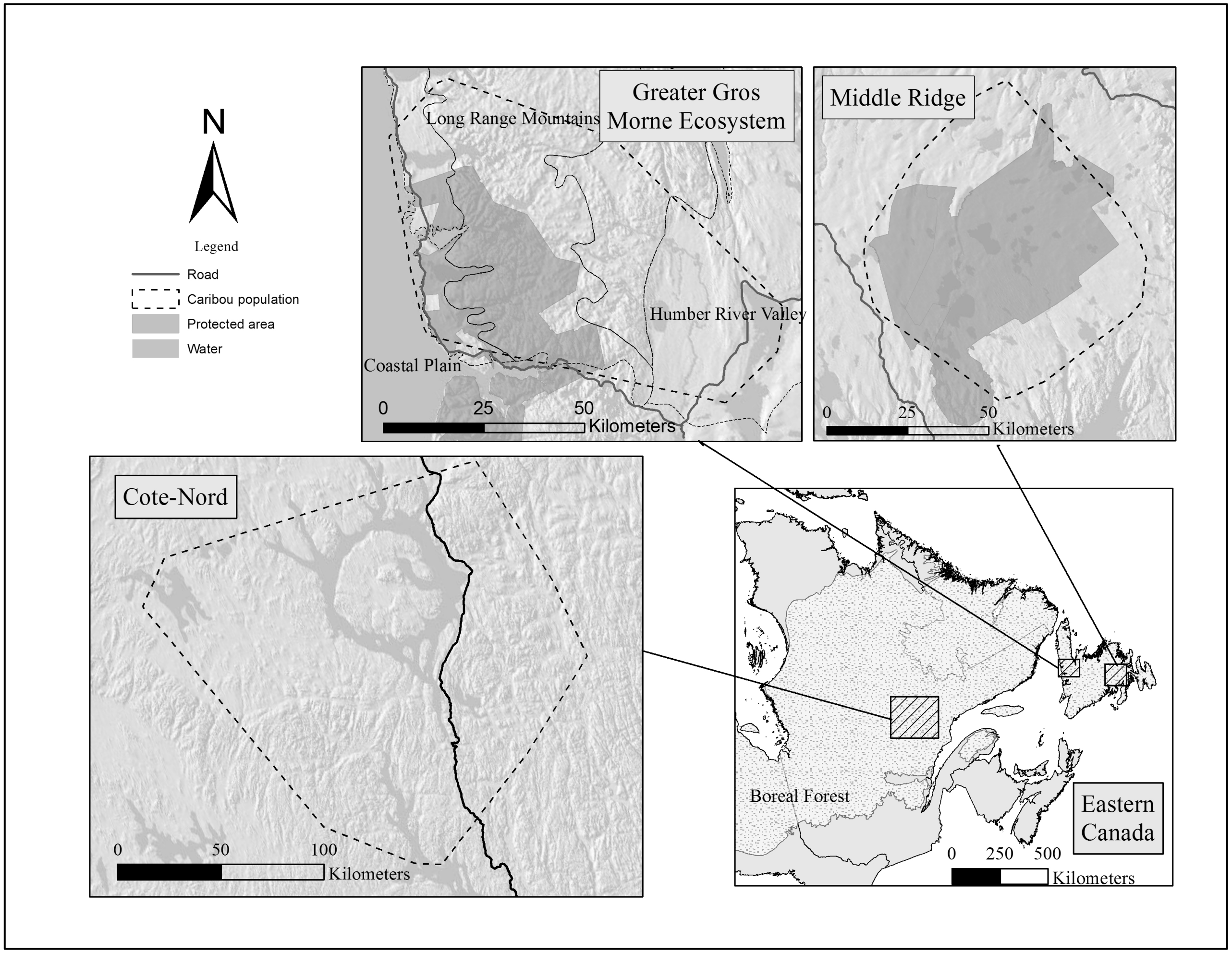

Figure 1. Map displaying the three regions where caribou data were collected; the Greater Gros Morne Ecosystem and Middle Ridge in Newfoundland, and the Côte-Nord region in Quebec.

Table 2. Summary of abiotic factors characterizing study regions in Newfoundland and Québec. Area occupied by caribou was estimated from the total area occupied by all collared caribou. Mean winter temperature was derived from climate normals from November through February (Ecological Stratification Working Group 1996).

| | Greater Gros Morne Ecosystem | | | | |
|---|---|---|---|---|---|
| | Coastal Plain | Long Range Mountains | Humber River | Middle Ridge | Côte-Nord |
| Area occupied by caribou (km$^2$) | 900 | 1,000 | 1,200 | 10,000 | 18,500 |
| Mean elevation (m asl) | 125 | 550 | 300 | 400 | 400 |
| Mean winter temperature (ºC) | −4.5 | −4.0 | −3.5 | −1.0 | −12.5 |
| Annual precipitation (cm) | 100-110 | 100-140 | 100-130 | 120-160 | 80-100 |
| Winter snow depth (m) | 0.5-1.0 | >2.0 | 1.0 | 0.5-1.0 | 1.0-1.5 |

Table 3. Summary of proportion of land cover types (% ± SE), disturbance regimes, and winter predator presence for caribou winter ranges in the Newfoundland (Coastal Plain n=31; Humber River n=5; Middle Ridge n=49) and Québec (n=43) study regions. Timber harvest refers to total proportion of the landscape consisting of regenerating cutblocks during the collection period of caribou telemetry data.

| | Greater Gros Morne Ecosystem | | | |
|---|---|---|---|---|
| | Coastal Plain | Humber River | Middle Ridge | Côte-Nord |
| Land cover type: | | | | |
| Dense conifer/mixed wood forest | 0.11 ± 0.01 | 0.19 ± 0.04 | 0.02 ± 0.00 | 0.20 ± 0.01 |
| Sparse-open conifer/mixed wood forest | 0.43 ± 0.01 | 0.46 ± 0.04 | 0.20 ± 0.01 | 0.65 ± 0.02 |
| Non-forest | 0.31 ± 0.01 | 0.18 ± 0.03 | 0.64 ± 0.01 | 0.06 ± 0.02 |
| Water | 0.12 ± 0.02 | 0.15 ± 0.08 | 0.14 ± 0.01 | 0.10 ± 0.02 |
| Other* | 0.02 ± 0.00 | 0.01 ± 0.00 | 0.00 ± 0.00 | 0.01 ± 0.00 |
| Disturbance: | | | | |
| Insects | frequent | occasional | occasional | occasional |
| Fire | rare | occasional | frequent | rare |
| Timber harvest | <10% | 2% | none | 4% |
| Winter predators | none | none | coyotes | wolves |

considered predator-free as wolves were extirpated from Newfoundland in the early 20th century and coyotes (*Canis latrans*) were rare until the early 2000s (McGrath 2004).

The Coastal Plain is comprised of a matrix of conifer forests and raised peat bogs, with kalmia (*Kalmia angustifolia*) heath occurring in the foothills of the Long Range Mountains. Topography is generally flat with some low hills, and, due to strong prevailing winds off the Gulf of St. Lawrence, there is very little snow accumulation. Forests are stunted in wind-exposed areas, and fires are very rare (Ecological Stratification Working Group 1996). Dominant tree species are balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*), while ericaceous shrubs such as kalmia, blueberry (*Vaccinium angustifolium*), and Labrador tea (*Rhododendron groenlandicum*) are dominant in open areas (Meades and Moores 1994). Recently, overbrowsing by moose (*Alces alces*) has contributed to poor regeneration of balsam fir forests in the Coastal Plain region (Gosse et al. 2011; McLaren et al. 2004).

In contrast to the wind-swept Coastal Plain, the Humber River valley, situated in the Central Newfoundland ecoregion, is sheltered from harsh winds and is more typical of a continental boreal forest. Topography is gentle and forests of black spruce and balsam fir dominate the landscape, interspersed with raised bogs containing moss, lichen, and ericaceous shrubs (Ecological Stratification Working Group 1996). Fires occur occasionally in the Humber River valley, but the primary natural disturbance, as for the Coastal Plain, is infestations of hemlock looper (*Lambdina fiscelaria*) and spruce budworm (*Choristoneura fumiferana*). Timber harvest for the pulp and paper industry resulted in roughly 2% of the landscape consisting of regenerating cutblocks during the collection period for telemetry data. While GMNP prohibits commercial harvest, small-scale cutting for domestic use is permitted in ~10% (193 $km^2$) of the park.

## Middle Ridge

Middle Ridge is located 150 km south of Grand Falls-Windsor in the Maritime Barrens ecoregion of central Newfoundland, which extends toward the south coast of Newfoundland and the Atlantic Ocean. The landscape is characterized by rolling topography with dwarf shrub heath barrens of reindeer lichen, *Vaccinium*, *Kalmia* and *Empetrum* spp., interspersed with fen and blanket bog communities containing sedges (*Carex* spp.) and mosses. Forest patches are infrequent, but where present consist of open balsam fir and black spruce forest (Ecological Stratification Working Group 1996). Fire has historically been the primary natural disturbance, and the present barren state is a result of intense fires during the 18th and 19th centuries, combined with thin, poorly developed soils that do not support forest regeneration (Newfoundland Parks and Natural Areas Division 1990). The proximity to the Atlantic Ocean causes winter precipitation to fall as rain or snow, and snow accumulation lessens toward the coast (Tucker et al. 1991). Topography is rolling with low relief, and elevation ranges from 300-500 m. Most of the area has been protected from timber harvesting since the designation of the Bay du Nord Wilderness Reserve and neighbouring Middle Ridge Wildlife Reserve in 1990, although some forestry activity takes place directly north of these reserves in the Gander River watershed (Chubbs et al. 1993; Newfoundland Parks and Natural Areas Division 1990).

Middle Ridge is home to one of Newfoundland's largest insular populations of caribou, and telemetry studies of caribou took place from 1987-1990 as well as from

2003-2007 (Mahoney and Weir 2009; Chubbs et al. 1993) A third collaring effort has followed caribou from 2009-present (Newfoundland and Labrador Department of Environment and Conservation unpublished data). Caribou spend the summer in the northern portion of Middle Ridge, where a higher proportion of forest occurs, and migrate to a winter range ~50 km south on the barrens (Chubbs et al. 1993). The population has declined from highs in the mid 1990s by roughly half, in part due to a high rate of calf predation by black bear (*Ursus americanus*), coyote, and lynx (*Lynx canadensis*) which has resulted in 90% mortality of calves (Mahoney and Weir 2009).

### Côte-Nord

In the Côte-Nord region, the study site is located 200 km north of Baie Comeau, Québec in the vicinity of the Manicouagan reservoir. It falls within the Central Laurentian ecoregion, and is characterized by undulating topography and humid forests dominated by black spruce and balsam fir, with *Kalmia* and lichen understory (Ecological Stratification Working Group 1996). Non-forested areas are less frequent than in the Greater Gros Morne Ecosystem and Middle Ridge regions, and consist primarily of rocky outcrops with lichen, but also of occasional sandy uplands, outwash plains, and forests with an overstory canopy closure of <10%. Fires are infrequent (>250 years between burns; Côté et al. 2010; Bouchard et al. 2008), and the primary natural disturbance is from hemlock looper and spruce budworm (Ecological Stratification Working Group 1996). Timber harvest for pulp and paper is ongoing, and roughly 4% of the total landscape consists of regenerating cutblocks (Basille et al. 2012).

Caribou in the Côte-Nord region were followed from 2005-present using GPS collars (Basille et al. 2012; Courbin et al. 2009). Movement patterns are typical of continental forest-dwelling caribou in that spatially discrete summer and winter ranges for the population do not exist. The Côte-Nord region differs from both Newfoundland regions in that wolves are the primary predator during winter (Courbin et al. 2009).

## METHODS

### Land cover classification for resource selection function modeling

A 30-m resolution Landsat EOSD land cover classification was obtained for the Greater Gros Morne Ecosystem, Middle Ridge, and Côte-Nord regions. Cover classes were initially collapsed from twenty-three into seven (Table 4) in order to maximize relevancy to caribou and minimize errors due to misclassifications of Landsat imagery (Freestone Digital Consulting 2012; Table 4). After completing field surveys for lichen and groundtruthing for land cover classification accuracy (see below), land cover types were collapsed further into three (dense conifer/mixedwood forest, sparse-open conifer/mixedwood forest, and non-forested areas) which represented the best trade-off between accurate classification and distinctions among land cover types regarding terrestrial and arboreal lichen abundance, the distribution of snow, and the likely function they serve to caribou.

## Field surveys for lichen abundance by land cover type

In order to ground-truth the EOSD land cover classification and test assumptions about habitat characteristics related to the relative abundance of lichen by land cover type, field surveys were conducted from July-September 2012 to sample plots located in the Greater Gros Morne Ecosystem and Côte-Nord regions. The boundary of the sampled area was defined as the winter range of caribou in each region, or the collective extent of all individual home range core areas. In each region an equal number of sample plots (n=21) were selected for each land cover type in the initial EOSD collapse using a random point generator in ArcGIS 10 (ESRI 2011). Sample plots in the front country were stratified to between 0.5 and 3.0 km from a road or trail to enable access on foot, whereas backcountry plots in GMNP were not stratified and were accessed by helicopter and multi-day hiking. Field visits were clustered in groups of four plots (> 300 m between plots) to increase sampling efficiency, which was limited by difficult terrain, impenetrable forests, and consequently long access times. Dominant tree species were determined at each plot, and four subplots were used as points to estimate percent overstory canopy using a densiometer, and to estimate percent lateral cover using a 0.5 m by 1.0 m cover board held vertical 15 m distant to the observer (Nudds 1977). Percent cover of ground vegetation was estimated using a 1-$m^2$ quadrat in each subplot. Land cover types classified using field data were compared to those determined from EOSD to calculate the accuracy of the remotely-sensed land cover classification (Wulder et al. 2003).

Table 4. Land cover classes, their parent EOSD classes, and their descriptions.

| Land cover type | Initial grouping | EOSD class | EOSD definition (Wulder et al. 2003) |
|---|---|---|---|
| Water | Water | Water | Lakes reservoirs, rivers, streams, or salt water |
| Non-Forest | Barren | Snow/Ice | Glacier, snow, ice |
| | | Rock/Rubble | Bedrock, rubble, talus, blockfield, rubbley mine spoils, or lava beds |
| | | Exposed Land | River sediments, exposed soils, pond or lake sediments, reservoir margins, beaches, landings, burned areas, road surfaces, mudflat sediments, cutbanks, moraines, gravel pits, tailings, railway surfaces, buildings and parking, or other non-vegetated surfaces. |
| | Herb/Low Shrub | Bryoids | Bryophytes (mosses, liverworts, and hornworts) and lichen (foliose or fruticose; not crustose); minimum of 20% ground cover or one-third of total vegetation must be a bryophyte or lichen. |
| | | Herb | Vascular plant without woody stem (grasses, crops, forbs, gramminoids); minimum of 20% ground cover or one-third of total vegetation must be herb. |
| | | Shrub Low | At least 20% ground cover which is at least one-third shrub; average shrub height less than 2 m. |
| | Wetland/Tall Shrub | Shrub Tall | At least 20% ground cover which is at least one-third shrub; average shrub height greater than or equal to 2 m. |
| | | Wetland Treed | Land with a water table near/at/above soil surface for enough time to promote wetland or aquatic processes; the majority of vegetation is coniferous, broadleaf, or mixed wood. |
| | | Wetland Shrub | Land with a water table near/at/above soil surface for enough time to promote wetland or aquatic processes; the majority of vegetation is tall, low, or a mixture of tall and low shrub. |
| | | Wetland Herb | Land with a water table near/at/above soil surface for enough time to promote wetland or aquatic processes; the majority of vegetation is herb. |

Table 4.
Continued

| Land cover type | Initial grouping | EOSD class | EOSD definition (Wulder et al. 2003) |
|---|---|---|---|
| Sparse-Open Conifer/Mixedwood Forest | Sparse Conifer/Mixedwood Forest | Mixedwood Sparse | Mixedwood Sparse: 10-25% crown closure; neither coniferous nor broadleaf tree account for 75% or more of total basal area. |
| | | Coniferous Sparse | 10-25% crown closure; coniferous trees are 75% or more of total basal area. |
| | | Mixedwood Open | 26-60% crown closure; neither coniferous nor broadleaf tree account for 75% or more of total basal area. |
| | Open Conifer/Mixedwood Forest | Coniferous Open | 26-60% crown closure; coniferous trees are 75% or more of total basal area. |
| | | Mixedwood Dense | Mixedwood Dense: Greater than 60% crown closure; neither coniferous nor broadleaf tree account for 75% or more of total basal area. |
| Dense Conifer/Mixedwood Forest | Dense Conifer/Mixedwood Forest | Coniferous Dense | Greater than 60% crown closure; coniferous trees are 75% or more of total basal area. |
| | | Broadleaf Dense | Broadleaf Dense: Greater than 60% crown closure; broadleaf trees are 75% or more of total basal area. |
| Other | Other | Broadleaf Open | 26-60% crown closure; broadleaf trees are 75% or more of total basal area. |
| | | Broadleaf Sparse | 10-25% crown closure; broadleaf trees are 75% or more of total basal area. |
| | | No Data | |
| | | Cloud | |
| | | Shadow | |

Percent cover of terrestrial lichen species was estimated at four 1-$m^2$ subplots, and the cover of arboreal lichen was measured in $cm^2$ on a random sample of trees, snags, and stumps in each plot, for which data were subsequently pooled (McMullin et al. 2011). Arboreal lichen cover was z-standardized to account for differences in the surface area sampled due to differences in the number and size of trees available to sample in each plot. Percent cover of terrestrial lichen did not conform to normality assumptions and was arc-sin transformed and ranked for analysis. Differences in lichen cover among land cover types were explored for all regions by performing analysis of variance (ANOVA) with land cover type nested within region. Significant differences for pairwise comparisons among land cover types were reported with Tukey’s post-hoc test.

### Snow distribution modeling

In GMNP, snow depths were monitored from 1994 to 1997 as part of a study of winter severity and caribou ecology (unpublished data). During this period, park staff measured snow depths every two weeks during the winter along paired transects in forested and non-forested areas at four stations located at 10, 50, 250, and 500 m above sea level. Whether differences occurred in snow depth between forest and non-forest transects was determined using a repeated-measures ANOVA. During sampling no distinction was made between dense forests and sparse-open forests. However, the relationships between overstory canopy cover and interception and sublimation of snow documented by Hedstrom and Pomeroy (1998) and Pomeroy and Gray (1995) led to the assumption that dense forests accumulate less snow than sparse-open forests.

For the Côte-Nord region, Courbin et al. (2009) modeled snow depth by establishing sample plots in twelve land cover types (Table 5) and measuring snow depth along 50-m transects once every three weeks. Coefficients of snow accumulation were derived for each cover type by comparing snow depth to that of shrub land cover, which was used as a reference category.

Table 5. Relative snow accumulation in collapsed and original (Courbin et al. 2009) land cover types in the Côte-Nord region. Coefficients are equal to the ratio of snow depth in the test land cover type to that in the reference land cover type, which was shrub.

| Land cover type (collapsed) | Relative snow accumulation | Land cover type (Courbin et al. 2009) | Relative snow accumulation |
|---|---|---|---|
| Water | 0.68 | Lake | 0.68 |
| Non-forest | 0.92 | Barren | 0.97 |
| | | Shrub | 1.00 |
| | | Barren with lichen | 0.78 |
| Dense forest | 0.97 | Dense conifer forest | 0.97 |
| Sparse-open forest | 1.06 | Conifer forest with lichen | 1.05 |
| | | Open conifer forest | 1.03 |
| | | Mixed forest | 1.12 |
| Other | 1.00 | Broadleaf forest | 1.12 |
| | | Regenerating clearcut | 1.00 |
| | | Recent clearcut | 1.00 |
| | | Road | 0.87 |

Caribou telemetry data

Telemetry location datasets for caribou in the Greater Gros Morne Ecosystem, Middle Ridge, and Côte-Nord regions were obtained from GMNP, the Newfoundland and Labrador Department of Environment and Conservation, and the Université Laval. As each dataset was collected under different circumstances and study objectives, there were a number of dissimilarities in sample size (number of individuals), collar technology, and sampling intensity (number of relocations per individual) among the three datasets.

In the Greater Gros Morne Ecosystem study, caribou locations were collected using a mixture of Argos (Service Argos, n=17), and GPS (Lotek Engineering, n=10) collars between 1993 and 1998. Capture and collaring details are described by Mahoney et al. (2001). Argos collars were programmed to attempt a fix once every 2 d, while GPS collars were programmed to attempt a fix every 3 h. Despite the difference in schedule and precision between Argos and GPS collars, the contribution of Argos collars to overall sample size resulted in the decision to keep them in the dataset. In the Middle Ridge study, locations were collected from 15 adult caribou between 2009 and 2012 using GPS collars (GPS4400M and IridiumTrack 3D; Lotek Wireless Inc., Newmarket, Ontario) programmed to attempt a fix every 1 (IridiumTrack 3D) or 5 (GPS4400M) h. Capture and collaring details are described by Lewis (2013). Caribou locations for the Côte-Nord study were collected from 15 adult caribou between 2005 and 2012 using GPS (Lotek Engineering) and Argos-GPS (Telonics Inc.) collars programmed to attempt a fix every 1-8 h. Capture and collaring details are described by Basille et al. (2012).

Inaccuracy in the telemetry locations was addressed by retaining GPS locations only if they were triangulated by three or more satellites (2-D or 3-D differential) and had an HDOP (horizontal dilution of precision) value ≤ 6 (GMNP; pre-2000 collars) or ≤ 10 (in the cases of Middle Ridge and Côte Nord post-2000 collars; Dussault et al. 2001). For Argos-collared animals, only locations of classes 2 or 3 were retained. A field-test of Argos and GPS collars conducted by GMNP indicated that GPS locations obtained by 2D and 3D differential fixes were accurate to < 30 meters when compared with a known location, and Argos collars of class 2 or 3 were accurate to within 300 meters (GMNP unpublished data; Appendices 1 and 2). GPS locations from Côte-Nord and Middle Ridge were collected using newer generation GPS and Argos-GPS collars with accuracy ≤ 25m (Giroux et al. 2012; Courbin et al. 2009; Dussault et al. 2001). Thus, two levels of accuracy, 300 m for Argos data and 30 m for GPS data, were assumed for all analyses.

Bias in home range estimation and RSF analysis resulting from too few locations for any individual was reduced by screening telemetry data after the delineation of the winter period (see below) to exclude individuals for a year when fewer than 10 locations were collected for a given winter. Of 123 home range core areas estimated, only 6 cases arose where between 10 and 20 locations were used to estimate home ranges. Given the broad land cover types being investigated and the importance of replication of individuals, these cases were deemed valuable enough to be included. The average number of locations per winter and individual was 858 for GPS collared caribou and 26 for Argos collared caribou.

### Delineation of winter season and home range core areas

Changes in movement rates of caribou have been shown to reflect seasonal transitions, as individuals migrate to make use of seasonally important resources such as occur in calving, summer and winter ranges (Basille et al. 2012; Ferguson and Elkie 2004). For this study, the winter season was defined separately for the Greater Gros Morne Ecosystem, Middle Ridge, and Côte-Nord regions, using a method developed by Rudolph and Drapeau (2012). The method employs a random-effects expectation maximization (RE-EM) regression tree model to select candidate onset dates based on inflection points between periods of high and low daily movement rates, while accounting for annual and individual variation by specifying a random intercept for each individual and nested individual-year combination. To minimize bias inflicted by varying time periods between telemetry relocations, the temporal window used to calculate movement rates was standardized by rarifying telemetry to one location per day, and excluding movement rates calculated for locations >2 d apart (Rudolph and Drapeau 2012). In this study, final onset dates for spring and winter were chosen as a singularly plausible candidate date, or the midpoint for a range of two or more plausible candidate dates, for each population studied.

Home range core areas were calculated for the winter period following the definition of Vander Wal and Rodgers (2012), such that home range cores exclude peripheries where proportional home range area begins to increase faster than the probability of use. Home range core areas were used instead of traditional home range estimators to ensure a conservative interpretation of areas used by caribou, so that subsequent samples of available resource units were not drawn from peripheral areas of the caribou home range where the proportion of land cover types occurring on the landscape might differ from the home range core and introduce bias in RSF calculations. To account for individuals using different areas in consecutive winters, home range core areas were calculated for each individual-year combination. Home range core areas were created using a fixed kernel method, and a trial and error approach was used to estimate the bandwidth parameter *h*, as this parameter is inherently subjective (Kie et al. 2010). For each home range core area, *h* was initially estimated using least-squares cross validation (LSCV). However, in some cases LSCV did not converge and produced tiny, fragmented home range core areas. For these cases, the reference value of *h* was decreased by increments of 100 until the resulting home range core area visually reflected the distribution of locations. Home range core areas were subsequently extended to include buffers of 30 m and 300 m to account for error associated with relocations from GPS and Argos collars, respectively. Calculations for season delineation and home range estimation were conducted using the statistical software R and the packages REEMtree and adehabitatHR (R Core Team 2012).

### Resource selection functions

Habitat selection by caribou was described by estimating resource selection functions in the Coastal Plain, Middle Ridge, and Côte-Nord regions for the winter period (McLoughlin et al. 2010; Manly et al. 2002). Three candidate models were compared: a simple generalized linear model with a fixed intercept for all individuals, a generalized mixed model with a random intercept specified for individual animals used to identify the individual as the sample unit and account for spatial and temporal autocorrelation between relocations as well as unbalance between numbers of locations per individual (Gillies et al. 2006), and a generalized mixed model with a random intercept as described above as well as a covariate allowing the non-forested proportion of the landscape to vary among individuals (Wagner et al. 2011). Resource units (land cover types) considered "used" were determined using telemetry locations from within the home range core area, and "available" resource units were random locations sampled within the home range core area of each individual sampled at a frequency equivalent to a ratio of 10 available units for each used unit. Available units were allowed to overlap used units. Fithian and Hastie (2012) state that the larger the ratio of available units to used units, the better the approximation of the model. Here, the choice of number of available units was also influenced by computational time, which increases with the size of the sample. Northrup et al. (2013) determined that estimates for resource selection functions converge as available units approach 10,000 samples, thus this number was used as the maximum available units per individual and year.

Each used and available location was buffered with a fixed radius of 30 m for GPS collars or 300 m for Argos collars (Visscher 2006), in order to address the potential error associated with telemetry locations and avoid isolated pixel error. For each buffered location, the land cover type occurring in the greatest proportion within the buffer was considered selected. Ties were rare (< 2% of locations), and in the case of a tie the least represented land cover type was considered selected in order to avoid under-representation of rare land cover types. Generalized linear mixed models were estimated using Laplace approximations, and all candidate models were compared using Akaike's Information Criterion corrected for finite sample sizes (AICc; Burnham and Anderson, 2002). Top candidate models for each region were validated using k-fold cross validation where k=5 (Boyce et al. 2002). Selection coefficients were presented as log-odds and interpreted only relative to other land cover types in the same region, as false-positive interpretations of selection can arise when comparing other metrics of selection such as probability of use odds-ratios when they are derived from resource selection functions estimated by logistic regression under a use-availability design (Keating and Cherry 2004). ArcGIS 10 was used to compute geospatial functions, and the statistical software R was used to calculate other statistics (R Core Team 2012; ESRI 2011).

# RESULTS

## Do land cover types contain different abundances of lichen and snow?

Dense forest and non-forested areas showed the most consistent differences across regions in lichen cover, with dense forest having significantly less terrestrial lichen cover than non-forested areas in all regions, and significantly more arboreal lichen cover in all but one region (Figure 2). Sparse-open forest tended to have an intermediate cover of both terrestrial and arboreal lichen. Generally, the Coastal Plain and Humber River regions displayed the same pattern of lichen cover, while land cover types in the Côte-Nord region had higher lichen cover overall and fewer differences among the three land cover types. As field sampling did not take place in the Middle Ridge region, relative trends in lichen cover among the land cover types were assumed to parallel the Greater Gros Morne Ecosystem, where climate patterns are similar.

The snow data collected from GMNP showed two trends: greater snow depth at higher elevation and greater snow depth on transects in forested areas compared to non-forested areas. Only at the lowest elevation (10 m above sea level) was there no difference between forested and non-forested transects in snow depth (Figure 3). The Côte-Nord snow model showed similar trends to GMNP, but with added distinction among forest types: lakes and non-forested areas had the lowest snow accumulation, followed by dense forest, and finally sparse-open forest (Table 5).

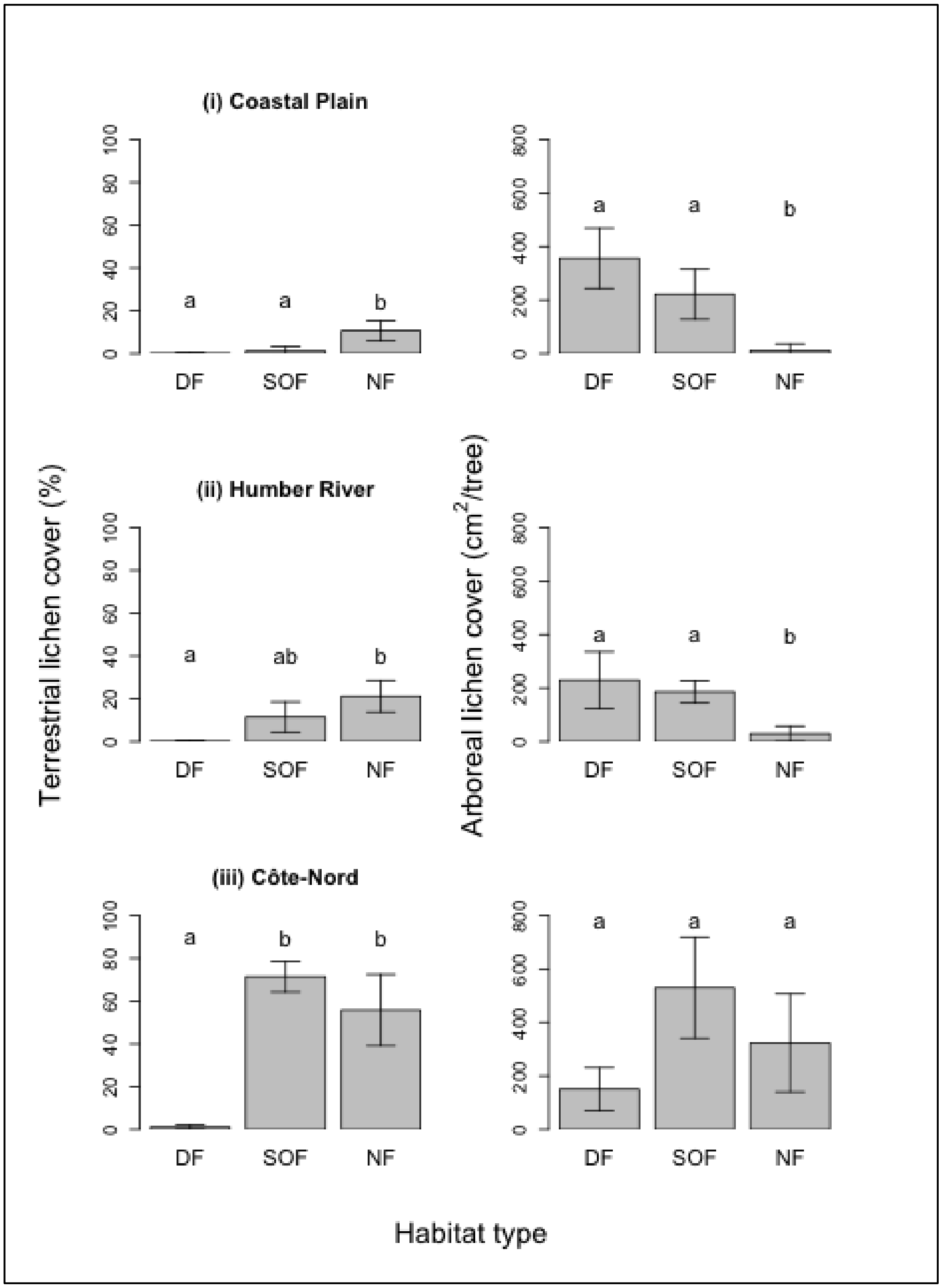

Figure 2. Mean abundance and 95% confidence intervals of terrestrial (left) and arboreal (right) lichen in three land cover types in the Coastal Plain (n=48), Humber River (n=48), and Côte-Nord (n=29) regions. Significant differences between land cover types are indicated with dissimilar letters, as determined by Tukey's post-hoc test for multiple comparisons. DF, SOF, and NF refer to dense forest, sparse-open forest, and non-forested areas, respectively.

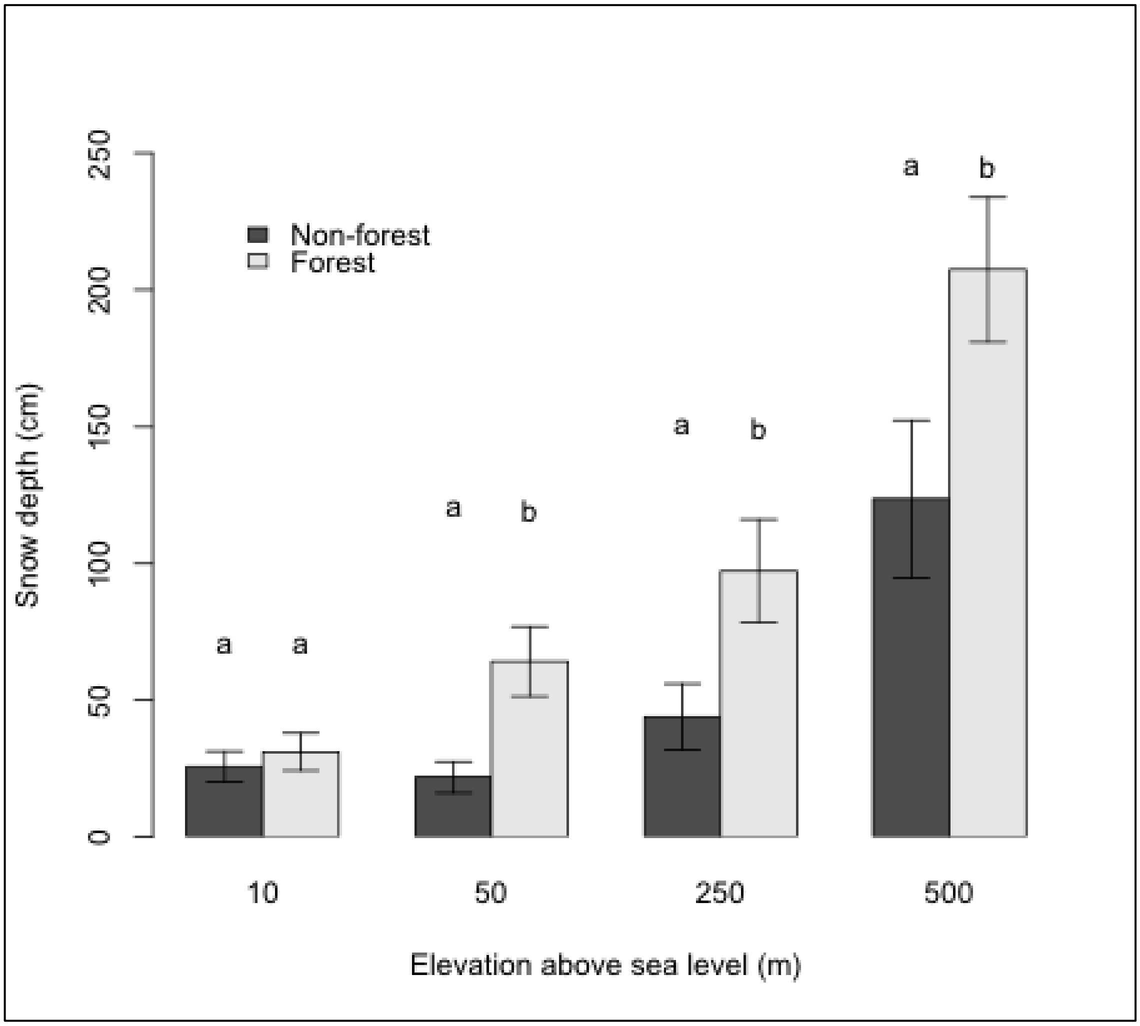

Figure 3. Mean snow depth and 95% confidence intervals for paired forested and non-forested sites (n=88) at four elevations in Gros Morne National Park. Pairwise significant differences are indicated by dissimilar letters as determined by Tukey's post-hoc test for multiple comparisons.

Regional differences in the availability and characteristics of land cover types

The composition of the landscape varied among regions, as summarized in Table 3. Land cover types varied most with regard to basal area, tree height, and lateral cover, as summarized in Table 6. Basal area in all regions was greatest in dense forest, intermediate in sparse-open forest, and least in non-forested areas ($p < 0.02$). Average tree height was taller in dense forest than sparse-open forest ($p < 0.005$), except in the

Coastal Plain region where tree height did not differ between the forested land cover types ($p = 0.96$). Average tree height in non-forested areas was significantly less than in either forested land cover type ($p < 0.001$). Lateral cover was similar in dense and sparse-open forests ($p > 0.27$), and there was significantly less lateral (shrub) cover in non-forested areas than in either forest class ($p < 0.001$) with the exception of sparse-open forest in the Côte-Nord region ($p = 0.59$). Moss, herb, sedges, and leaf litter dominated ground cover in the dense and sparse-open forest land cover types, while non-forested areas had less moss and herb cover and a greater cover of ericaceous shrubs. The Côte-Nord region differed from both the Coastal Plain and Humber River regions in that ground cover was almost exclusively moss, ericaceous shrubs, and terrestrial lichens.

### EOSD accuracy and landcover characteristics

The initial EOSD land classification was only 50% accurate overall (Table 7), while the final collapsed land classification was 72% accurate overall (Table 8). Class-specific accuracy rates were similar among regions, and were pooled. Non-forested areas and dense forest had class-specific accuracies of 89% and 84% respectively, while the sparse-open forest class frequently included non-forested areas and was only correctly classified 42% of the time (Table 8). Field visits revealed that confusion in the sparse-open forest class tended to occur where stunted or extremely sparse forests had an overstory canopy closure of <10% but had been classified as sparse-open forest (10-60% canopy closure).

Table 6. Summary of land cover characteristics for dense forest, sparse-open forest, and non-forested areas in Coastal Plain, Humber River, and Côte-Nord regions. Shown are ground cover of vegetation types (% ± SE), arboreal lichen, basal area, tree height, lateral cover, canopy cover, dominant tree species, and number of plots sampled. Dissimilar letters indicate significant differences (ANOVA and Tukey's post hoc test) among land cover types within regions.

| | Greater Gros Morne Ecosystem | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Coastal Plain | | | Humber River | | | Côte-Nord | | |
| | Dense forest | Sparse-open forest | Non-forest | Dense forest | Sparse-open forest | Non-forest | Dense forest | Sparse-open forest | Non-forest |
| Ground cover (%): | | | | | | | | | |
| Moss | $38.0 \pm 7.5_{a}$ | $28.1 \pm 7.6_{ab}$ | $14.8 \pm 3.3_{b}$ | $47.5 \pm 5.8$ | $35.4 \pm 4.6$ | $31.8 \pm 3.5$ | $68.0 \pm 7.6_{a}$ | $7.8 \pm 3.3_{b}$ | $11.1 \pm 5.5_{b}$ |
| Ericaceous shrub | $1.3 \pm 1.0_{a}$ | $7.4 \pm 4.5_{a}$ | $30.1 \pm 4.5_{b}$ | $11.9 \pm 6.5_{a}$ | $31.4 \pm 5.6_{b}$ | $20.0 \pm 2.9_{b}$ | $22.2 \pm 6.4$ | $14.7 \pm 1.3$ | $28.3 \pm 6.9$ |
| Sedge | $9.4 \pm 5.1$ | $16.7 \pm 5.0$ | $16.3 \pm 2.9$ | $8.6 \pm 5.0_{a}$ | $9.0 \pm 6.4_{a}$ | $22.4 \pm 4.1_{b}$ | $0.0 \pm 0.0$ | $0.0 \pm 0.0$ | $< 1.0$ |
| Herb | $34.3 \pm 7.9_{a}$ | $44.3 \pm 6.7_{a}$ | $14.9 \pm 3.4_{b}$ | $16.9 \pm 5.1_{a}$ | $8.1 \pm 4.2_{ab}$ | $< 1.0_{b}$ | $4.3 \pm 2.2$ | $2.4 \pm 2.0$ | $< 1.0$ |
| Rock/earth/litter | $16.5 \pm 6.9$ | $1.7 \pm 0.8$ | $9.3 \pm 3.1$ | $12.8 \pm 6.4$ | $1.3 \pm 0.6$ | $4.0 \pm 3.3$ | $2.8 \pm 1.0$ | $2.7 \pm 2.1$ | $2.6 \pm 1.2$ |
| Basal area ($m^2$/ha) | $19.2 \pm 3.7_{a}$ | $8.7 \pm 1.9_{b}$ | $< 1.0_{c}$ | $25.7 \pm 3.4_{a}$ | $6.9 \pm 1.4_{b}$ | $< 1.0_{c}$ | $27.3 \pm 3.1_{a}$ | $6.8 \pm 1.0_{b}$ | $< 1.0_{c}$ |
| Tree height (m) | $6.9 \pm 0.8_{a}$ | $5.7 \pm 0.9_{a}$ | $0.4 \pm 0.3_{b}$ | $12.8 \pm 1.0_{a}$ | $7.4 \pm 0.9_{b}$ | $0.6 \pm 0.3_{c}$ | $13.5 \pm 1.4_{a}$ | $8.8 \pm 0.9_{b}$ | $4.5 \pm 0.9_{c}$ |
| Lateral cover (%) | $82.4 \pm 5.3_{a}$ | $70.5 \pm 5.8_{a}$ | $7.2 \pm 3.5_{b}$ | $62.1 \pm 7.9_{a}$ | $62.6 \pm 3.9_{a}$ | $4.0 \pm 2.0_{b}$ | $49.8 \pm 9.8_{a}$ | $27.0 \pm 3.9_{ab}$ | $15.8 \pm 4.6_{b}$ |
| Canopy cover (%) | $89.1 \pm 2.5_{a}$ | $36.6 \pm 6.8_{b}$ | $< 1.0_{c}$ | $88.2 \pm 2.5_{a}$ | $30.7 \pm 6.8_{b}$ | $< 1.0_{c}$ | $80.3 \pm 3.5_{a}$ | $23.8 \pm 3.0_{b}$ | $2.7 \pm 1.0_{c}$ |
| Dominant tree spp. | bS, bF | bF, bS | - | bS | bS | - | bS | bS | - |
| Number of plots | 12 | 9 | 27 | 13 | 7 | 28 | 6 | 12 | 11 |

Table 7. Confusion matrix showing accuracy of land cover types in the initial collapse mapped by EOSD. Mapped sites are categorized based on EOSD data, and reference sites are the true land cover types as determined by field visits. Sites were pooled across Coastal Plain, Humber River, and Côte-Nord regions.

| | Reference sites | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Mapped sites | Dense forest | Open forest | Sparse forest | Barren | Herb/low shrub | Wetland/ tall shrub | Total | User's accuracy |
| Dense forest | 16 | 3 | 0 | 0 | 1 | 0 | 20 | 0.84 |
| Open forest | 13 | 5 | 3 | 0 | 0 | 0 | 21 | 0.23 |
| Sparse forest | 2 | 7 | 3 | 0 | 6 | 3 | 21 | 0.14 |
| Barren | 0 | 0 | 0 | 11 | 6 | 3 | 20 | 0.52 |
| Herb/low shrub | 0 | 1 | 3 | 0 | 15 | 4 | 22 | 0.68 |
| Wetland/tall shrub | 0 | 1 | 3 | 3 | 2 | 12 | 21 | 0.57 |
| Total | 31 | 15 | 11 | 14 | 30 | 22 | 125 | 0.50 |
| Producer's accuracy | 0.52 | 0.33 | 0.27 | 0.79 | 0.50 | 0.55 | 0.49 | |

Table 8. Confusion matrix showing accuracy of land cover types after the final collapse mapped by EOSD. Mapped sites are categorized based on EOSD data, and reference sites are the true land cover types as determined by field visits. Sites were pooled across Coastal Plain, Humber River, and Côte-Nord regions.

| | Reference sites | | | | |
|---|---|---|---|---|---|
| Mapped sites | Dense forest | Sparse-open forest | Non-forest | Total | User's accuracy |
| Dense forest | 16 | 3 | 1 | 20 | 0.84 |
| Sparse-open forest | 15 | 18 | 9 | 42 | 0.42 |
| Non-forest | 0 | 7 | 56 | 63 | 0.89 |
| Total | 31 | 28 | 66 | 125 | 0.72 |
| Producer's accuracy | 0.52 | 0.64 | 0.85 | 0.67 | |

Preparation of telemetry data

The number of telemetry locations remaining after screening, as well as the details regarding the winter period, the size of home range core areas, and caribou density is summarized for each region in Table 9. Winter onset dates varied among regions from December 17 to January 1, and spring onset dates from April 13 to April 19 (Figure 4). Insufficient data resulted in the Humber River region being excluded from home range core area and resource selection function calculations.

Resource selection functions: Caribou select land cover types with the most lichen and least snow

In all regions, the top candidate model chosen by AICc included random intercepts for individuals and a covariate for the non-forested proportion of the landscape available within the home range core of an individual (Table 10). Top candidate models were robust to cross validation ($\bar{r}_s = 0.75$). In all regions, non-forested areas were selected at a rate greater than expected by chance (Table 11). This land cover type had an equal or higher fraction of ground cover in terrestrial lichen than dense or sparse-open forest (Figure 2), and the least snow accumulation (Figure 3). Sparse-open forest was selected at a rate greater than expected by chance in Middle Ridge and Côte-Nord regions, but not in the Coastal Plain region (Table 11). There was also a greater fraction of terrestrial lichen ground cover in sparse-open forest than in dense forest in the Côte-Nord region, but this difference did not occur in the Coastal Plain region (Figure 2). Dense forest showed the most variation in selection by caribou when comparing the three regions, being selected at a rate less than expected by chance in the Coastal Plain region, but greater than expected by chance in the Côte-Nord region (Table 11). While the inclusion of a covariate accounting for the non-forested proportion of the landscape improved model fit, in itself this covariate was not significant in explaining habitat selection by caribou.

Table 9. Summary details for telemetry data, winter period, home range core area, and caribou density in the Coastal Plain, Humber River, Middle Ridge, and Côte-Nord regions.

| | Greater Gros Morne Ecosystem | | | |
|---|---|---|---|---|
| | Coastal Plain | Humber River | Middle Ridge | Côte Nord |
| Number of individuals | 23 | 3 | 17 | 15 |
| Collar type | Argos (13),<br>GPS (11) | Argos (2),<br>GPS (1) | GPS | GPS |
| Individual & year combinations | Argos (18),<br>GPS(13) | Argos (3),<br>GPS(2) | 49 | 43 |
| Number of relocations | Argos (466),<br>GPS (2374) | Argos (79),<br>GPS (582) | 51,724 | 35,958 |
| Collection period | 1993-1998 | 1993-1998 | 2010-2012 | 2005-2012 |
| Winter period | Dec 23 – Apr 19 | Dec 23-Apr 19 | Dec 17 – Apr 13 | Jan 1 – Apr 14 |
| Home range core area (km$^2$) | 38.17 ± 5.83 | - | 230.07 ± 15.46 | 79.13 ± 22.13 |
| Density (caribou/km$^2$)* | 1.94 | 2.92 | 0.89 | 0.02 |

*Details regarding density calculations are in Appendix 3.

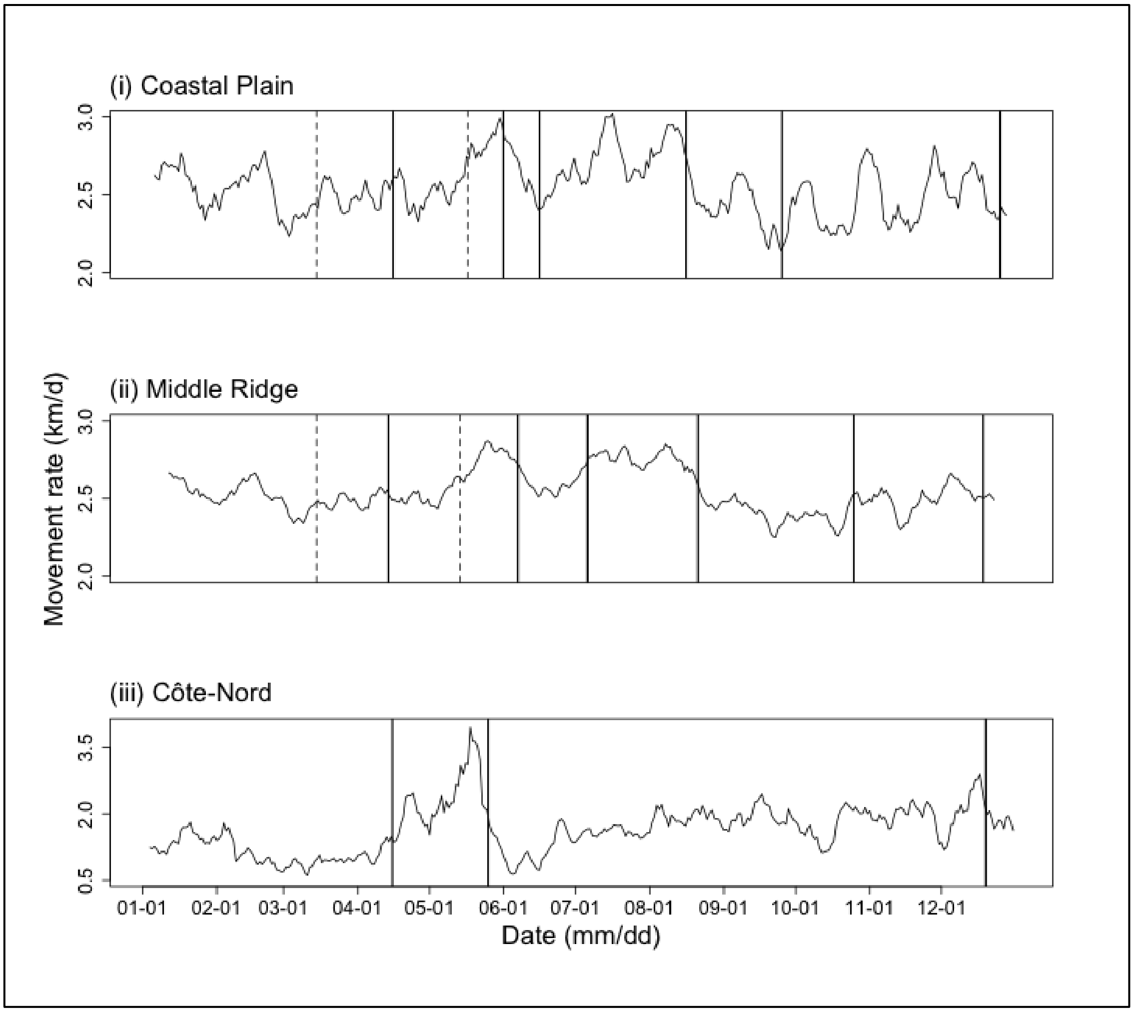

Figure 4. Population-averaged movement rate (km/d) plotted against date for caribou in the Coastal Plain, Middle Ridge, and Côte-Nord regions. Solid lines indicate seasonal onset dates, while dashed lines indicate ranges of candidate onset dates where movement rates were highly variable with high variability among individuals; the midpoints of these ranges were used as spring onset dates.

Table 10. Candidate models of habitat selection for woodland caribou on Coastal Plain, Middle Ridge, and Côte-Nord regions. The number of parameters in the model (*K*), Akaike's Information Criterion corrected for finite sample sizes (AICc), the difference in AICc (ΔAICc), the AICc weight (*w*), and Spearman correlation coefficients of model cross validation ($\bar{r}_s$) are provided. *Habitat* refers to the fixed effect variables of dense forest, sparse-open forest, and non-forested areas, ID refers to individual animals, and *prop_nf* refers to the non-forested proportion of the landscape in the home range.

a. Coastal Plain

| No. | Model | *K* | AICc | ΔAICc | *w* | $\bar{r}_s$ |
|---|---|---|---|---|---|---|
| 3 | *Habitat* with random intercept by ID and covariate *prop_nf* | 11 | 18,884 | 0 | 1.000 | 0.722 |
| 1 | *Habitat*; no random intercept by ID | 4 | 18,933 | 49 | 0.000 | - |
| 2 | *Habitat* with random intercept by ID | 5 | 18,935 | 51 | 0.000 | - |

b. Middle Ridge

| No. | Model | *K* | AICc | ΔAICc | *w* | $\bar{r}_s$ |
|---|---|---|---|---|---|---|
| 3 | *Habitat* with random intercept by ID and covariate *prop_nf* | 11 | 301,007 | 0 | 1.000 | 0.928 |
| 2 | *Habitat* with random intercept by ID | 5 | 302,701 | 1694 | 0.000 | - |
| 1 | *Habitat*; no random intercept by ID | 4 | 304,242 | 3235 | 0.000 | - |

c. Côte-Nord

| No. | Model | *K* | AICc | ΔAICc | *w* | $\bar{r}_s$ |
|---|---|---|---|---|---|---|
| 3 | *Habitat* with random intercept by ID and covariate *prop_nf* | 11 | 215,111 | 0 | 1.000 | 0.614 |
| 2 | *Habitat* with random intercept by ID | 5 | 215,444 | 333 | 0.000 | - |
| 1 | *Habitat*; no random intercept by ID | 4 | 218,031 | 2920 | 0.000 | - |

Table 11. Resource selection coefficients (β; log-odds) and 95% confidence interval (95% CI) for land cover variables estimated from the top candidate models for Coastal Plain, Middle Ridge, and Côte-Nord winter ranges. A positive value for β indicates a land cover type was selected more frequently than expected by chance, while a negative value indicates a land cover type was selected less frequently than expected by chance. In all cases "Water" was used as the reference land cover type.

| | Coastal Plain | | | Middle Ridge | | | Côte-Nord | | |
|---|---|---|---|---|---|---|---|---|---|
| | β | 95% CI | | β | 95% CI | | β | 95% CI | |
| | | Lower | Upper | | Lower | Upper | | Lower | Upper |
| Intercept | −2.69 | −3.41 | −1.97 | −4.26 | −5.99 | −2.54 | −2.65 | −3.00 | −2.31 |
| Dense forest | −2.31 | −3.36 | −1.25 | 0.35 | −1.19 | 1.90 | 0.39 | 0.32 | 0.46 |
| Sparse-open forest | 0.64 | −0.13 | 1.40 | 0.89 | 0.37 | 1.40 | 0.73 | 0.67 | 0.80 |
| Non-forested | 0.97 | 0.12 | 1.81 | 1.09 | 0.61 | 1.56 | 1.03 | 0.94 | 1.12 |
| Non-forested proportion of the landscape | 1.12 | −1.06 | 3.30 | 1.35 | −1.37 | 4.08 | −3.22 | −23.25 | 16.82 |

# DISCUSSION

## Are broadly characterized land cover types valid for studying habitat selection in multiple populations of animals?

In this study the boreal forest was classified into three general land cover types, and relative selection of these land cover types in winter by caribou in three geographically and ecologically distinct regions corresponded to the relative abundance of lichen and distribution of snow among land cover types. Calculation of a set of relatively simple resource selection functions from existing satellite telemetry data for caribou and freely available satellite land cover maps represents a departure from the fine-focus increasingly employed in studies of animal behaviour and made possible by advances in satellite technology. Whereas fine-scale studies are valuable in the detail they provide, they require highly accurate and precise data in order to be reliable. Using coarse scale habitat characteristics can alleviate the issues of misclassification in satellite land cover data, while offering an opportunity to investigate ecological situations such as resource selection by animals on a more widely applicable and comparable basis. Underlying this opportunity is the fact that the ecological processes determining the distribution, abundance, and behaviour of a species are fundamental, and arguably applicable over large extents at broad and fine scales (Urban 2005, Johnson et al. 2001). In addition, as it is widely recognized that animals respond to resources at multiple scales (Leblond et al. 2011; Hebblewhite et al. 2008; Johnson 1980), conceptually it may be easier to hone an understanding of a broad scale ecological pattern such that it applies to specific locales and situations, rather than condense a fine-scale understanding of an ecosystem such that it applies to a greater whole.

For woodland caribou populations, which have declined throughout North America to the point where united and speedy enactment of recovery strategies is paramount, the identification and understanding of ecological driving forces that transcend geographical boundaries is invaluable. Therefore, the merit of land cover classifications derived from broadly applicable variables lies in their ability to help wildlife managers understand habitat selection by caribou in a manner that is unified and useful to planning their recovery on a national scale, while simultaneously facilitating further study and understanding of caribou ecology at local scales.

A potential roadblock in the classification of a single broad set of land cover typess for multiple populations is the influence of landscape composition on measures of habitat selection in a resource selection function framework (Moreau et al. 2012; Hins et al. 2009; Fortin et al. 2008; Osko et al. 2004). Authors such as DeCesare et al. (2012) and O'Brien et al. (2006) were successful in predicting habitat selection by multiple populations of caribou by basing their studies in the fundamental reasons *why* caribou should select habitat instead of *how*, the latter being more sensitive to the influence of varying availability and configuration of land cover types on the landscape. Resource selection functions developed for caribou in the Coastal Plain, Middle Ridge, and Côte-Nord regions showed similar trends and non-forested areas were consistently identified as the most selected land cover type despite differences in the availability and configuration of land cover types on the landscape. This is an indication that the predictions of this study were indeed based on the factors driving habitat selection, and further suggests that broadly characterized land cover types were successful in describing differences in *why* caribou select habitat despite variation in landscape composition.

An important consideration in the application of broad land cover types to many regions of a species' occurrence is the effect that habitat availability may have on how animals perceive land cover types on the landscape (Moreau et al. 2012). For example, dense forest makes up only 2% of the landscape in the Middle Ridge region, and as predicted this land cover type was selected at a rate no greater than expected by chance. At such a low occurrence, it is possible that caribou do not perceive dense forest as an available land cover type and neither select or avoid it (Manly et al. 2002). This difference underlines the importance of defining land cover types that realistically reflect the decisions that animals are making (Knight and Morris 1996). Where non-forested areas make up 65% of the landscape in the Middle Ridge region, caribou may distinguish only between non-forested and forested areas, and pay no heed to characteristics that distinguish forest types. However, in the Côte-Nord and Coastal Plain regions the distinction between dense and sparse-open forest is logical, as these classes make up significant portions of the landscape, and they are associated with differences in terrestrial lichen abundance and snow accumulation.

In the Côte-Nord region, dense forest land cover was selected less than sparse-open forest, but still at a rate greater than expected by chance. In relation to the abundance of lichen and distribution of snow between these land cover types, this finding supports the hypothesis that as snow accumulates and makes access to terrestrial lichens in sparse-open forest and non-forested areas more energy-intensive, caribou may select land cover types such as dense forest, where there is less snow but still access to arboreal lichens (Brown and Theberge 1990). If dense and sparse-open land cover types had been combined, this trend would not have been observed. Middle Ridge represents an exception to the applicability of three boreal forest land cover types in this study, and serves as a reminder that while broadly characterized habitat types have potential in unifying the understanding of habitat selection by caribou among regions, their application still requires some consideration regarding adaptations that ensure relevancy to a given landscape. An extension to this logic is the fact that predation risk and anthropogenic changes to the landscape are additional factors not considered here but known to influence habitat selection by caribou in most of the boreal forest (Latombe et al. 2013; Creel et al. 2005; Altendorf et al. 2001; Bøving and Post 1997). Studies applying a similar method of collapsing land cover types to a few relevant land cover types in regions where predation and anthropogenic disturbance occur should consider these additional factors as criteria when defining land cover types to investigate.

In summary, for studies aiming for applicability to other regions and for wildlife conservation measures applied at a broad scale, and when uncertainty in the accuracy of finer land cover classifications is an issue, the classification of a set of broad land cover types that are defined according to real distinctions in ecological value has clear benefits over studies of a greater number of locally available land cover types that, despite arguably providing a more thorough understanding of animal behaviour within their study areas, rely on assumptions about land cover classification accuracy and may be difficult to compare to studies where not all of the land cover types are present.

### How relevant is snow accumulation and lichen abundance in systems with caribou predators?

Resource selection functions in the Côte-Nord region allowed an examination of how habitat selection related to forage abundance and snow accumulation to predict habitat selection by caribou in the presence of wolves. Habitat selection did not relate solely to the relative abundance of lichen associated with land cover types, as terrestrial and arboreal lichen abundance did not differ between non-forested areas and sparse-open forest. The greater selection of non-forested areas may be explained by a lower accumulation of snow as compared to sparse-open forest. However, while this pattern of resource selection can be explained solely by forage abundance and snow distribution, it does not exclude the possibility that non-forested area served another important ecological function: minimization of predation risk.

Brown (1999) proposed that predation risk be considered as a cost that varies by land cover type, and that to minimize the cost of predation risk and maximize foraging efficiency, foragers select land cover types that maximize vigilance and forage opportunities. Untangling the effect of predation risk from other factors driving habitat selection requires caution due to their additive nature and the potential for positive reinforcement in the selection of high-quality land cover types that serve many purposes (Terry et al. 1996). For example, across their range, caribou have been observed occupying large peatland areas, lichen ranges bordering lakes, and areas near forest edges, all places where good visibility and abundant lichen must together drive habitat selection (McLoughlin et al. 2005; Ferguson and Elkie 2004; Bradshaw et al. 1995). Similarly, non-forested areas In the Côte-Nord region commonly occur on barren hilltops and may provide good vantage points, scent refuges from wolves, and an abundance of terrestrial lichen.

Other studies of caribou behaviour in the Côte-Nord region support the idea that caribou select areas of higher elevation, which decreases their chance of encountering wolves that are targeting moose at lower elevations (Basille et al. 2012). However, Latombe et al. (2013) found that caribou showed stronger selection for open forest cover types during the passage of wolves, followed by a switch to stronger selection of non-forested stands rich in lichen. This offers empirical evidence that caribou shift habitat selection according to multiple factors, and also shows that habitat selection is a dynamic process. The pattern observed by Latombe et al. (2013) suggests that caribou in the Côte-Nord display chronic anti-predator behaviour, but that after the passage of a wolf caribou perceive a lower risk of predation and forage in non-forested areas where lichens are most abundant. This interpretation is at odds with the overall strong selection for the non-forest cover type observed in this thesis, but the two interpretations agree that lichen abundance is an important factor in habitat selection by caribou. Caribou seem to trade off predation risk with foraging opportunities in a dynamic way that depends on spatial proximity to predators, as well as how cognizant caribou are of their proximity.

Outside of experimental manipulations of predation risk that are logistically limiting in caribou-wolf systems, predation risk can be disentangled from other factors through an examination of differences in habitat selection in predated and non-predated landscapes. Caribou, as well as most other ungulates, are known to alter their behaviour based on perceived predation risk (Latombe et al. 2013). Foragers in landscapes with high predation risk should select land cover types with the best foraging opportunities at a greater rate than in landscapes with low predation risk, as occupying areas with high-quality foraging opportunities leaves a greater proportion of time available for activities that can include vigilance (Andruskiw et al. 2008; Oyugi and Brown 2003; Brown 1999). Low variation in model coefficients and small, non-overlapping confidence intervals in the selection of non-forested areas and sparse-open forest in the Côte-Nord region may be indirect evidence of a stronger selection for land cover types with the best foraging opportunities in this region than in Newfoundland, where variance in coefficients was higher and confidence intervals between coefficients for different land cover types had a greater tendency to overlap. It is unlikely that this result was due to sample size deficiencies, as telemetry locations from the Middle Ridge and Côte-Nord regions were amply replicated. While not direct evidence of increased vigilance or more efficient foraging in the presence of predators, the comparison nevertheless provides a base for further investigation of the interactive effects of foraging and anti-predator behaviour on habitat selection by caribou. Another possibility is that while patterns of habitat selection related to forage abundance were detectable using broad land cover types and seemed unchanged by the presence of predators, the influence of predators may alter caribou behaviour at a broader or finer scale than examined here. For example, Rettie and Messier (2000) suggested that predators should most influence caribou in their distribution on the landscape, while Latombe et al. (2013) and Courbin et al. (2013) suggest that caribou alter their behaviour in a dynamic way to trade-off between predator avoidance and foraging based on perceptions of predator proximity. These studies serve as reminders that the factors influencing habitat selection may vary in importance based on the scale of investigation.

Patterns of habitat selection in all regions support the hypothesis that snow accumulation is an important factor for habitat selection by caribou, regardless of predator presence. However, habitat selection seemed most related to lichen abundance, and perhaps the most realistic approximation of the influence of snow distribution and predation risk on habitat selection are as cumulative costs that must be balanced by forage abundance, with the relative role of each depending on factors such as winter severity and predator density.

## The search for ideal land cover data continues: limitations of EOSD

EOSD land cover data performed reasonably well in defining land cover types that were meaningful to caribou. However, EOSD is not without drawbacks, and inaccurate classification of land cover was not entirely mitigated by combining land cover types that were frequently confused. Some problem areas were addressed by combining those habitat classes that are known to be regularly misclassified (Freestone Digital Consulting 2012), and ground-truthing efforts shed light on some of the factors that might have influenced EOSD accuracy and can be attributed to some of the misclassifications that were observed. Primarily, habitats that were highly fragmented at a resolution finer than the 30 m pixel size of EOSD were often misclassified. This error was especially apparent in classifications of non-forested areas on lake edges and on bogs. Patches of herb and low shrub were sometimes classified as barren, particularly when interspersed with patches of standing water. The inaccuracy of EOSD in distinguishing these habitat types was minimized by the combination of all non-forested areas into one habitat type.

However, some misclassification errors could not be resolved by collapsing land cover types due to the need to preserve meaningful distinction among land cover types in the abundance of lichen and distribution of snow. For example, the largest misclassification error arose in the classification of sparse-open forest, in which overstory canopy closure was frequently overestimated and confused with dense forest. This problem could have been reduced by collapsing all forest land cover types into one, but the cost of doing so was a lack of distinction in predicted abundance of lichen between forest types, which is more important in interpreting habitat selection by caribou than land cover classification accuracy.

Another potential cause for discrepancies between EOSD and field classifications is the occurrence of natural disturbances such as insect or wind events. This is primarily of concern in interpreting the resource selection functions from the Coastal Plain region, where insect and wind disturbance are frequent. The most recent major insect outbreak took place in 1996 (McLaren et al. 2009), and EOSD data was developed using imagery after this point. During field visits, it was observed that some areas classified as dense or sparse-open forest had been obviously disturbed and were in fact meadows with coarse woody debris and few standing trees. However, due to the rarity of these occurrences (2 of 21 forested plots), no correction to the land cover map was deemed necessary to account for insect disturbance.

A final potential concern regarding the use of EOSD land cover data is the time lag existing between the development of land cover data and field sampling of land cover characteristics. While there was a 10 y time difference between EOSD mapping and field sampling, this time difference is much shorter than the time scale of canopy-altering succession and field surveys confirmed that EOSD land cover maps were still relevant to sample land cover characteristics related to each land cover type.

One of the primary reasons EOSD land cover was used was the classification of land cover types that were relevant to caribou in their relation to lichen abundance. Terrestrial lichen is known to be an important food source for caribou, and its availability is known to influence habitat selection by caribou (Mayor et al. 2009). While broad-scale lichen abundance has been mapped using remote sensing, most studies occurred in tundra or forest-tundra where lichen ground cover was directly identifiable without interference from overstory canopy (Théau et al. 2005; Nordberg and Allard 2002; Käyhkö and Pellika 1994). In the boreal forest, the definition of land cover types by characteristics associated with lichen abundance has been employed at local scales for some time (Cichowski 1989), but the potential for broad-scale implication has only recently been considered. Lesmerises et al. (2011) used forest characteristics from eco-forest maps to estimate the terrestrial lichen biomass available to caribou in the Saguenay region of Québec, but only > 50 year-old spruce-dominated stands (41.8% of the study area) were sampled, precluding any inference regarding the relationship between lichen abundance and relative selection of other land cover types by caribou.

As remote sensing technology becomes more advanced and accessible to researchers, it is reasonable to expect that custom land cover maps will become increasingly prevalent in future studies. In their absence, the results of this study show that despite limitations of available land cover data, careful consideration of the relationship between EOSD land cover types and relevant factors such as lichen and snow distribution aided in the application of a set of broadly characterized land cover types to three regions of caribou occurrence, which resulted in the identification of common and important land cover types. In considering the contribution of custom mapping and remote sensing to this kind of study, it is reasonable to expect greater insight and understanding of habitat selection by animals as increasingly relevant land cover data become available over broader spatial scales.

### Towards a comprehensive model of snow distribution in the boreal forest

The predictions and results of this study rely heavily on a model of snow distribution that is simple yet based on real patterns of snow accumulation observed in the boreal forest (Pomeroy and Gray 1995). While the model likely holds for the broad land cover types investigated here according to the relationship between snow accumulation, overstory canopy closure in forested areas, sublimation, and wind clearing in non-forested areas, and was supported by measurements of snow depth in the Côte-Nord region and GMNP, a study with a finer focus would benefit from additional parameterization to approximate the effects of wind speed, ablation, sublimation, and elevation that are only implicitly considered here.

The snow model did not incorporate snow characteristics such as hardness, density, or crusting that potentially influence habitat selection by caribou, nor did it consider an index of winter severity that might vary inter-annual snow conditions (Tucker et al. 1990). However, Fancy and White (1985) provide evidence that crusting only increases the cost of foraging in a significant way if it is extreme, and it seems reasonable to expect that generally that hardness and density are cumulative effects that interact with the accumulation of snow to limit accessibility of forage to caribou. Modeling snow accumulation in land cover types relative to one another controls for inter-annual variation in snowfall, outside of the case where there is little or no snowfall and accumulation in all land cover types is essentially zero. Freezing rain can create difficult foraging conditions for caribou by reducing accessibility to lichens, and while these events are expected to increase with the progression of global warming (Vors and Boyce 2009), they are still rare enough to justify not including them in a general model of snow conditions by land cover type.

An easily visualized limitation of the snow model used here is in the expected differences in snow accumulation between clearings of large and small diameter. Literature states that in small clearings snow accumulates more than in surrounding forest, due to the lack of wind clearing and lack of interception by a forest canopy (Gelfan et al. 2004; Pomeroy et al. 2002). It is only for clearings with a diameter greater than 2-3 times the average tree height that snow accumulation is expected to accumulate to lower depths than in surrounding forests as a result of wind and heat radiation (Golding and Swanson 1988). In the regions examined here, snow may reach maximum accumulation depths in clearings 30-40 m diameter (2-3 times maximum tree height). Given that pixel size of EOSD land cover is 30 m, the assumption that snow would accumulate less in non-forest land cover than in forest land cover would only be incorrect in the case of isolated non-forest pixels. As EOSD generally identified land cover patches consisting of clusters of pixels as opposed to isolated pixels, the assumptions of the snow model used in this study likely hold true. Thus, the snow model used in this study provides a reference point from which future studies could model snow distribution among land cover types in the boreal forest in greater detail.

# CONCLUSION

One of the greatest challenges faced by ecologists using satellite telemetry data to study habitat selection is to relate inference from studied populations to broad-scale conservation objectives (Hebblewhite and Haydon 2010). One approach is to develop habitat selection models and land cover classifications that are generalized to reflect factors influencing habitat selection that are relevant on a broad scale. This study was able to successfully collapse boreal forest land cover types into three that minimized the misclassification errors associated with EOSD land cover classification while showing relevant differences in forage abundance and snow accumulation, and confirmed their selection by caribou by estimating resource selection functions. This approach is one by which wildlife managers can identify important land cover types across the range of woodland caribou and aid in their recovery. The land cover types explored here can be further investigated with data from other regions in the boreal forest, and the approach can be further refined toward a unified approach to caribou conservation.

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# APPENDICES

## APPENDIX 1: ACCURACY OF GPS COLLARS IN GMNP

Appendix 1. Accuracy assessment of GPS collars in GMNP. Shown are the distance of relocations from a ground control point (mean ± SE) and the proportion of locations collected via 3-D and 2-D differential fixes* in four land cover types for test collars.

| Land cover type | Distance (m) | Proportion of 3D and 2D differential fixes |
|---|---|---|
| Park compound | 26.0 ± 2.3 | 0.96 |
| Open | 24.6 ± 4.5 | 0.95 |
| Steep slope | 22.2 ± 1.3 | 0.94** |
| Thick brush | 32.0 ± 5.7 | 0.96*** |

*2-D fixes were removed as they made up a small proportion of fixes and were always less accurate than the 3-D and 2-D differential fixes.

**68% of fix attempts in this land cover type were unsuccessful

***45% of fix attempts in this land cover type were unsuccessful

## APPENDIX 2: ACCURACY OF ARGOS COLLARS IN GMNP

Appendix 2. Accuracy assessment of Argos collars in GMNP. Shown is the proportion of locations occurring in each location class, the reported accuracy from Service Argos, and the measured distance of test collar locations from a ground control point (mean ± SE).

| | Location Class | | |
|---|---|---|---|
| | 1 | 2 | 3 |
| Proportion of total locations | 0.78 | 0.14 | 0.07 |
| Service Argos accuracy (m) | 150 | 350 | 1000 |
| Distance from ground control (m) | 117.3 ± 12.4 | 224.1 ± 42.6 | 684.5 ± 224.3 |

## APPENDIX 3: CALCULATION OF CARIBOU DENSITY

Caribou density during the winter period was calculated for each region using historical population estimates from the study period and dividing by the area of the population range. Population ranges came from unpublished spatial estimates defined by the Newfoundland and Labrador Department of Environment and Conservation. For the Middle Ridge and Humber Valley regions, population estimates came from mark-recapture surveys that were conducted during the winter from a helicopter (Newfoundland and Labrador Department of Environment and Conservation, unpublished data). Population estimates of caribou in GMNP were calculated from mark-recapture surveys of radio-collared animals conducted in July of 1995 and 1997 from a helicopter above the Long Range Mountains where calving takes place. The density of caribou in the Coastal Plain region during winter was estimated as the total population estimate multiplied by the fraction of collared caribou that migrated to the Coastal Plain to spend the winter. Côte-Nord density estimates were taken from Courbin et al. (2009).