2018

Is Ruggedness a Key Habitat Feature for Woodland Caribou Along the Lake Superior Coast?

McClinchey, Jack

IS RUGGEDNESS A KEY HABITAT FEATURE FOR WOODLAND CARIBOU ALONG THE LAKE SUPERIOR COAST?

by

Jack McClinchey

Source: Roberta Bondar, 2001

FACULTY OF NATURAL RESOURCES MANAGEMENT
LAKEHEAD UNIVERSITY
THUNDER BAY, ONTARIO

April 20th, 2018

IS RUGGEDNESS A KEY HABITAT FEATURE FOR WOODLAND CARIBOU
ALONG THE LAKE SUPERIOR COAST?

by

Jack McClinchey

An undergraduate thesis submitted in partial fulfillment
of the requirements for the degree of
Honours Bachelor of Science in Forestry

Faculty of Natural Resources Management
Lakehead University

April 20th, 2018

_____   _____
Major Advisor   Second Reader

LIBRARY RIGHTS STATEMENT

In presenting this thesis in partial fulfillment of the requirements for the HBScF degree at Lakehead University in Thunder Bay, I agree that the University will make it freely available for inspection.

This thesis is made available by my authority solely for the purpose of private study and research and may not be copied or reproduced in whole or in part (except as permitted by the Copyright Laws) without my written authority.

Signature: _____

Date: _____

A CAUTION TO THE READER

This HBSCF thesis has been through a semi-formal process of review and comment by at least two faculty members. It is made available on loan by the Faculty of Natural Resources Management for the purpose of advancing the practice of professional and scientific forestry.

The reader should be aware that the opinions and conclusions expressed in this document are those of the student and do not necessarily reflect the opinions of the thesis supervisor, the faculty, or Lakehead University.

iv

ABSTRACT

McClinchey, J. M. 2018. Is Ruggedness a Key Habitat Feature for Woodland Caribou Along the Lake Superior Coast?. NRMT 4030. 73 pp.

Keywords: density-dependence (DD), inverse density-dependence (IDD), moose, moose growing season forage, Lake Superior Coast Range (LSCR), Pukaskwa National Park (PNP), ruggedness, refuge habitat, refuge islands, wolves, woodland caribou

Woodland caribou (*Rangifer tarandus caribou* Gmelin) in the Lake Superior Coast Range are at risk, having been extirpated in portions of their range including Lake Superior Provincial Park and Pukaskwa National Park (PNP). A resource selection function has yet to be formulated for this population. I chose to examine the population between Terrace Bay and Marathon, Ontario, where the most recent observations of mainland individuals has occurred, hypothesizing that rugged terrain was a mechanism for caribou to escape predation from wolves (*Canis lupis* L.). These animals do not appear to use rugged terrain, as they were found to be spaced away from rugged areas. Ruggedness is likely important at the landscape scale, segregating caribou from moose (*Alces alces* L.) and consequently wolves. At the finer scale caribou probably avoid rugged terrain to lower energetic costs. Alternatively, refuge islands appear to act as the primary means of spatial segregation between caribou, moose and wolves. Heavy selection for these features is not a viable long-term survival strategy for caribou in the LSCR, as shown by an extirpated population in PNP. I suggest that caribou will be extirpated from the LSCR, as populations on Michipicoten and Slates Islands which have likely sourced the mainland coast have recently become extirpated or nearly so.

CONTENTS

TABLES

FIGURES

ACKNOWLEDGMENTS

INTRODUCTION

Large-scale declines of boreal woodland caribou (*Rangifer tarandus caribou* Gmelin) began in the early 20th century as human settlement negatively impacted caribou habitat, which is characterized by large tracts of mature coniferous tree species (Bergerud 1974). Early forest harvesting practices favoured regeneration of hardwood species in the boreal forest, creating browse for moose (*Alces alces* L.) and white-tailed deer (*Odocoileus virginianus* Zimmermann) (Peterson 1955a; Bergerud 1974). Greater numbers of alternate ungulate species on the landscape raised wolf (*Canis lupis* L.) densities, the primary predator of woodland caribou (Peterson 1955a; Bergerud 1974). Road development also fragmented woodland caribou habitat, creating ecological traps whereas caribou settled in poorer quality habitats, which enhanced predator success rates through corridor creation (Ontario Ministry of Natural Resources and Forestry [OMNRF] 2014c; Newton et al. 2017). Caribou are far more susceptible to predation than other ungulate species, given their lower reproductive capacity (Skoog 1968; Bergerud 1971, 1974). Hence, predation is considered the limiting factor for woodland caribou, as they can travel long distances for food and should logically not be food limited (Bergerud 1974; Bergerud and Elliot 1986; Bergerud et al. 2007; OMNRF 2009; Environment Canada 2012).

Woodland caribou (*Rangifer tarandus caribou* Gmelin) are now threatened across Ontario, and have faced range reductions of 40-50% since the mid 1800s (Ontario

Woodland Caribou Recovery Team [OWCRT] 2008b). A population that is part of a discontinuous distribution is currently persisting in very small numbers along the north shore of Lake Superior, between Terrace Bay and Marathon, Ontario. The area is different ecologically, and the caribou occupying it are different genetically from the continuous distribution within the boreal forest (OMNRF 2014a; Drake et al. 2018). A resource selection function has yet to be formulated for this population, which is alarming given drastic declines in population levels and presumed extirpation from portions of its range occupied in the recent past, such as Pukaskwa National Park (PNP, Lake Superior Provincial Park and Sleeping Giant Provincial Park (Bergerud et al. 2007, 2014; OMNRF 2009).

Woodland caribou rarely travel along the coast more than 2 km from Lake Superior (Bergerud 1985; Bergerud et al. 2014). This coastal area supports higher instances of deciduous or mixed forest types than surrounding landscapes, and therefore does not fit traditional habitat models within the boreal forest (Racey et al. 1999; OMNRF 2014b; Hornseth and Rempel 2016). The topography within this area is extremely rugged, and caribou both inside and outside the study region have been documented using rugged terrain as a means to lower predation risk, so its ruggedness may serve as an advantage (Ferguson 1982; Bergerud and Page 1987).

The objective of this thesis is to quantify caribou habitat along the Lake Superior coast, between Terrace Bay and Marathon, Ontario. Habitat elements such as ruggedness, elevation, moose forage density, caribou refuge areas, distance to refuge islands and distance to the Lake Superior shoreline will be correlated to caribou point data using a Digital Elevation Model and Ontario's Landscape Tool. It is hypothesized that caribou select rugged terrain along the coast, allowing them to escape predation

from wolves. It is also hypothesized that refuge habitat is unimportant to caribou in the study area, as the forest is dominated by mixedwood and deciduous forest types.

LITERATURE REVIEW

WOODLAND CARIBOU IN ONTARIO

Woodland caribou currently persist in a continuous distribution in northern Ontario (Fig. 1). This range includes a region from the Quebec to the Manitoba border, extending southward towards Sioux Lookout, Geraldton, Hearst, and nearly Timmins, and extending northward towards to the northern limit of the boreal forest. Limited numbers of caribou persist in a discontinuous distribution south of Geraldton towards Lake Superior, extending westward towards Nipigon, and eastward towards Wawa.

The Ontario Ministry of Natural Resources, today renamed the Ontario Ministry of Natural Resources and Forestry (OMNRF), released a Range Delineation Report in 2014, which separated continuous and discontinuous ranges, and identified 14 ranges within the continuous distribution (OMNRF 2014a) (Fig. 1). The Lake Superior Coast Range (LSCR) forms part of the discontinuous distribution (Fig. 2). The OMNRF defines the LSCR as a 10 km wide coastal strip extending inland from the coast, including adjacent islands such as the Slate Islands, Pic Island, and Michipicoten Island (OMNRF 2014, Glen Hooper, personal communication, 2017). The 10-km strip provides a significant buffer on the true range of LSCR caribou, which often occupy a range within 2-3 km of the coast (Glen Hooper, personal communication, 2017).

Figure 1. Woodland caribou continuous and discontinuous ranges in Ontario. Source: OMNRF (2014a).

Figure 2. Lake Superior Coast Range for woodland caribou, including observations by decade. Source: OMNRF (2014a)

Ontario's Woodland Caribou Conservation Plan includes policies on caribou within the discontinuous distribution and the LSCR to "enhance connectivity between the northern continuous range and the southern coastal Lake Superior populations," which will "improve the prospects for persistence of the coastal population," (OMNRF 2009). However, through recent meetings with Regional Planning Biologist Glen Hooper, it was revealed that the OMNRF is now focused on increasing connectivity within the LSCR. This shift in habitat management goals for caribou within the LSCR offers important context as the purpose of this thesis, which involves the evaluation of habitat within the LSCR.

Habitat

There has been a significant number of sources exploring this topic, especially since the objectives of modern forest management shifted from timber management to ecosystem management after the 1992 Earth Summit. The OMNRF's Woodland Caribou Conservation Plan (2009), the Caribou Discussion Paper (OWCRT 2008a), and Environment Canada's Recovery Strategy for Woodland Caribou (2012) all offer thorough synthesis of such primary scientific sources, and these documents will be the primary references for this section.

At the landscape scale, woodland caribou in the boreal forest require large contiguous tracts of undisturbed, mature (60 years or older) coniferous forest types, preferably jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) Britton, Stems & Poggenburg) (OWCRT 2008a). Much of the boreal forest is naturally in an unsuitable condition for caribou at discrete time intervals, but caribou evolved to

use an entire landscape over time as habitat within it changes with disturbances caused by fire, wind and insects (OWCRT 2008a; Environment Canada 2012).

The OMNRF classifies woodland caribou habitat into two broad categories: winter habitat and refuge habitat (OWCRT 2008a). Winter habitat in northwestern Ontario consists of large areas of relatively monospecific stands of jack pine and black spruce, but in the province's northeastern area where the fire cycle is much longer, winter habitat largely consists of lowland black spruce stands (OWCRT 2008a; OMNRF 2009). Both ground and arboreal lichens are important food sources in traditional winter habitats, which few other wildlife species can survive on (OWCRT 2008a; Environment Canada 2012). During the winter, caribou also traverse frozen lakes as a means to spot wolves at long distances, while also hydrating themselves through the slush layer under the snow. They also tend to feed on lichen-rich lake shorelines (OWCRT 2008a).

Refuge, or all-season habitat, exists in large landscape patches, and consists of low diversity coniferous forest types. These areas support very little forage for moose and deer, and thus lower densities of predators, primarily wolves, but also black bears (*Ursus americanus* Pallas) (OWCRT 2008a).

Boreal caribou have specific habitat requirements during the calving period. To reduce predation risk, pregnant cows travel to isolated areas during the spring and summer. These habitats can include islands, shorelines, peninsulas, or peatlands in the mainland forests. Caribou are exceptional swimmers and can effectively escape from predators using water (OWCRT 2008a; OMNRF 2009).

RANGE REDUCTIONS AND POPULATION DECLINES

Across Canada, the southern limit of woodland caribou has progressively receded northward since the early 1900s (Fig. 3). A similar situation has unfolded in Ontario. Cumming and Beange (1993) chronologically describe the northerly contraction of woodland caribou distribution in Ontario, stating that this decline began in 1880 (Fig. 4) (Cringan 1957).

The recession of caribou along the coast of Lake Superior has appeared to proceed in a somewhat slower manner compared to latitudinally adjacent regions on the mainland. Caribou were eliminated from southern regions of the Kenora district and the mainland northeast of Lake Superior around the 1920s, but persisted along the coast until about the 1950s (Cumming and Beange 1993). Cringan (1956) stated that caribou were present near Black Bay Peninsula, Thunder Bay, and Simpson Island until 1946, 1955 and 1956, respectively. Caribou also persisted on Sibley Peninsula, modernly known as Sleeping Giant Provincial Park, until the 1970s (Ted Armstrong, personal communication, 2017).

Figure 3. Woodland caribou range reduction in Canada. Source: Environment Canada (2012).

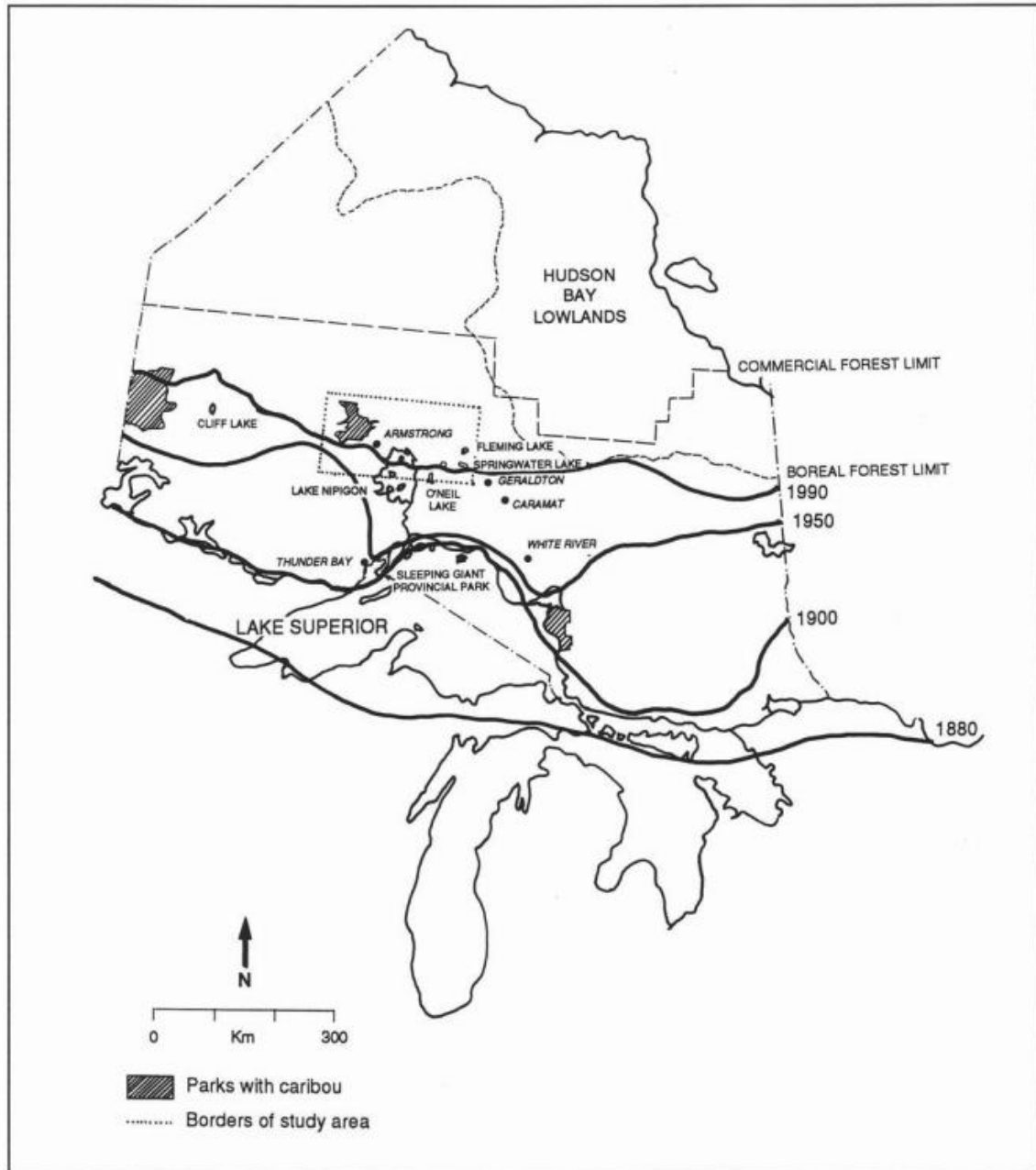Figure 4. Woodland caribou range reduction in Ontario. Source: Cumming and Beange (1993)

The overall reduction of woodland caribou ranges and populations can likely be attributed to multiple factors, each having a compound effect on one another. Human hunting likely played a role in the onset of their decline (Bergerud 1974). Caribou often congregate, traveling as part of small groups or large herds. They often use traditional

routes of travel, which can facilitate hunter access. Little evidence suggests that caribou will become more wary of humans, even after continual harassment (Bergerud 1974). Additionally, caribou do not perceive danger at great distances and are very susceptible to high powered rifles. Early declines of some caribou populations has been attributed solely to overhunting. Bergerud (1974), Mercer et al. (1985) and Bergerud (1978) have all stated that caribou populations of 50 or fewer individuals, similar to size of the LSCR caribou population (Shuter et al. 2016), are very sensitive to even slight changes in birth or mortality rates. Populations at these levels may exhibit inverse (or positive) density dependence, in which population growth rates decrease as populations become very small (Cumming 1992; Wittmer et al. 2005; Bergerud et al. 2014).

Accidents with motor vehicles and trains have increased with development projects encroaching on caribou habitat. For example, 27 caribou deaths occurred over a two year period for an Alberta population of 150-200 caribou (Dzus 2001). Again, the possibility of inversely density dependent population dynamics increases the importance of even occasional accidents (Cumming 1992; Wittmer et al. 2005; Bergerud et al. 2014). Within this study area , the Trans-Canada highway and the Canadian National Railway are within 2-3 km of the Lake Superior shoreline between Terrace Bay and Marathon, overlapping with caribou habitat (Fig. 9) (OMNRF 2014a; Shuter et al. 2016).

Some of the other historic hypotheses on the regulating factors of caribou populations have focused on the importance of lichen reserves and habitat alterations (Bergerud 1974). The hypothesis of lichen reserves as a limiting factor has largely been rejected, as caribou have persisted in record densities where lichen reserves are absent, or nearly so, and lichen is therefore not considered a necessary food source (Bergerud

1996; Bergerud et al. 2007). Destruction of habitat, namely old growth coniferous forests, was also considered a separate hypothesis. Bergerud (1967) first proposed the now widely acknowledged theory that wolf predation might be limiting caribou. He stated that the anthropogenic removal of vast tracts of mature forests created habitat favorable for other ungulate species, which supported unnaturally high wolf densities to which caribou have never evolved (Bergerud 1967, 1974).

Impacts of Wolf Populations

Bergerud (1974) defended his hypothesis of predation as a limiting factor for caribou by comparing it to other acknowledged hypotheses at the time, and revisited the hypothesis again over twenty years later (Bergerud 1996). Bergerud and Elliot (1986) supported Bergerud's (1974) initial hypothesis by critically evaluating the dynamics of caribou, wolf and moose populations.

Bergerud and Elliot (1986) examined three woodland caribou populations in the interior of British Columbia after the occupation of moose in the area. Moose had expanded their range into northwestern British Columbia in a manner similar to the post-glacial dispersion of moose to the coast of Lake Superior, which will be discussed later (Peterson 1955b). Once moose began to invade northwestern B.C., wolf densities quickly rose, and caribou populations declined (Peterson 1955b).

In their study, Bergerud and Elliot (1986) examined adult mortality and recruitment for the three populations, the Level Kawdy, the Spatsizi-Lawyers Pass, and the Horseranch populations. Only the Horeseranch population had undergone an artificial wolf reduction program. Both herd size and range size of caribou increased

when wolf populations were artificially decreased. More precisely, it was demonstrated that caribou cannot maintain their numbers when wolf populations reach densities above 6.5 wolves per 1000 km^2, yet moose populations can persist in low numbers with >8 wolves per 1000 km^2. Thus, caribou cannot coexist except in refuge habitat when moose biomass allows wolf numbers to increase to high levels, as moose populations will support densities of wolves inhospitable to woodland caribou even if moose is the primary prey (Bergerud and Elliot 1986).

Bergerud and Elliot (1986) also synthesized recruitment and mortality rates of various caribou populations across North America and correlated these to localized wolf densities. In all cases where recruitment was below a critical threshold for population persistence (12%), wolf densities exceeded 6.5 wolves per 1000 km^2 for at least 2 consecutive years (Table 1). One of the main reasons that woodland caribou cannot maintain recruitment when wolf populations are above this density, commonly exceeded below the line of continuous caribou distribution (OMNR 2005), is that they have a lower reproductive output than other ungulate species. Deer, moose, and elk (*Cervus canadensis* Erxleben) frequently conceive as yearlings (Buechner and Swanson 1955; Pimlott 1959; Verme 1969). Female caribou, on the other hand, do not generally reach sexual maturity until 28 months, and this period can exceed 40 months (Skoog 1968; Bergerud 1971). In addition, caribou typically have one young, while other ungulates commonly have two. Even when caribou do give birth to twin litters, small calves are often the result, and they are more susceptible to mortality from predation compared to larger calves from single litters (Bergerud 1974).

Table 1. Recruitment rates of caribou when wolf densities exceeded a critical threshold. Source: Bergerud and Elliot (1986).

Herd	Cohorts	Recruitment (%)	Remarks	Reference
Nelchina, AK	1964, 1965, 1966	5, 8, 6	Recruitment improves to 24% (1967) after wolves reduced	Bergerud 1983
Forty Mile, AK	1956, 1957	5, 5	Recruitment improves to 31% (1958) after wolves reduced	Davis et al. 1978, Valkenburg and Davis 1985
Delta, AK	1971, 1972, 1973, 1974	9, 7, 7, 1	Recruitment improves to 25% (1976) after wolves reduced	Gasaway et al. 1983, Davis and Valkenburg 1985
Denali, AK	1972, 1973, 1975, 1976	1-18 calves per 100 females (<10-12% recruitment)	In National Park not hunted; population low, 1972-1985; calf mortality was due to predation	Haber 1977
Beverly, N.W.T.	1955, 1956	7, 8	Recruitment improves to 20% (1958) and 25% (1959) after wolves	Kelsall 1968

The OMNRF concluded moderate to high level of support for an additional factor, that road use by wolves can lead to increased hunting efficiency and higher predation rates on woodland caribou, and synthesized relevant evidence in part three of their State of the Woodland Caribou Resource Report (2014c). Wolves in managed areas select secondary and tertiary roads at both the pack and landscape scales, as hunting efficiency is higher when roads are used. Predation-related mortality rates were higher in managed landscapes where roads were present when compared to unmanaged landscapes that were absent of roads. Further, caribou may avoid roads, especially when traffic levels are higher, so roads serve to fragment their habitat. An ecological trap is created when wolves continue to use roads successfully (OMNRF 2014c). A recent publication of a set of collar data from wolves shows roads are preferred over natural

linear features, and areas of higher kill rates associated with high road density, supporting the OMNRF's (2014) findings (Newton et al. 2017).

Moose Dispersion Patterns

Peterson (1955b) found that moose failed to colonize former portions of the Cordilleran and Laurentide Ice Sheets or were absent from these areas for hundreds of years until the early 20th century (Fig. 5). The reasons for this pattern are unknown, but Peterson (1955b) hypothesized that population pressure, especially in the direction of dispersal, may have influenced it. Logging could have played an important role in the later creation of favourable habitat for moose. Revisiting the implications of these distribution patterns to this thesis, Peterson (1955a) stated that "all available evidence confirms that moose have actually expanded their ranges to meet somewhere north of Lake Superior, … [and] not that moose had previously occurred in that area within recent time."

Writing for National Geographic, Shiras (1912) claimed there were emigrations of moose since about 1885 from the east and west into the area north of Lake Superior. "About 1885, a steady movement of the moose westerly from Quebec was observed and a slower easterly migration from northern Minnesota. Eventually, these animals commingled and took possession of the entire shore, later extending into the interior until they reached the waters flowing into Hudson Bay."

Figure 5. Post-glacial dispersion of moose in North America. Source: Peterson (1955b).

Peterson (1955a) reproduced a personal letter from District Biologist for the Ontario Department of Lands and Forests at the time, Mr. C. A. Elsey. Through interviews with several older residents of the Longlac region, Elsey found that First Nations near Longlac and Mobert, Ontario hunted moose for the first time in the late 19th century and they were "unfamiliar with moose and would not eat the flesh." Elaborating on these migrations of moose, Grant (1902) documented instances of moose in the upper Ottawa River and Temiskaming regions of Ontario. He stated that moose arrived in the Ottawa River area early in the 20th century and proceeded to spread westward, likely reoccupying range lying between the shores of Lake Superior and James Bay (Peterson 1955a). Peterson (1955a) synthesized his findings in a map displaying the spread of moose in Northern Ontario (Fig. 6). Further to his findings, I personally undertook an

interview with Pukaskwa National Park biologist Christine Drake. Drake agrees with

Peterson's (1955a) findings. Drake revealed that, through her correspondence with local

First Nations, moose meat has been increasing in the diets of Indigenous Peoples

surrounding Pukaskwa National Park (PNP), which is almost immediately southeast to

the study site (Christine Drake, personal communication, 2017).
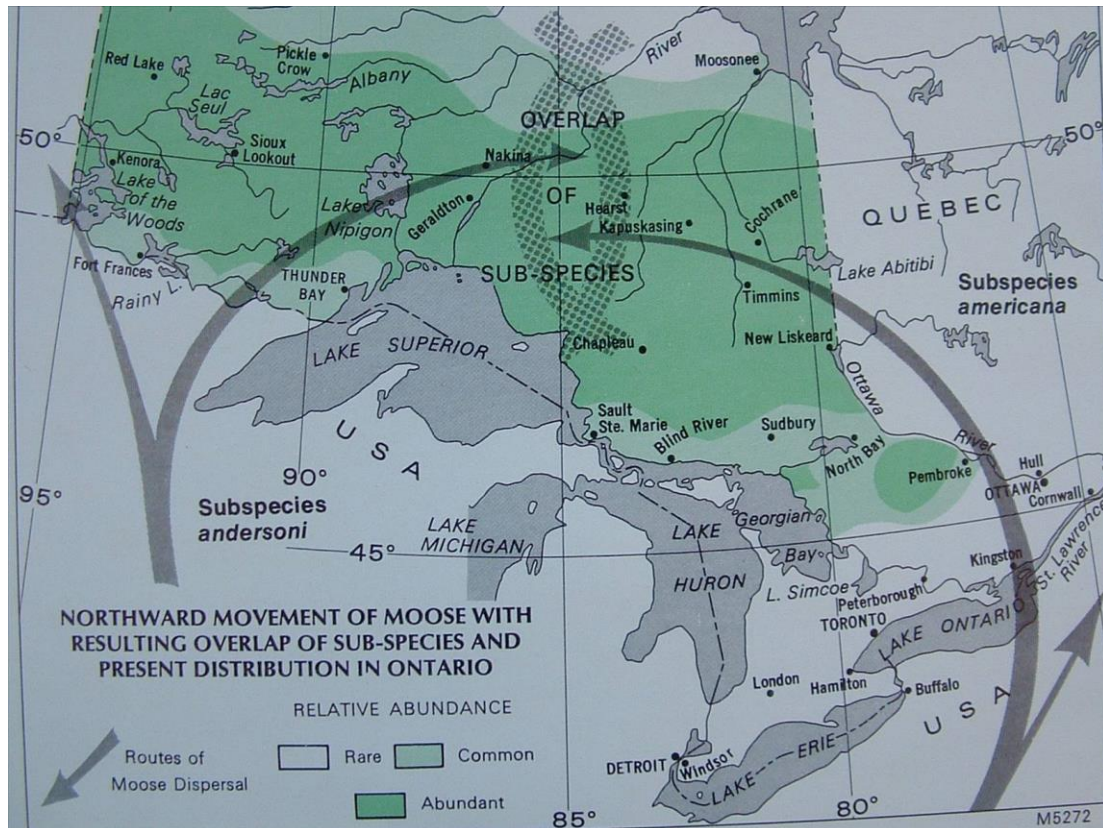

Figure 6. Post-glacial dispersion of moose in Ontario. Source: Peterson (1955a).

LAKE SUPERIOR COAST RANGE

Peer reviewed publications and MSc theses relevant to this thesis can broadly be

separated into two categories: studies conducted on Pic Island (Ferguson 1982; Ferguson

et al. 1988) and studies conducted in PNP (Bergerud 1985, 1989; Neale 2000; Bergerud

et al. 2007, 2014). These publications offer interpretations of habitat selection and population dynamics of woodland caribou in the LSCR, specifically on the mainland coast. Despite being in the LSCR, caribou subpopulations on Michipicoten Island and the Slate Islands (both provincial parks) have, until recently, been routinely predator-free (Glen Hooper, personal communication, 2017). Further, the terrain on these islands is considerably less rugged than either the mainland or Pic Island, and there is less migration of animals from the mainland to these islands compared to Pic Island (Ferguson 1982). Thus, findings related to the park subpopulations will not be discussed as heavily.

Additional relevant information covering caribou in the LSCR includes the results of a 2016 aerial survey conducted throughout the LSCR by Parks Canada and the OMRNF (Shuter et al. 2016), reports of migrations of caribou within the LSCR (Foster and Harris 2012; Ray Tyhuis, personal communication, 2017), and genetic analyses on caribou in PNP and Pic Island (Drake et al. 2015, 2018). Though no caribou were directly observed in the 2016 aerial survey, caribou sign was recorded between Terrace Bay and Marathon, offering validation of the selection of the study site for this thesis. Incidents of caribou migrating from the Slate Islands to the mainland, as well as comparative genetic analyses between caribou on Pic Island and Pukaskwa National Park offers some insight into the movements of caribou in the LSCR, and consequently, the study area. Findings from the aerial survey, reports on genetics, and personal communications with OMNRF staff regarding caribou migrations from the Slate Islands will be summarized.

Pic Island

Ferguson (1982) and Ferguson et al. (1988) examined why caribou persisted on Pic Island, a 1038-ha island opposite Neys Provincial Park, or Coldwell Peninsula (Fig. 5), but were less numerous on adjacent mainland shoreline regions. They tested the following hypotheses: food resources were inadequate on the mainland, mainland caribou had contracted diseases that Pic Island caribou did not, mainland caribou were more susceptible to predators than Pic Island caribou, and mainland caribou dispersed, becoming victim to inverse density dependence, while caribou on the islands were prevented from recolonizing the mainland.

The bulk of the evidence, though circumstantial, suggests predation limited caribou on the mainland and allowed for persistence of caribou on Pic Island. Animals only occupied the adjacent Coldwell Peninsula when predators were absent. More abundant and nutritious forage options were available on the mainland, yet caribou remained on Pic Island. There was also little to no sign of white-tailed deer on Pic Island over a three-year study period (1978-1980), and there was no evidence that moose became inflicted with a neurological disease transmitted from white-tailed deer on the mainland. Caribou were observed moving onto Pic Island from the mainland, while a caribou released onto the mainland from the island swam back onto the island two weeks later, rejecting the dispersal hypothesis (Ferguson 1982; Ferguson et al. 1988).
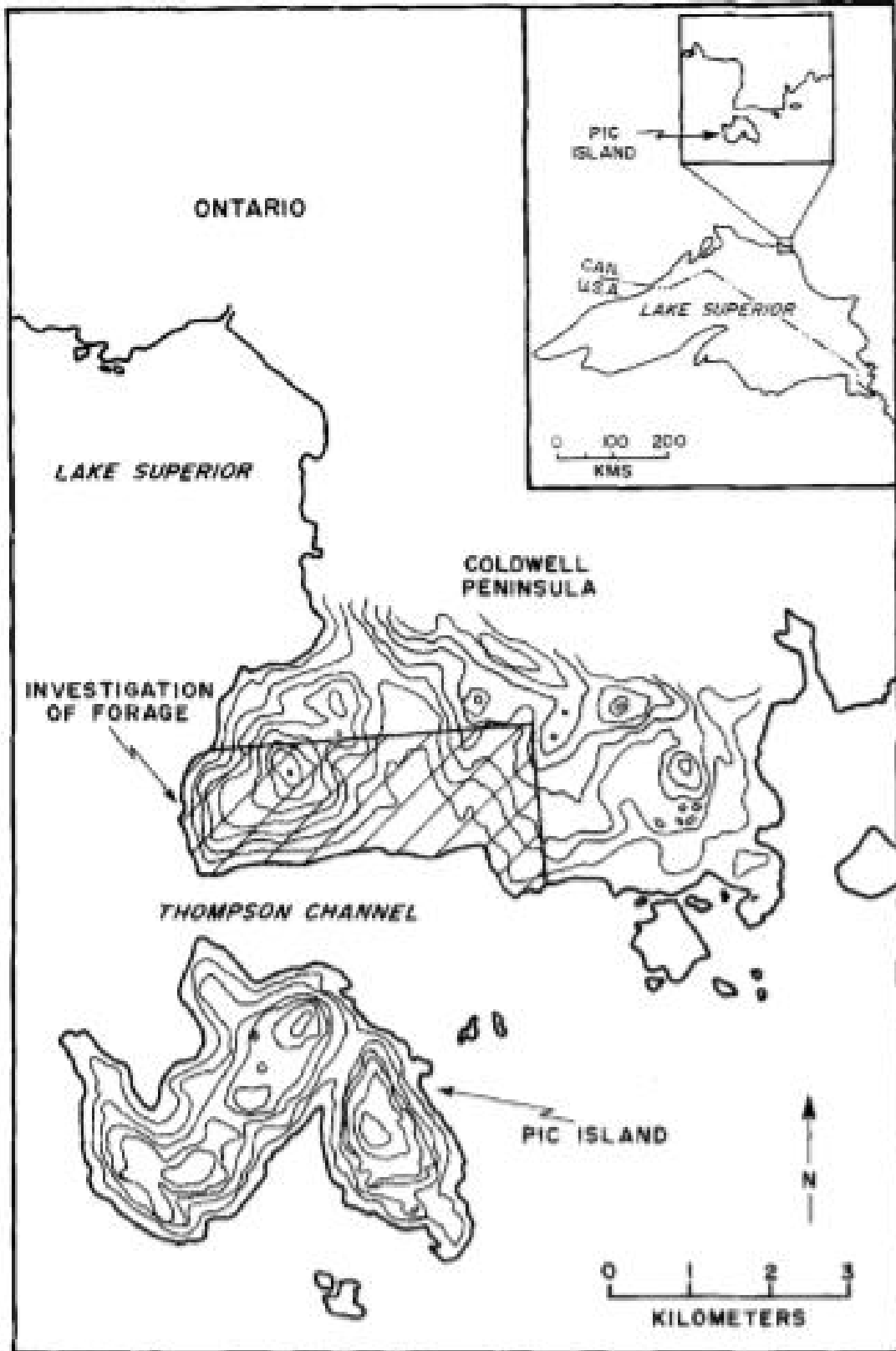
Figure 7. Pic Island and Coldwell Peninsula, Ontario. Source: Ferguson et al. (1988).

Ferguson (1982) and Ferguson et al. (1988) also proposed the presence of escape habitat from predators on Pic Island allowed for persistence of woodland caribou. Of particular interest is the fact that caribou were "found to respond to predators by running uphill in predator avoidance studies on the island," offering background to the selection of rugged terrain as an escape feature (Ferguson 1982). In predator simulations, which involved having a domestic dog (*Canis lupus familiaris* L.), either an elk hound or beagle, chase caribou to observe escape behavior, on three out of five occasions, caribou were found to run uphill in an initial reaction. Some other escape tactics included the use of the Lake Superior shoreline, evident caribou trails, and easy running areas (Ferguson 1982). Escape behavior of caribou in Pukaskwa National Park was also recorded in telemetry work between 1983 and 1986 documented by Bergerud (1989). Similar to Ferguson's (1982) findings, caribou responded by generally moving uphill or adjacent to the shoreline. Such consistency in escape behavior within the LSCR is indicative of the importance of both ruggedness and elevation to woodland caribou as escape habitat.

Ferguson (1982) furthered his discussion on predation by evaluating the relative importance of black bears, lynx (*Lynx canadensis* Kerr) and wolves as predators. A single bear lived on the island for roughly a year during the study period, and one caribou was found near its den. The caribou was found to be injured from a 4-m fall off a nearby ledge, from which it survived for a period of time before dying and being dragged 5 m to the entrance of the adjacent bear den. Thus, death may have been accidental, and the bear was not considered an important predator factor for this study (Ferguson 1982). Lynx sign was observed at the mouth of Pic River within the Neys area (Coldwell Peninsula) at the height of the snowshoe hare (*Lepus americanus* Erxleben) population cycle, but at no other time on the mainland. There were also no

lynx observations on the island, and there has historically been little evidence of lynx predation on caribou calves outside of Newfoundland. Lynx too was not considered an important predator (Bergerud 1971; Ferguson 1982).

Wolves, have however, been found to have a significant influence on the evolutionary development of caribou, as previously discussed. An estimated five wolves traversed from the mainland to Pic Island in late winter of 1976-1977. The caribou population was reduced by half that winter. Both starvation and predation were considered to be important factors in the population's decline (Ferguson 1982).

Pukaskwa National Park

Bergerud (1985) and Bergerud et al. (2007, 2014) tested the predation hypothesis as a limiting factor for woodland caribou by examining the small persisting coastal population in PNP, and Bergerud (1989) synthesized woodland caribou behavior and population dynamics up to 1989 in a review for PNP. Neale (2000) examined the effects of natural and human land use on the distributions of wolves, moose and woodland caribou in PNP, focusing heavily on the effects of snow depth and elevation. Similar to Ferguson (1982) and Ferguson et al. (1988), Bergerud (1985, 1989) and Bergerud et al. (2007, 2014) concluded that unique escape features along the coast of Lake Superior have allowed woodland caribou to persist much longer than populations in the adjacent, more continental, mainland. Neale (2000) found that years of heavy snowfall result in moose movement towards low elevation areas, which may coincide with movement towards the Lake Superior coast.

The hypothesized escape/avoidance features can be separated into two categories: features linked to Lake Superior, and those associated with terrain. Escape features reliant on Lake Superior includes the shoreline itself and offshore islands, or winter refuge islands that are less frequently connected to the mainland by land-fast ice than their adjacent counterparts. Terrain features include rugged terrain, high elevation areas, and more specifically, "balds" or rounded, alpine hilltops occurring at high elevations above river valleys as a means to spot predators (Bergerud 1985, 1989; Bergerud et al. 2014).

Caribou in PNP select the shoreline because of a reduced predation risk in the open water season. Lake Superior is generally ice-free for about 10 months of the year, catering to the caribou's excellent swimming ability as a means of escape. Bergerud (1989) observed caribou mean distances from the shoreline between 1976-1986, reporting that 136 sightings of radio collared caribou occurred at 1.3 ± 0.1 km from the shoreline, while the distance inland for 212 aggregations of tracks on winter surveys was 0.55 ± 0.05 km. Bergerud et al. (2014) later reported that caribou were located within 2 km of the shoreline of Lake Superior about 98% of the time between 1974-1988. Bergerud (1989) and Bergerud et al. (2014) also demonstrated that the Lake Superior shoreline was likely used by caribou as part of a spatial segregation strategy from both moose and wolves, as caribou declines were resultant of a proportional increase of moose, and thus wolves, traversing the shoreline during several years of heavy snowfall. Snowfall amounts are lessened very close to the shoreline compared to the interior of the shoreline, and moose therefore occupied the shoreline to reduce predation risk and energetic cost associated with deep snow areas (Neale 2000; Bergerud et al. 2014).

The use of ice-free winter refuge islands by woodland caribou in PNP is another example of a unique escape feature unavailable to other woodland caribou populations within the boreal forest. Bergerud (1989) and Bergerud et al. (2014) examined the importance of refuge islands. A total of 48 islands and islets are present along the Lake Superior shoreline in PNP, and those which are large enough and far enough away from the mainland are available as winter refuges for caribou in the absence of land-fast ice. Bergerud (1989) described islands as small as 5 ha in size as potential temporary refuges from wolves, and Bergerud (1989) and Bergerud et al. (2014) reported that islands protected from wind were rarely ice-free and were not frequented by caribou.

The presence of land-fast ice resulted in a greater presence of wolves along the shoreline, and therefore increased the frequency of predation on woodland caribou (Bergerud et al. 2014). Wolves were able to force inverse density dependence and population decline in PNP caribou when land-fast ice enabled them to cross Lake Superior to the islands. The only instances of predation on caribou on offshore islands were observed when land-fast ice connected the islands to the mainland and wolf tracks were observed crossing the ice (Bergerud et al. 2014). When tracks revealed that wolves had reached an island via land-fast ice, caribou tracks were also observed leaving said island. Caribou had also been killed on the land-fast ice itself (Bergerud et al. 2014).

In winters when land-fast ice provided access to Otter Island (212 ha), the most commonly used refuge island in PNP, the number of wolf track aggregations on the adjacent shoreline was 10.2 ± 1.4. Significantly fewer wolf tracks were counted in nine years with minimal land-fast ice coverage, while no wolf tracks were observed along the entire coast in years with no land-fast ice. Wolves were also most commonly spotted

around Oiseau Bay, where concentrations of refuge islands are present, when land-fast ice occurred (Bergerud et al. 2014).

Given the measurable increase in wolf activity around offshore islands when land-fast ice connected these islands to the mainland, it is not surprising that Bergerud et al. (2014) found lower rates of calf recruitment and higher rates of missing adults during years of extensive land-fast ice coverage. In six winters with some land-fast ice, calves comprised 13.3 ± 1.6% of caribou counted in surveys and the number of adults missing in subsequent-year surveys amounted to 6.8 ± 1.7%, whereas in five winters with very little land-fast ice, both the number of calf recruits was higher (22.6 ± 3.6%) and missing adults were fewer (1.2 ± 2.2%), indicative of higher predator success rates when land-fast ice is present (Bergerud et al. 2014).

Neale (2000) reported that moose winter ranges were significantly closer to the coast of Lake Superior than their summer ranges ($P = 0.003$). However, directional movement from summer to winter ranges was not significantly correlated to movement towards the coast ($P = 0.5$). Of 13 moose winter ranges evaluated, only six moved towards the coast, while seven moved either parallel or away from the coast. There was, however, a statistically significant movement across snow depth zones to lower snow depth zones ($P = 0.000$). Moose moved towards the coast, not necessarily reaching the shoreline. Instead, they seemed to select for low snow depth areas within their winter range. There was no statistically significant trend in range relocation between summer and winter ($P = 0.15$), indicating that ranges provided year-round habitat needs. Moose were also found to move to zones of lower elevation at interiors. Neale (2000) arrived at results somewhat different than those of Bergerud et al. (2014). Bergerud et al. (2014) describes that moose observations were more numerous <10 km from the shoreline

during years of heavy snowfall, and that moose distance was negatively correlated with midwinter snow depth ($P < 0.01$). Bergerud et al. (2014) observed moose for nine years, longer than Neale's (2000) two years, perhaps offering more insight into moose movements.

Support for the use of "balds" as escape features resides with the following findings. Caribou aggregations >200 m from the shoreline most often occurred on these "balds," demonstrating the ability for individuals to adapt behaviors similar to those of other boreal-dwelling caribou (Bergerud et al. 2014). Woodland caribou in both the boreal and mountain ecotypes tend to use high elevation areas like "balds" to spatially segregate themselves from other ungulates that are less agile in rugged, steep terrain, and caribou are therefore able to limit their encounters with wolves (Bergerud et al. 1984; Hatler 1986; Pinard Véronique et al. 2011).

Results of the 2016 Lake Superior Coast Range (LSCR) caribou (*Rangifer tarandus caribou*) aerial survey

A systematic, stratified, aerial survey of woodland caribou was designed and undertaken by the OMNRF and Parks Canada staff in 2016 in order to develop and standardize a survey design to characterize caribou distribution and to estimate caribou population size and recruitment rates of mainland caribou in the LSCR. Transects were delineated between Camp 81 Road (20 km east of Nipigon) and Montreal River to include the mainland, as well as nearshore islands (<5 km offshore) that were greater than 100 ha or on which there were recent caribou observations. Transect spacing was based on methods similar to those used in moose aerial surveys, as well as systematic

caribou surveys conducted at similar altitudes and in similar terrain, which assume that moose and caribou tracks can be reliably detected up to 250 m from the flight path (Oswald 1998; Patterson et al. 2014). These transects were flown with a rotary wing aircraft between late February to early March. Survey flights were conducted on Feb. 22, Feb. 24-26 and Mar. 1-5, 2016, and breaks in transects flown were due to violations of appropriate survey conditions. None of the transects south Gargantua Bay in Lake Superior Provincial Park were completed due to poor survey conditions that extended from Mar. 5 to Mar. 31, 2016.

Results from this survey, as well as personal communication with Northwest Regional Planning Biologist Glen Hooper, appear to offer some support for the selection of the region between Terrace Bay and Marathon as the study site. A minimum of 10 animals were estimated to be associated with four groupings of caribou sign (Fig. 8). A minimum of four animals, two per grouping, were associated with two groupings inside the study site (grouping 3 & 4). No caribou sign was detected east of Neys Provincial Park. These findings should not be interpreted as caribou being absent from these areas, as incomplete transects and an inherently low probability of ungulate sign detection along transect lines suggests that sign could have been missed in surveyed areas. Alternatively, the lack of caribou observations is likely more indicative of low density populations persisting in these areas (Shuter et al. 2016).

The population size estimate for the entire study area is 55 caribou, with 95% confidence that the population falls between 13 and 227 individuals. Small sample sizes contributed to the wide confidence intervals. The estimate of caribou population size was based on treating surveyed areas as representative of the study area, and thus the

density of caribou within the surveyed area was applied to the entire study area (Shuter et al. 2016).
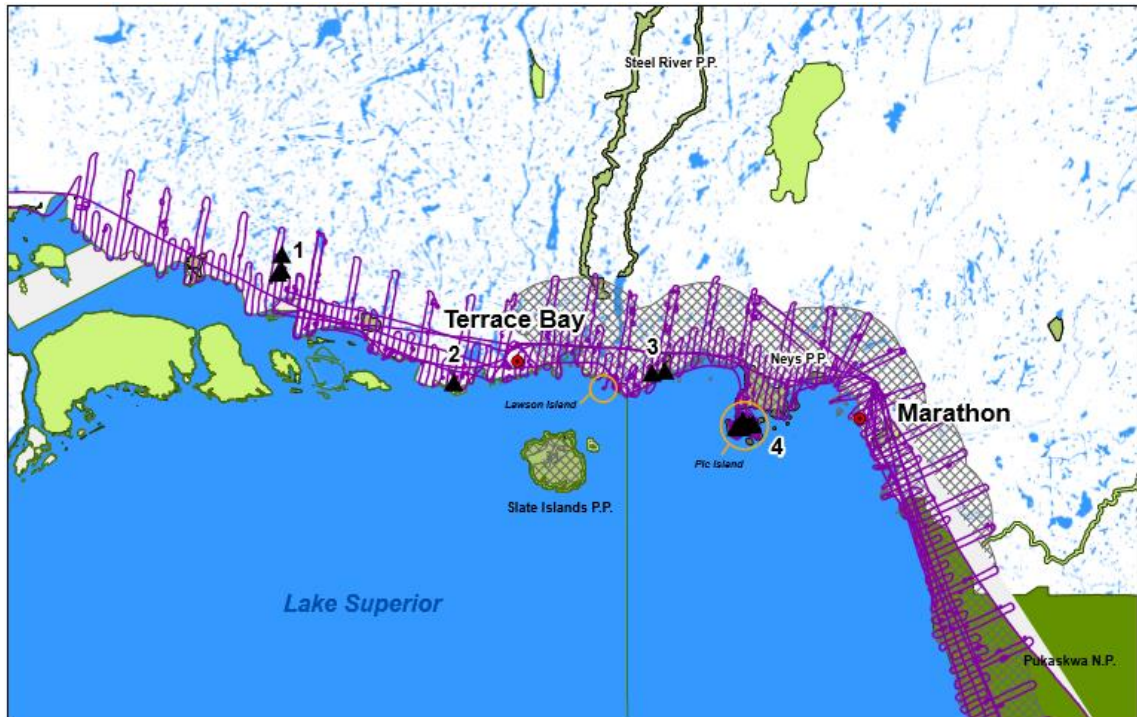
Figure 8. General location of caribou sign derived from the 2016 CNFER survey.

Migrations within the LSCR and exodus from the Slates Islands

Occasional exodus of caribou from the Slate islands to the mainland during winters of ice bridge formation is thought to have contributed to the maintenance of the LSCR population between Terrace Bay and Marathon. About 10 caribou are known to have emigrated from the Slates in the winter of 1978-1979 (B. Snider, personal communication, in Bergerud, 1985). Four animals were documented crossing the ice to the mainland in 2014, and it is likely undocumented migrations have also occurred when

ice bridges formed in other cold winters, facilitating wolf migration onto the Slates and potentially promoting caribou exodus (Ray Tyhuis, personal communication, 2017).

Foster and Harris (2012) synthesized movements of three tagged caribou translocated from the Slates to the mainland in 1984, as part of the Woodland Caribou Impact Assessment for the Marathon Platinum Group Metals Copper Mine Project. These findings offer additional insight into the dispersal habits of caribou emigrating the Slate Islands. Two caribou (one male and one female) occupied areas within the study site for at least a year. The male was documented using the shoreline between the Steel River and Jackfish Bay (Fig. 9). The female caribou traveled both east and west of Victoria Cape (peninsula immediately west of Jackfish Bay), traveling as far east as Prairie River, and well west of the study area, almost reaching Rossport. A third caribou had a tremendous journey over a nearly three-year period. It travelled eastward from Victoria Cape, occupying Neys Provincial Park and Pic Island in 1985, then joined the Manitouwadge herd in January 1986, then traveled to the mouth of White River in August 1986, dying at the Swallow River in central PNP in April 1987: a total straight line distance of 200 km (Bergerud 1989; Foster and Harris 2012).

Despite documented occupancy of the study area by Slate Islands animals, genetic analyses of woodland caribou populations on Pic Island conclude that individuals on the Slate Islands and Michipicoten Island are more closely related to those in PNP, while caribou on Pic Island are more closely related to those in the Hearst area (Drake et al. 2015, 2018). These results are based on fecal samples of five individuals from PNP and not preclude migrations from the Slates towards the study area, but perhaps demonstrate continued connectivity from the discontinuous distribution to the north and Pic Island. One sample collected at the north end of PNP

was more closely related to samples from Pic Island and Hearst, perhaps supporting the continued connectivity hypothesis, given its location relative to Pic Island and Hearst when compared to the other four samples, which were located towards the center of PNP at Otter Island.

It is worth noting that during the time this thesis was undertaken, the author and the supervisor became aware that populations on the Slates Islands and Michipicoten Island approached extirpation. Caribou on both islands were reduced within a few years by the immigration of wolves to the islands over ice bridges in 2014. The herd on the Slate Islands had been reduced to 2-4 males, which had been occupied by several hundred animals in the 1990s (Bergerud et al. 2007). Similarly, the Michipicoten population was reduced to 20 individuals, half of which were airlifted to the Slates, while the other half were airlifted to Caribou Island in an effort to retain this small island population. Should caribou become extinct from the Slates and Michipicoten Island, it may have serious implications on the future of caribou between Terrace Bay and Marathon, Ontario.

METHODS

Determining and mapping various indices of ruggedness along the coast of Lake Superior between Terrace Bay and Marathon was the first priority of this project. Five additional main habitat variables were chosen based on the literature review: elevation, based on the use of "balds" or high elevation areas, caribou refuge habitat (%), moose growing season forage density (kg/ha), distance to the Lake Superior shoreline, and distance to refuge islands. Further explanation and rationale for choosing these variables is presented in the following sections.

DATA PREPARTION & STUDY SITE SELECTION

A data sharing agreement was signed with the OMNRF to secure caribou location data between Terrace Bay and Marathon. A total of 172 entries existed between Terrace Bay and Marathon, Ontario. Entries that were not point locations were eliminated immediately. They included an extensive network of mapped caribou trails adjacent to the Steel River, and a polygon covering the entire Coldwell Peninsula, which described when an estimated eight caribou arrived on the peninsula from Pic Island in the winter of 1975. Point entries included both observations of individuals and caribou sign. There was a significant amount of variability associated with search effort and reliability of the points. Certain points were delineated from aerial transects and

confirmed by OMNRF biologists, while other point locations were derived from public observations. However, no distinction was made between the type of observation or the search effort for each point to maintain as many caribou locations as possible in the analysis.

All points occurring after 1985 were eliminated, as an analysis of recent forest resource inventories was necessary to map refuge habitat and moose growing season forage. Given that inventories used were sourced generally between 2005-2007, it was reasoned that a 30-32-year time lag would be the maximum allowable time difference to assess forest composition and structure. The number of points was consequently reduced from 172 to 85. Reducing this limit to 10 or even 20 years would have limited an already compressed data set. Caribou locations observed on Pic Island were also eliminated, as it was reasoned that caribou residing on Pic Island would not be actively searching for escape features related to terrain or forest type, as the island itself presents a significant refuge from predators. Furthermore, if caribou had spent their entire life on Pic Island, it is possible that they may have a lessened behavioral response to predators compared to individuals on the mainland where wolves are much more common. Bergerud et al. (2017) observed this phenomenon on the Slate Islands, which was absent from wolves except for 1993-1994 and 2003-2004. Eliminating Pic Island from the study area reduced the number of caribou locations from 85 to 55.

Caribou locations occurring north of Highway 17 were also eliminated, given that only 4/55 points were present north of this line. A 1.5-km buffer was placed east of Terrace Bay and West of Marathon, in order to eliminate bias associated with the exponentially greater potential for public observations in these centers compared to other, more remote areas along the coast. The data set was reduced to a final count of 49

caribou points. Boundaries for the study area were then delineated (Fig. 9), and within it 490 random points (10 times the number of caribou points) were generated to be used in a binary logistic regression (resource selection function) predicting the caribou points.
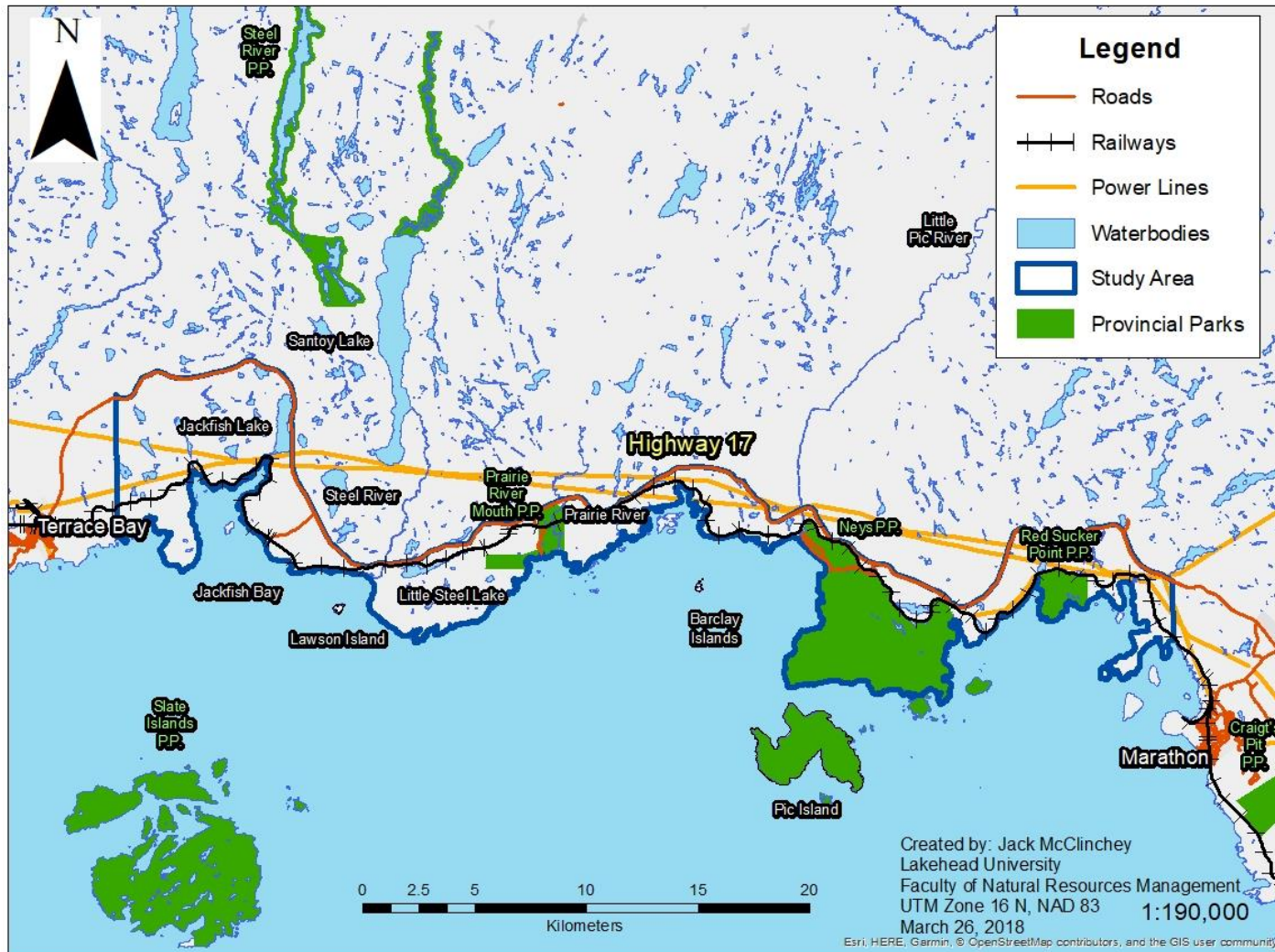
Figure 9. Significant waterbodies, streams, bays, islands, Provincial Parks and towns in the study area.

CARIBOU AND MOOSE HABITAT MEASURES

Mapping a measure of what is considered typical caribou habitat in the boreal forest and mapping moose carrying capacity in the study area were necessary components of this thesis. Ontario's Landscape Tool (OLT) was selected to map these features. It projects a relatively simple spatial representation of prescriptive and evaluative indicators on the landscape using forest resource inventories (FRI) (Elkie et al. 2013). Such inventories encompassing the study area were acquired and imported into the tool from the Kenogami Forest Management Unit and the Marathon Block, which incorporates the Pic River, Big Pic, White River and Nagagami Forest Management Units.

Caribou refuge habitat is measured at several spatial scales, including 500, 6000 and 30,000 ha. The simplest measure of caribou refuge habitat identifies the proportion of suitable refuge forest units within 0.8-ha polygons (Appendix I) (Elkie et al. 2013). Winter habitat was excluded as a variable, as it is incorporated into refuge habitat (Appendix I), which is already limited in the study area (Figure 15). Refuge habitat is described as year-round habitat, and therefore it was an appropriate measure given the limited number of caribou points derived from year-round observations. Further descriptions of refuge habitat are found in Elkie et al. (2013, 2014).

Moose growing-season forage density (kg/ha) was chosen a measure of moose carrying capacity or moose occupancy. Other candidate measure of moose habitat included moose carrying capacity, range, and cover, all of which had measure for both the growing and dormant seasons. Measures of carrying capacity, range and cover

produced almost uniform results across the entire study area. Measures of forage produced the most stand-level, and thus practical results, as they identify biomass of forage in 1-ha polygons. Similar to winter and refuge caribou habitat, in a preliminary analysis, moose growing-season forage mostly captured dormant-season browse. The total area of high-density dormant season browse was considerably less than that of growing season forage, but where present, there was considerable overlap in the biomass values derived for the dormant and growing seasons.

REFUGE ISLAND SELECTION

The classification of islands as refuge was based on the criteria set out by Bergerud (1989) and Bergerud et al. (2014), as synthesized in the literature review. Islands had to be >5 ha, less frequently connected by ice to the mainland than adjacent counterparts, and "far" from shore. There was no definitive measure of frequency of winter access to the shoreline or distance from the shore. Further, accessing consistent coverage of ice data was difficult, and limited by consistent cloud coverage, likely due to the lake effect and rising topography in the study area. The characteristics of the most frequently used refuge islands in PNP were thus further investigated. Bergerud (1989) and Bergerud et al. (2014) described three primary refuge islands in their observations of caribou over a nearly 30-year period. From north to south, the main refuge islands include One-Lake Island (a group of three islands totalling 23 ha), Refuge Island (5 ha) and Otter Island (212 ha). None of these islands was sheltered by harbours, bays or peninsulas, and they averaged roughly 400 m from the nearest point on the adjacent shoreline. Thus, island in the study area which were considered refuge were delineated

based on the degree to which they were sheltered by harbours, bays, or peninsulas assuming a prevailing wind from the west, provided that they were at least 400 m from the nearest point on the adjacent shoreline and greater than 5 ha in area.

MAPPING

All of the five habitat variables were mapped using ArcGIS. Outputs from OLT were imported into ArcGIS and elevation was mapped using a digital elevation model (DEM), while values of ruggedness were derived from this DEM. Measures of habitat variables were then determined at each random point and caribou location. Raster and vector values for ruggedness, elevation, refuge habitat and moose forage density were extracted at each point with the "Extra raster values" tool for raster images and "Join by location" tool for vectors. The distance to the various refuge islands and the shoreline was determined by measuring the distance between each point and the closest point on either the shoreline or the shoreline of the closest island with the "Near" tool.

RESOURCE SELECTION FUNCTIONS

Model Sets

Three different model sets were created to explain the distribution of caribou points along the Lake Superior coast. The first set included the distance to difference combinations of islands. In this model set, the three models included the distance to three refuge islands based on Bergerud's (1989) and Bergerud et al.'s (2014) criteria

(D3), the distance to Pic or Slates Islands (D2) and the distance to Pic island (D1). Model D2 was a hypothesis that the Terrace Bay area islands were acting as a source for caribou in the study area, and that caribou became subject to inverse-density dependence shortly after arriving to the mainland (Ferguson 1982; Bergerud 1985; Ferguson et al. 1988). Model D1 was based on the idea that Pic Island is closer to the mainland than the Slates, and because it has a greater number of confirmed observations compared to other refuge islands, as well as the body of literature describing its importance as a refuge island to caribou occupying the mainland coast (Ferguson 1982; Ferguson et al. 1988; Neale 2000).

The second model set included models of independent variables. The results of the first model were incorporated into the independent variable model, as the best distance to islands (m) model was selected as an independent variable. Other models in the second set included ruggedness (VRM), elevation (m), moose forage density (kg/ha) and refuge habitat (%). Once the results of the second model set were reviewed, only those models performing as expected were used to form a multiple-factor model set.

Akaike's Information Criterion

Resource selection functions were built to obtain values proportional to the probability of use of each of the tested variables (Boyce et al. 2002). Model comparisons used Akaike's Information Criterion (AIC), which estimates the quality of a statistical model relative to a collection of models for a given set of data (Akaike 1973; Wagenmakers and Farrell 2004). A binary logistic regression was estimated in SPSS

version 22 and the relative weight of each model was calculated using Akaike weights,

following Wagenmakers and Farrell's (2004) formulas:

$$AIC_i = -2Log\ likelihood + 2Vi \qquad \text{Equation (1)}$$

where Vi is the number of variables in model i. Raw AIC values for each of the tested

variables were then transformed into relative weights the following formula:

$$w_i\ AIC = \frac{exp(-0.5(\Delta_i AIC))}{\sum_{k=1}^{k} exp(-0.5(\Delta_i AIC)} \qquad \text{Equation (2)}$$

where

$$\Delta_i AIC = AIC_i - min\ AIC$$

RESULTS

RUGGEDNESS INDEX SELECTION

Whether used in the context of predator avoidance, insect avoidance, forage availability, or snow depth, ruggedness measures in past caribou habitat models have followed similar methodologies. A review of the literature on ruggedness in caribou resource selection functions concludes that Beasom et al.'s (1983) and Sappington et al.'s (2007) ruggedness indices are the primary measures of ruggedness referenced in previous of caribou habitat models. Further, ruggedness has been incorporated in habitat models of mountain caribou (Apps and Kinley 2000; Apps et al. 2001) and certain Arctic populations (Nellemann and Thomsen 1994; Nellemann and Fry 1995; Wilson et al. 2012). Beasom et al. (1983) quantified ruggedness by assessing the total length, or density, of topographic contour lines in a given area, and dubbed this measure the land surface ruggedness index (LSRI). Nellemann and Thomsen (1994) and Nellemann and Fry (1995) outlined a terrain ruggedness model for reindeer populations in Norway, using a variation of Beasom et al.'s (1983) index. They incorporated both the number of contour lines and the number of fluctuations ("ups and downs") in a given area, defined by the number of separate aspects along the transects. This modified LSRI perhaps increased the accuracy of the index to true terrain ruggedness.

More recently, Riley et al. (1999) established the terrain rugged index (TRI). They were attempting to create a quantitative and easily comparable measure of terrain

heterogeneity, as they felt existing models (Beasom et al. 1983; Nellemann and Thomsen 1994; Nellemann and Fry 1995) were too labour intensive and site specific. This measure computes the sum change in elevation between grid cells of a selected size and eight neighbor grid cells using a Digital Elevation Model (DEM) paired with Geographic Information Systems (GIS).

The Vector Ruggedness Measure (VRM) derived by Sappington et al. (2007) appears to be best suited for this thesis. Sappington et al. (2007) wanted to quantify escape habitat for desert bighorn sheep (*Ovis canadensis nelsoni* Merriam) in the American Southwest, while remaining skeptical of the independence of existing ruggedness measures (Beasom et al. 1983; Nellemann and Thomsen 1994; Nellemann and Fry 1995; Riley et al. 1999) to slope and elevation. It was emphasized that separating ruggedness from slope could be important as bighorn sheep may perceive these characteristics differently when assessing escape terrain. Further, a sheep's perception of escape terrain may vary as a function of the physiography of the mountain range. Sappington et al. (2007) compared their VRM to the TRI and LSRI to determine which index was most independent of slope and elevation, and therefore the truest measure of ruggedness (Fig. 10). Three separate mountain ranges in the Mojave Desert of the American Southwest including the Black Mountains, the Eagle Mountains and the Eldorado Mountains, were utilized as test sites for the comparison of the three indices.
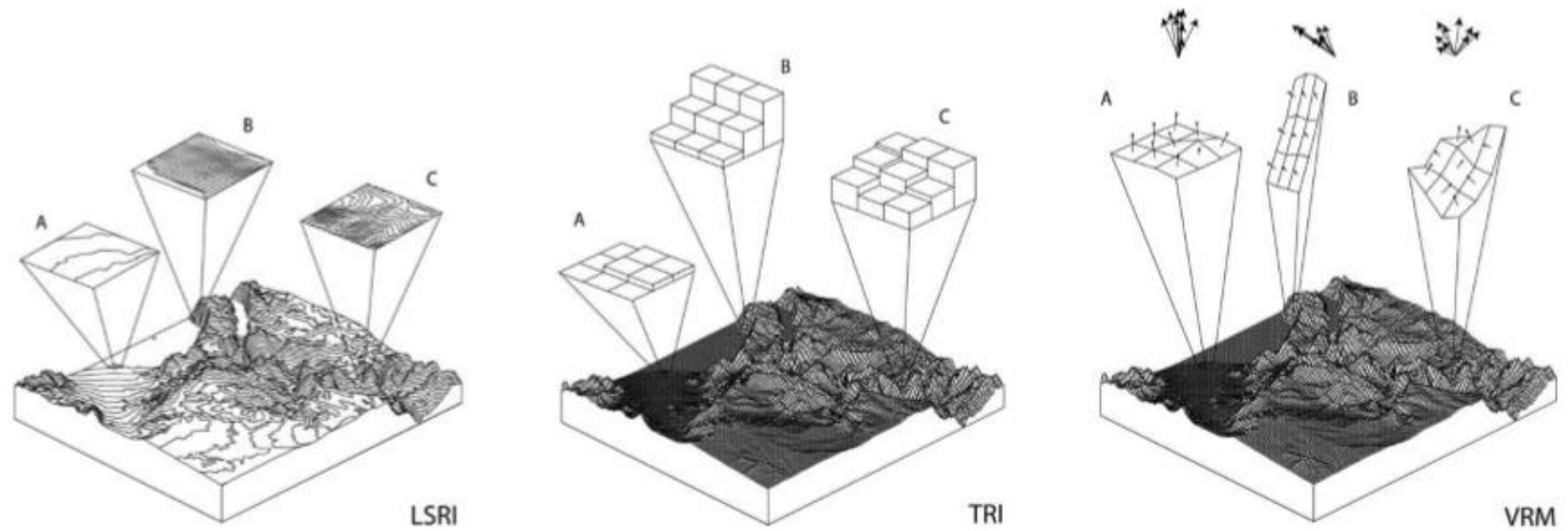
Figure 10. Graphic representation of three common methods for measuring landscape ruggedness, from left to right; Landscape Ruggedness Index (LSRI), Terrain Ruggedness Index (TRI) and the Vector Ruggedness Measure (VRM). Source: Sappington et al. (2007).

VRM values were created in an ArcView script by Sappington et al. (2007) to calculate the three-dimensional dispersion of vectors normal to grid cells composing each landscape. Sappington et al. (2007) adapted the VRM from Hobson's (1972) method for measuring surface roughness in geomorphology, which considers heterogeneity of both slope and aspect. This measure of ruggedness uses three-dimensional dispersion of vectors normal (orthogonal) to planar facets on a landscape (Fig. 8). Using Spearman's rank correlation, Sappington et al. (2007) found that point measurements of LSRI and TRI were highly correlated with slope in all three mountains ranges ($r > 0.9$ for all ranges). In contrast, the correlation between VRM and slope was much lower in the Eldorado Mounts ($r = 0.713$) and even less in the Eagle Mountains ($r = 0.418$) and the Black Mountains ($r = 0.312$). There was much more variation in the patterns of correlation between slope and ruggedness when comparing the VRM to the LSRI and TRI. Additionally, the LSRI and TRI were so heavily dependent on slope that low values for these indices were not possible when slope was high. VRM was able to differentiate smooth, steep hillsides from irregular terrain that varied in gradient and aspect. This was most evident along a gradual escarpment on the western side of Black Mountains. Random points along the escarpment yielded relatively small values of VRM, but high values of slope, LSRI and TRI. Given these findings, the Vector Ruggedness Measure was chosen for this thesis.

REFUGE ISLAND SELECTION

Three islands were deemed appropriate as refuge: Lawson Island (12 ha), Barclays Islands (3 small islands totalling 9 ha) and Pic Island (1038 ha), together on

average 1200 m from the Lake Superior shoreline. Other islands greater than 5 ha in size

were most often excluded on the basis of being sheltered by landforms such as bays,

peninsulas or other islands, offering more regular winter access to wolves over land-fast

ice (Fig. 11). This set included, from east to west, St Patrick Island (15 ha), McKellar

Islands (56 ha), Foster Island (4 ha), Detention Island (59 ha), Hawkins Island (70 ha),

and Blondin Island (30 ha). The average distance of non-refuge islands from shoreline

was roughly 380 m. Hawkins and Blondin Island were also assessed as being close to

the town of Marathon and it was rationalized that utilization of these islands may have

been lessened due to this proximity. This selection of refuge islands matches the caribou

survey described by Shuter et al. (2016), who observed caribou sign on Pic Island, and

in their report noted that an observation had occurred on Lawson Island in the past 10

years.

HABITAT VARIABLE MAPS

The most rugged part of the study area, and the area with the greatest changes in

elevation, was Neys Provincial Park, (Fig. 9, 12-13.) Other rugged areas included

Victoria Cape (peninsula west of Jackfish Bay) and the shoreline east of Lawson Island.

Refuge habitat and moose growing-season forage density measures performed well,

because refuge habitat was non-existent where moose growing season forage densities

exceeded 30 kg/ha. (Fig. 14-15). Moose growing season forage density was high in Neys

Provincial Park, in a region stretching south of Little Steel Lake towards the shoreline, at

the mouth of Prairie River and immediately east of Jackfish Bay (Fig. 9 & 14). The

most significant patches of refuge habitat were a semi-contiguous tract extending from

Victoria Cape north towards Highway 17 and a patch between Lawson Island and the

Prairie River (Fig. 9 & 15).
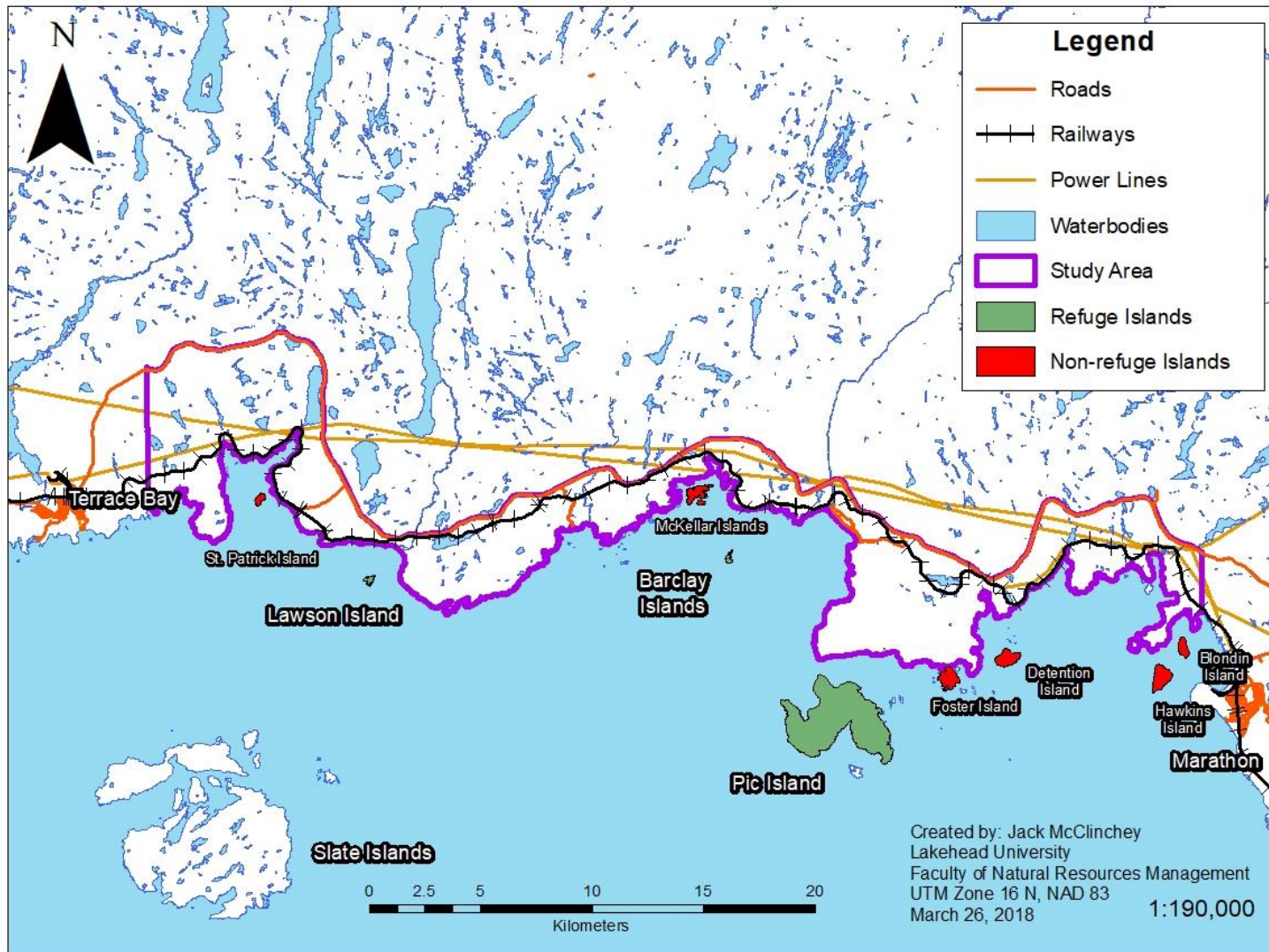
Figure 11. Woodland caribou refuge and non-refuge islands in the study area between Terrace Bay and Marathon, Ontario.
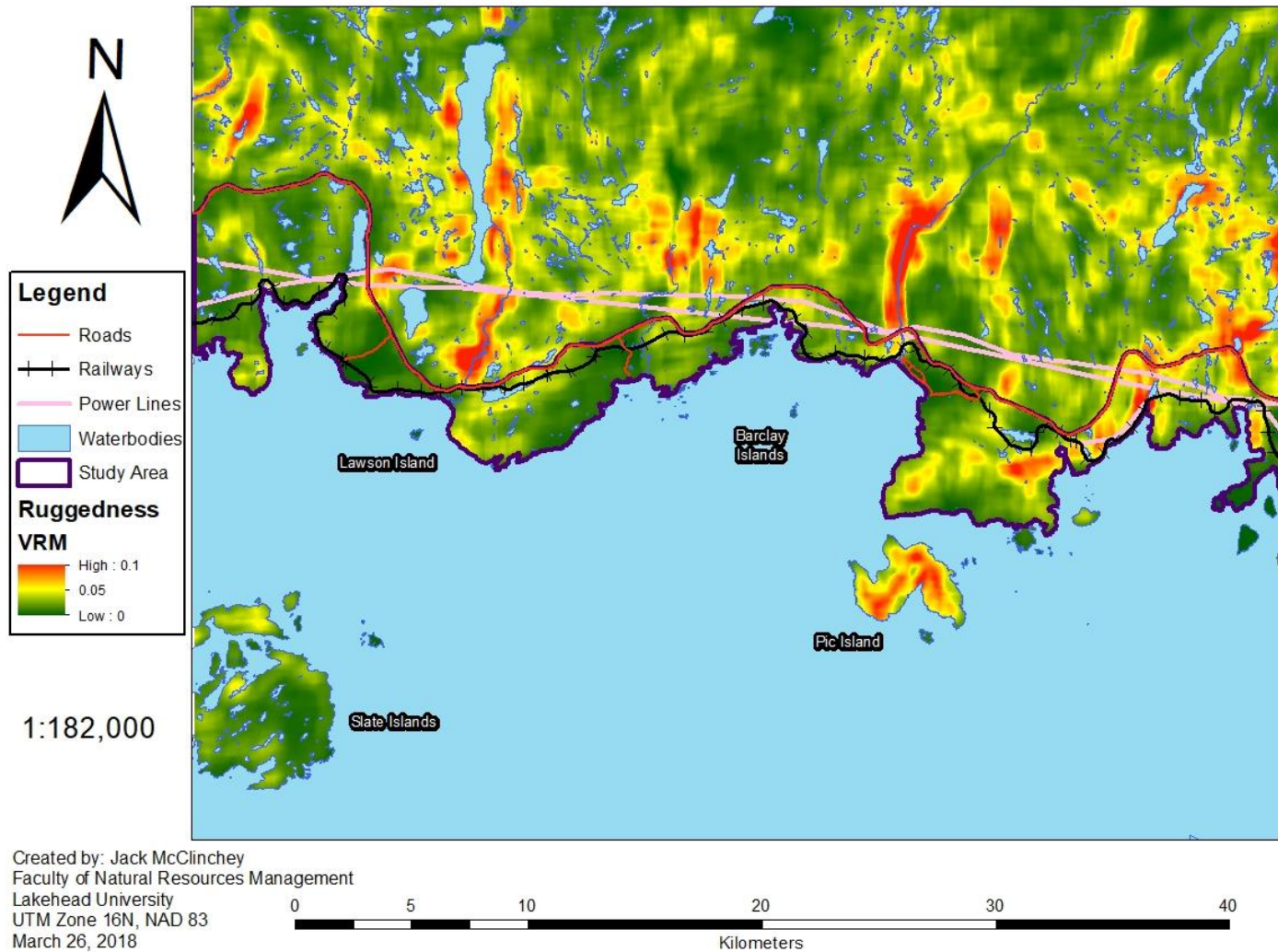
Figure 12. Terrain ruggedness values according to the vector ruggedness measure (VRM) in the study area between Terrace Bay and Marathon, Ontario.

Legend

— Roads
─┼─ Railways
— Power Lines
▨ Waterbodies
▢ Study Area

600
380
160

1:182,000

Lawson Island

Barclay Islands

Pic Island

Slate Islands

Created by: Jack McClinchey
Faculty of Natural Resources Management
Lakehead University
UTM Zone 16N, NAD 83
March 26, 2018

0 5 10   20   30   40
Kilometers

Figure 13. Digital elevation model (m) in the study area between Terrace Bay and Marathon, Ontario.

Figure 14. Moose growing season forage density (kg/ha) in the study area between Terrace Bay and Marathon, Ontario.
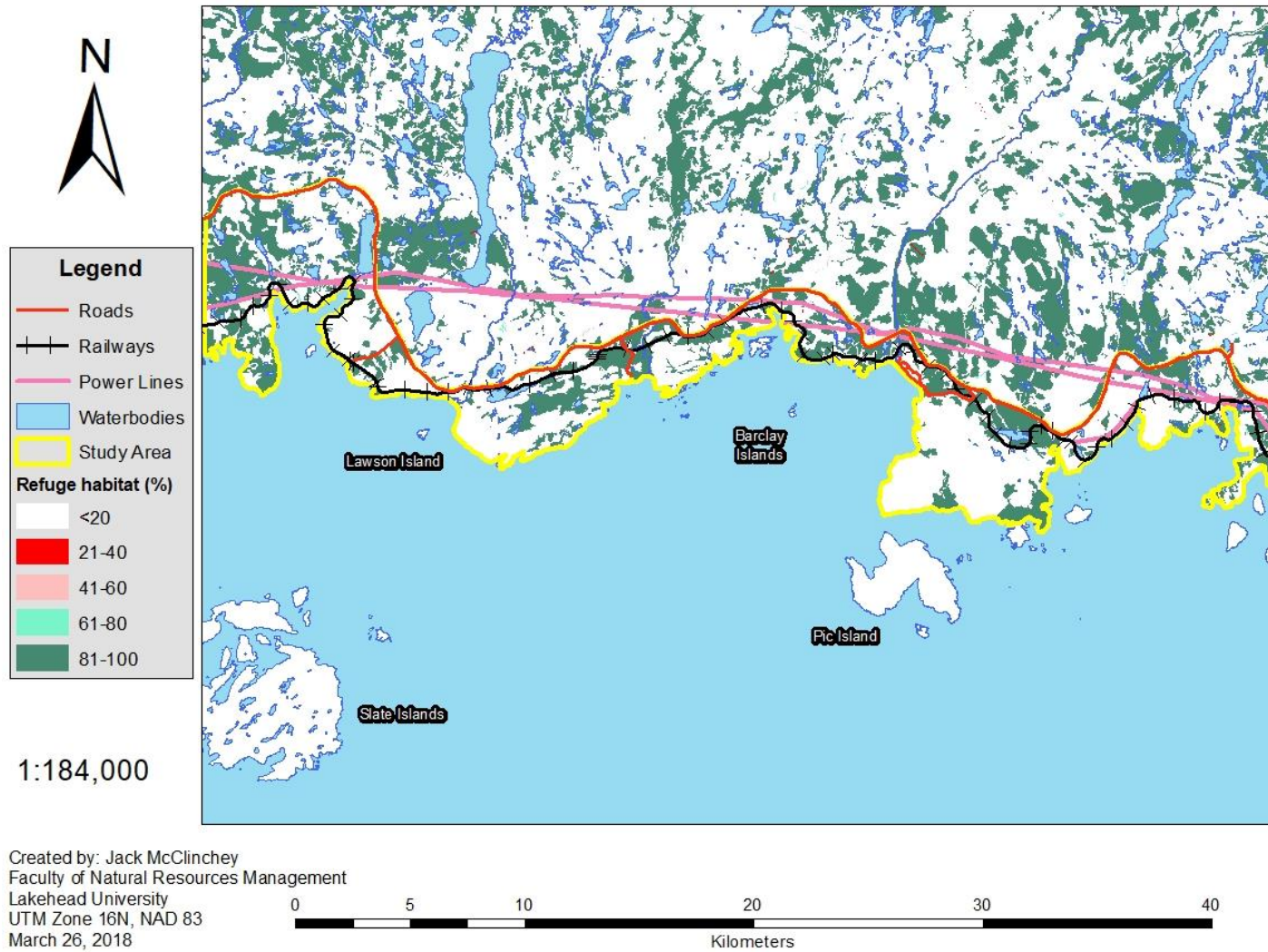
Figure 15. Woodland caribou refuge habitat (% suitability of 0.8ha polygons) in the study area between Terrace Bay and Marathon, Ontario.
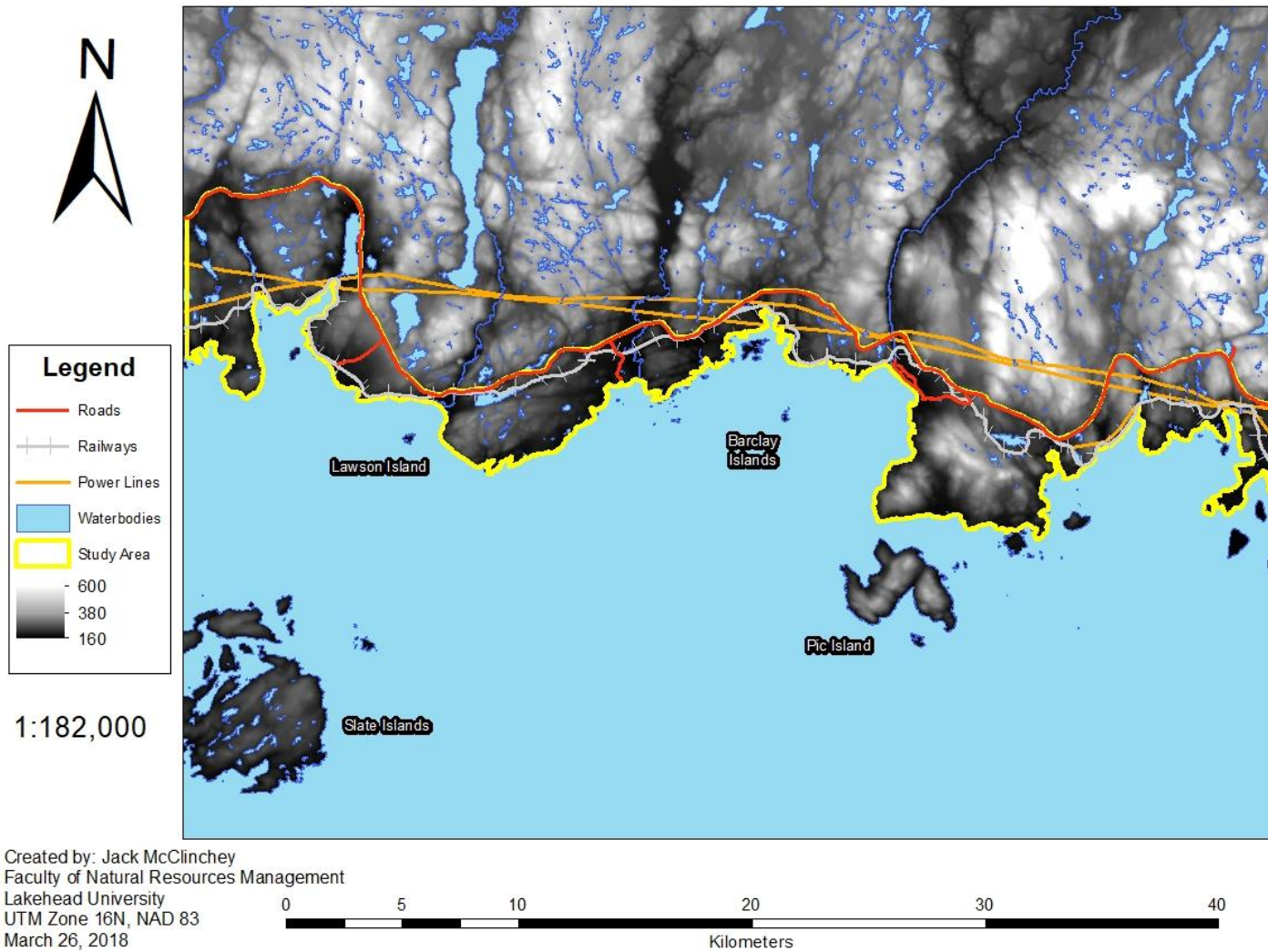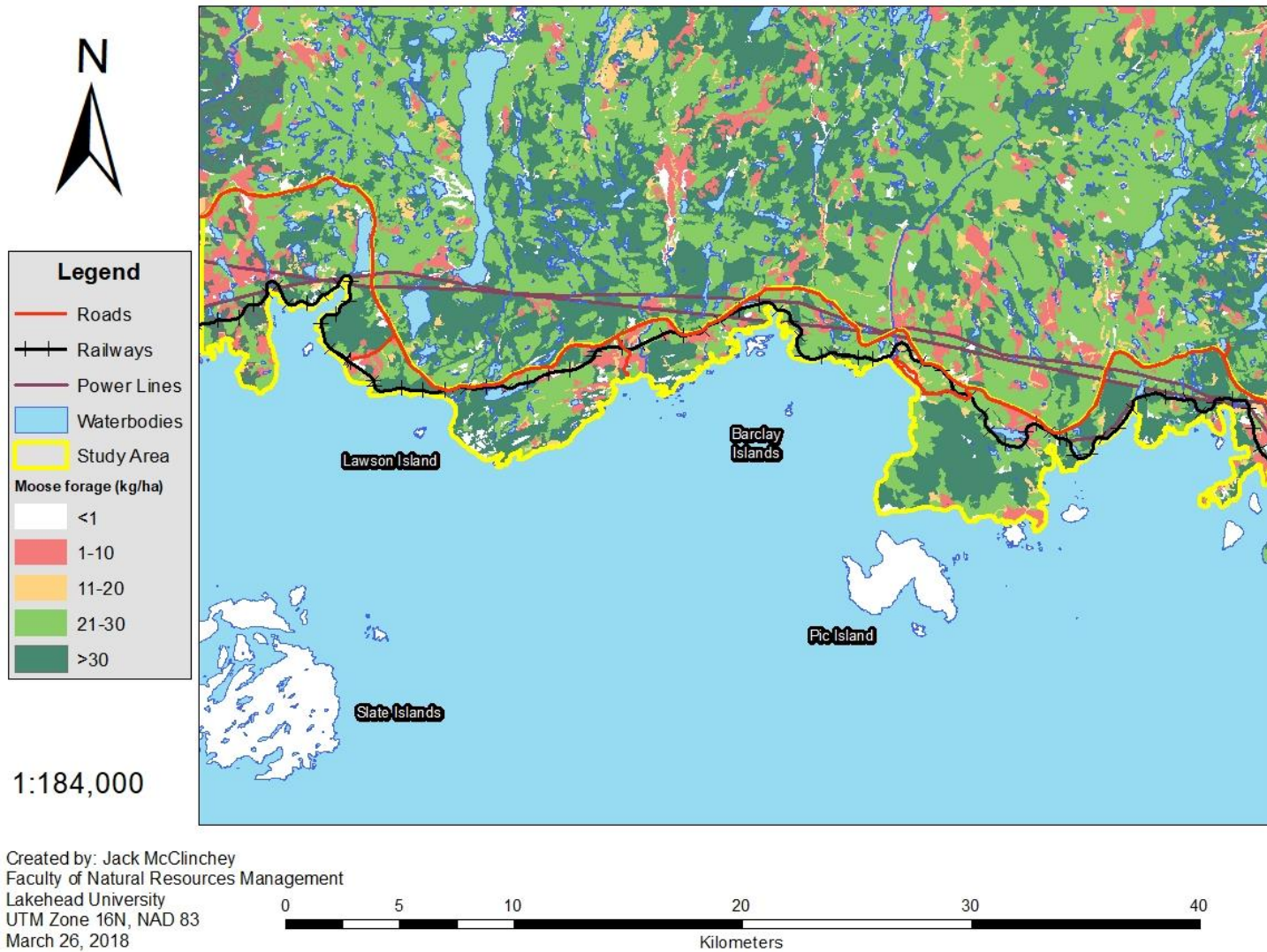
RESOURCE SELECTION FUNCTIONS

Based on the distance to islands model set, it appears that distance to the three refuge islands (D3) best fit the distribution of caribou in the study area when compared to distance to Pic or Slates (D2) and the distance to Pic (D1) (Table 2.). Caribou were also distributed significantly closer to both Pic and Slate Islands ($P = 0.02$), as well as Pic Island alone ($P = 0.001$), when compared to randomly generated points. Based on its AIC weight, the D3 model was 49 times more likely to be the best model compared to the next best model (distance to Pic & Slates).

Table 2. Distance to refuge islands model set for woodland caribou along the Lake Superior coast in Ontario, Canada, 1985-2018.

Model	No. of parameters	-2 Log likelihood	AIC	ΔAIC	wAIC	β	P
D3 (Lawson, Barclays, Pic)	3	310.493	312.493	0	0.98	-0.379	0.001
D2 (Pic or Slates)	2	319.596	320.596	8	0.02	-0.230	0.02
D1 (Pic)	1	385.711	387.711	74	0.00	-0.143	0.001

The D3 model was incorporated into the new independent model set, which included distance to the Lake Superior shoreline, moose growing-season forage density (kg/ha), ruggedness (VRM), elevation (m) and refuge habitat (% occupancy of polygons; Table 3). The D3 model was again the best model in the independent model set. In fact, based on its Akaike weights, the D3 model was over 1 650 000 times more likely to be the best model explaining caribou distribution when compared to the next best independent variable model, which was the distance to the shoreline (Table 3). Caribou were also significantly distributed away from 1-ha polygon areas were moose growing-season forage densities were high ($P = 0.001$). Ruggedness did not perform as expected,

as caribou were significantly distributed away from rugged terrain ($P = 0.001$).

Similarly, caribou avoided high-elevation areas and 0.8-ha polygons with high

percentages of refuge habitat ($P = 0.001$; Table 4).

Table 3. Independent variables model set for woodland caribou along the Lake Superior coast in Ontario, Canada, 1985-2018.

Model	No. Par	-2 Log likelihood	AIC	ΔAIC	wAIC	β	P
D3	1	310.493	312.493	0	1.00	-0.379	0.001
Shoreline	1	348.346	350.346	38	0.00	-2.670	0.001
Moose	1	419.894	421.894	108	0.00	-0.071	0.001
Ruggedness	1						
Elevation	1						
Refuge	1						

Table 4. Variable coefficients, chi-square values and probability values of models performing against predicted outcomes for woodland caribou distribution along the Lake Superior coast in Ontario, Canada, 1985-2018.

Model	No. Par	β	P	Wald (x^2)
Ruggedness	1	-205.722	0.001	150.495
Elevation	1	-0.009	0.001	225.469
Refuge	1	-0.23	0.001	80.407

Variables performing as expected and those that significantly explained the

distribution of caribou in the study area were combined into a multiple factor model set

(Table 5). The D3 model was combined with the shoreline variable and growing-season

forage densities were incorporated with these two factors in a separate model. Further,

the D3 model was combined with the moose-forage density model and a final model was

tested including moose growing-season forage density and the distance to the shoreline.

The distance to three refuge islands (D3) and the distance to shoreline variable

comprised the best multiple-factor model, predicting the caribou points 1.27 times better

than the next best model. When moose growing-season forage density was added to this

model, this variable was not a significant predictor of caribou distribution ($P = 0.220$).

The other models were not comparable. The difference in AIC values between these

models and those which were reported was greater than 2.

Table 5. Multi-factor model set for woodland caribou along the Lake Superior coast in Ontario, Canada, 1985-2018.

Model	No. Par	-2 Log likelihood	AIC	ΔAIC	wAIC	P (D3)	P (S)	P (M)
D3 + Shoreline	2	297.680	301.680	0	0.56	0.001	0.001	0.001
D3 + Shoreline + Moose	3	296.127	302.127	0	0.44	0.001	0.001	0.220

DISCUSSION

PITFALLS IN METHODOLOGY

Before interpreting the results of this thesis, I will provide context on their

significance and discuss some of their limitations. Major deficiencies in the

methodologies of this thesis included the time between caribou observation and

classification of forest-related attributes, high variability in quality of the caribou

observations, and uncertainties in the success of the Vector Ruggedness Measure. The

Ontario Landscape Tool (OLT) outputs to map caribou refuge habitat and moose forage

density are the most compromised by the first issue, because of various ages in the FRI

for the Kenogami Forest Management Unit, and the collective Marathon Block, which

incorporates the Pic, Big Pic, Nagagami and White River Forest Management Units.

There may have been up to a 35-year difference between the time of a caribou

observation and the classification of habitat variables. Even in the absence of large-scale

fires in the study area since that time, forest stand characteristics such as age, species

composition and canopy closure would have undoubtedly changed in the study area.

On the second issue, certain points were delineated during helicopter flights to

locate radio-collared animals and multiple hours of flight time were undertaken to

observe caribou tracks. Other points were derived from public observation of individual

caribou. There was also considerable variation in the type and age of caribou sign

observed, as certain signs included very fresh cratering activity, while many signs were

acknowledged as "old" observations of caribou tracks. Considering all points as equal representations of caribou habitat selection likely compromised the comparison of the predictive model sets. Finally, the use of the Vector Ruggedness Measure may have led to uncertainty in the classification of rugged terrain in the study area. This measure was designed based on the topography and relief in the Mojave Desert. The neighbourhood size used in the evaluation of rugged terrain was 8100 m^2. It quite possible that ruggedness was over-or underrepresented in the study area given either the use of an overly large or overly small neighbourhood size.

STUDY SITE ECOLOGICAL CHARACTERISTICS

It is likely that the condition of the forest has remained relatively consistent over the course of the study period, supporting high densities of moose at least since their hypothesized arrival to the study area in the early 20th century (Peterson 1955a, 1955b). Newmaster (2010) differentiates the boreal forest in the study site from more continental locations inland from Lake Superior, as the lake effect significantly prolongs fire return intervals along the coast. Trees along the Lake Superior coast are not very old, but it is suspected that significant stretches of forests within the study site have not been disturbed for hundreds or even thousands of years. Lightning strikes along the Lake Superior coast often result in single-tree fires. As a result, extensive byophyte and lichen communities occur that are otherwise not common to the boreal forest, and they occur on specific habitats.

Newmaster (2010), as well as OMNRF staff Steve Kingston and Glen Hooper (personal communications, 2017), describes forests in the study area dominated by white birch (*Betula papyrifera* Marshall), white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill). All of these species are capable of self replacement in the absence of a stand-replacing fire (Newmaster 2010). Especially white birch can self-replace from basal sprouting when small canopy gaps are formed, although this species is conventionally thought of as a shade-intolerant pioneer species (Kneeshaw and Bergeron 1998; Bouchard et al. 2006; Taylor and Chen 2011). White birch is also a significant source of moose browse (Naylor et al. 1999).

Hence, without large-scale disturbances, and a forest composed of species with self-replacement abilities, we can assume that the coast has likely been void of significant areas of black spruce of jack pine dominated stands for hundreds or possibly even thousands of years. In turn, we would expect that refuge habitat would be absent from the study area for the same period, as these stands largely comprise what is classified as refuge habitat in the boreal forest (Appendix I).

CARIBOU HABITAT SELECTION

Barring uncertainty in the vector ruggedness measure, I have rejected the initial hypothesis that rugged terrain is a key habitat feature for woodland caribou in the Lake Superior coast range. Not only did highly rugged terrain fail to predict caribou locations, caribou were distributed away from it; i.e. avoiding, rugged areas. Apps and Kinley (2000) and Apps et al. (2001) suggest that caribou selected rugged terrain and high elevation areas at the broader scale, while they used gentler terrain at the finer scale.

Bergerud and Page (1987) concluded that woodland caribou occupy high elevation areas during the calving period, whereas moose generally occupy lower elevation forested areas during the same period. Rugged and high elevation areas should promote spatial segregation between caribou and larger alternate prey such as moose an elk (Bergerud et al. 1984; Hatler 1986; Pinard Véronique et al. 2011). However, caribou will avoid rugged terrain at the finer scale due to increased energetic cost associated with traveling through undulating terrain compared to flatter areas (Leblond et al. 2011).

The population dynamics of woodland caribou in the study area may also explain their avoidance of rugged terrain. Bergerud et al. (2014) observed that woodland caribou in PNP reduced their activity as the population declined, occupying only the shoreline. Only when the population was higher did movements inland occur towards higher elevations ("balds"), especially during years of land fast-ice formation.

The rejection of refuge habitat as important was an expected result of this thesis. Refuge habitat was limited along the Lake Superior coast (Fig. 15). Avoiding encounters with moose, and consequently wolves, by selecting large contiguous tracts of mature coniferous forests is not a viable survival strategy for caribou in the study area, as the presence of these forests is simply non-existent. Instead, a landscape with birch-dominated and mixedwood forests likely supports high densities of moose and no escape areas (Appendix II). Further, it is worth considering the classification of refuge habitat in the OLT. Refuge habitat includes conifer mixedwood forest, which consists of at least 50% coniferous species; with an onset of 70 years (Appendix I). I argue that this forest unit should not be considered suitable refuge habitat. Mixedwoods most often occur rich sites, and even in the absence of stand-replacing disturbances, regeneration of deciduous shrubs or pioneer species is likely to occur on these stands, renewing moose browse

(Kneeshaw and Bergeron 1998; Naylor et al. 1999; Taylor and Chen 2011). Refuge habitat also includes balsam fir dominated stands, even though balsam fir can act as an important winter food source for moose (Belovsky 1981; McLaren and Janke 1996; Naylor et al. 1999). Without mixedwood and balsam fir dominated stands included, an even more restricted distribution of suitable caribou refuge habitat occurs in the study area, limited only to small patches north of Victoria Cape and at the mouth of Prairie River. However, the Victoria Cape patch, bisected by two powerlines, easily loses its effectiveness as caribou refuge. One of the most significant tracts of refuge habitat in the study area was identified between Steel River and Prairie River (Fig. 9 and Appendix II), but caribou likely actively avoided areas that supported high densities of moose forage within it, as this is a conifer mixed wood stand.

With or without suitable refuge habitat, caribou still actively avoided the highest densities of moose forage ($P = 0.001$) in a landscape dominated by moose habitat (Table 3, Fig. 14 & Appendix II). Caribou are well documented spatially segregating themselves from areas of high moose density in order minimize predation risk, and in fact, caribou ranges are often constrained by extensive areas of mixed or deciduous forest types which harbour high moose densities (James et al. 2004; OMNRF 2014a). The results of this this confirm previous works that caribou will avoid areas of high densities of moose habitat at both the landscape and stand scales (James et al. 2004; Wittmer et al. 2005; Fortin Daniel et al. 2008).

A possible explanation for the poor performance of the shoreline model relative to the D3 model could be the presence of linear landscape features immediately adjacent to the shoreline throughout the study area. Though the negative influence of linear features on woodland caribou in Ontario has already been summarized in the literature

review (OMNRF 2014c), a recently published paper by Newton et al. (2017) offers further insight into the selection of these features by wolves, and the potential consequences on woodland caribou in the study area. Newton et al. (2017) examined the selection of habitat features for 52 wolves in northern Ontario using telemetry data. The study areas included both natural and human altered forests, as they aimed to determine if wolves first selected linear features, and if so, whether selection of anthropogenic linear features was stronger than those which were natural or anthropogenic. Anthropogenic features included primary, secondary and tertiary roads, railways and hydro lines. Natural linear features included the shoreline of large lakes and waterlines (rivers) which were greater than 500m in length and all but the smallest streams. They found that wolves first selected linear features, and as the density of anthropogenic linear features increased on the landscape, selection for those features increased and selection for natural linear features decreased. Wolves did not increase total time on linear features, either anthropogenic or natural, but instead selected for anthropogenic linear features over natural ones (Newton et al. 2017)

The Canadian National Railway literally follows the Lake Superior shoreline from Terrace Bay to Marathon, with the only buffered areas occurring at Victoria Cape, Coldwell Peninsula, and a stretch between Lawson Island and Prairie Cove (Fig. 9). Caribou observations were abundant in all three of these areas (34 out of 49 observations). Where the railway was closest to the shoreline, from Jackfish Bay to Steel River, and from the eastern edge of Coldwell Peninsula to the eastern boundary of the study area, caribou aggregations were minimal (6 observations). Predator travel routes along the railway may be the reason.

The Trans Canada highway confines the northern boundary of study area, and where utility corridors are also present in the study site, immediately north of McKellar Harbour and Jackfish Bay, both of these features could promote moose occupancy and predator movement. The natural linear features in the study area include major rivers, the Steel River, Prairie River, and Little Pic River, all of which run perpendicular to the coast (Fig. 9). Bergerud (1989) and Bergerud et al. (2014) describe the major rivers in PNP acting as both pack boundaries and travel corridors for wolves. The shoreline itself may also act as a natural linear feature, running parallel to the coast. However, the proximity of the railway to the shoreline likely results in consistent selection of this feature by wolves over the shoreline, as travel on anthropogenic features requires less energy and can increase travel rates and hunting efficiency (Whittington et al. 2011; Dickie et al. 2016). If Newton et al.'s (2017) findings can be applied to the study area, then wolves would be more likely to travel parallel to shoreline than perpendicular to the shoreline, selecting the railway and utility corridors over major rivers, increasing the likelihood of encounters with caribou.

The scale of linear features in the study area should also be evaluated relative to the range of woodland caribou in the study area. The study area incorporates approximately 17,000 ha. Though the study area inevitably excludes the total range of woodland caribou that occupy this zone, it still pales in comparison to common range sizes of woodland caribou in Ontario, 300,000 to 500,000 ha (OMNRF 2014a). Thus, even small linear features would be likely to have a proportionally more significant impact on woodland caribou in the study area, as their density relative to the range size would be much higher.

Neale (2000) describes that construction of the coastal hiking trail in PNP began in 1973, which was envisioned to traverse the entire shoreline throughout the park and was halted after it was roughly 50% complete. Concerns were raised regarding the facilitation of human, moose and wolf access to portions of the coast occupied by woodland caribou. Their concerns appeared to be legitimate, as Bergerud et al. (2014) reported increased co-occurrence of moose and caribou along the coastal trail between 1982 and 1986 when compared to more southern portions of the caribou's range in PNP, and later described the range of caribou in PNP becoming restricted to the southern portions of its historical extent, away from the coastal trail. Further, Neale (2000) reported increased instances of bear scat on the coastal hiking trail. Even though Ferguson (1982) concluded that black bears are likely not a significant predator for caribou on Pic Island, even the occasional kill by a black bear might have a significant impact on a small caribou population.

Given the presence of linear landscape features along significant sections of the shoreline, high densities of moose forage and moose habitat in the study area, and limited presence of suitable refuge habitat, caribou are likely selecting refuge islands, which offer the most isolated escape in the models tested and the greatest degree of spatial segregation from moose and wolves. The antipredator strategy of caribou in the LSCR is to reduce their activity to areas that offer the greatest refuge from predators. They are found to have the smallest aggregation size and some of the smallest home range sizes of caribou in North America (Bergerud 1985, 1989). Bergerud et al. (2014) described that caribou in PNP underwent two distinct periods of differing population regulation by predators: density-dependent (DD) regulation (1972-1988) and inversely density-dependant (IDD) regulation (1989-2009). During the DD phase, predation rates

by wolves would increase as caribou populations increased, maintaining a stable carrying capacity of about 24 individuals. The population entered IDD when the overall moose population in PNP declined and consecutive years of heavy snowfall resulted in a proportional increase of moose, and thus wolves, occupying the shoreline, and caribou were extirpated from the park as a result (Bergerud et al. 2014)

As mentioned in the literature review, Ferguson (1982) hypothesized that caribou exiting Pic Island likely became subject to inverse density dependence once they occupied the mainland. Based on a declining number of observations over time within the study area, we can assume that caribou were subject to IDD during the study period or entered this regime of population regulation at some point. Whether caribou along the mainland coast are, or were in, a phase of DD or IDD population regulation during the occurrence of observations reported may be important in explaining caribou habitat selection. Bergerud et al. (2014) noticed considerable differences in caribou activity during the two period of population regulation, and these observations offer clear explanations for the selection of refuge islands as a the primary escape habitat for woodland caribou.

Specifically, Bergerud et al. (2014) found that range sizes and activity levels in PNP were reduced when the population became subject to IDD. The average home range size and distance from the shoreline both decreased significantly ($P < 0.05$ and $P < 0.01$). Further, caribou in PNP began occupying Otter Island significantly more during the IDD period ($P < 0.01$). Woodland caribou in PNP increased their safety net by remaining on Otter Island and other small islands for extended periods of time in an effort to reduce encounters with wolves. Hence, if distance refuge islands is the most parsimonious model explaining woodland caribou habitat selection in the study area, it is

likely they were subject to IDD. Thus, the findings of this thesis would support those of Bergerud et al. (2014), in which declining populations of woodland caribou in the LSCR restrict their movements to refuge islands, and narrow their occupancy of the shoreline to areas close or immediately adjacent to these islands. If woodland caribou in the study area were subject to density dependant regulation by wolves, we might have expected significant results relating to rugged terrain, elevation, and refuge habitat, as well as a stronger performance of the moose forage density and shoreline models.

The poor performance of the distance to Pic or Slate Islands, and the distance to Pic Island models relative to the distance to Barclays, Lawson and Pic Island model does not preclude the importance of these islands to caribou in the study area. Both of these models still delivered significant results (Table 2). The Slates Islands may yet offer a source of caribou to the study area, but it is likely that caribou arriving to the mainland from the Slates travel over a broad region within the study area (Foster and Harris 2012). Pic Island likely continues to act as a significant anchor for caribou on the mainland coast, given recent observations of caribou there and its documented selection over the adjacent mainland (Ferguson 1982; Ferguson et al. 1988; Shuter et al. 2016). In sum, the results of this thesis emphasize the importance of a suite of refuge island, and are consistent with the interpretation of their importance in PNP (Bergerud 1989; Bergerud et al. 2014).

CONCLUSION

The results of this thesis should be interpreted cautiously. A considerable time-lag exists between the classification of forest-dependant caribou habitat and many observations of caribou or caribou sign. There were inconsistencies in the search effort afforded to various caribou points, as certain points included sign of caribou activity, while other points include observations of actual caribou. Many points were derived from systematic linear aerial transects, while others were derived from members of the public.

Having said this, the results show that woodland caribou in the Lake Superior Coast Range between Terrace Bay and Marathon do not appear to be selecting rugged terrain as a means to avoid predation from wolves, rejecting my hypothesis. Rugged terrain likely acts as an important landscape feature to promote the spatial segregation of caribou from moose, who have larger body sizes than caribou and are less agile in steep, rugged terrain. However, within the LSCR, caribou likely select less rugged areas to reduce their own energetic costs.

Wolves have likely subject caribou in the LSCR inverse-density dependence, prompting caribou to restrict their activities to a small area of the shoreline immediately adjacent to refuge islands. Caribou may have selected for higher elevation areas where "balds" occur if the population was higher, and under density dependant regulation.

Caribou did not use refuge habitat and avoided high densities of moose forage. The occurrence of patches of refuge habitat was too sparsely distributed to act as a measure of spatial segregation from moose and wolves, and the misclassification of mixedwoods as refuge habitat perhaps forced caribou to avoid certain patches of refuge habitat.

Refuge islands appear to be the most important escape feature explored, even more so than any random point on the Lake Superior shoreline, likely due to the fact that the shoreline is paralleled by linear features throughout much of the study site. These features are consistently selected by wolves over natural linear features, and they enhance travel and kill rates.

Restricting activity to areas on the shoreline immediately adjacent to refuge islands is not a viable survival woodland caribou in the LSCR, as shown in PNP. Wolves eventually focus their efforts on these islands and can force inverse-density dependence on caribou in years when land-fast ice connects these islands to the mainland. The last stronghold for mainland caribou in the LSCR was shown to exist between Terrace Bay and Marathon in a 2016 aerial survey, as populations have been extirpated from Pukaskwa National Park and Lake Superior Provincial Park. Given the extirpation of woodland caribou from Michipicoten Island, and drastic declines of caribou on the Slate Islands, both of which have likely been sourcing mainland populations, I suggest caribou are destined for extirpation from the Lake Superior Coast Range.

LITERATURE CITED

Akaike, H. 1973. Information Theory and an Extension of the Maximum Likelihood Principle. P. 199–213 *in* Springer Series in Statistics.Springer, New York, NY.

Apps, C., and T. Kinley. 2000. Multiscale habitat modeling for mountain caribou in the Columbia highlands and northern Columbia mountains ecoregions, British Columbia. Aspen Wildlife Research, Calgary, AB

Apps, C. D., B. N. McLellan, T. A. Kinley, and J. P. Flaa. 2001. Scale-Dependent Habitat Selection by Mountain Caribou, Columbia Mountains, British Columbia. J. Wildl. Manag. 65(1):65–77.

Beasom, S. L., E. P. Wiggers, and J. R. Giardino. 1983. A Technique for Assessing Land Surface Ruggedness. J. Wildl. Manag. 47(4):1163–1166.

Belovsky, G. E. 1981. Food Plant Selection by a Generalist Herbivore: The Moose. Ecology. 62(4):1020–1030.

Bergerud, A. T. 1967. Management of Labrador Caribou. J. Wildl. Manag. 31(4):621–642.

Bergerud, A. T. 1971. The Population Dynamics of Newfoundland Caribou. Wildl. Monogr. (25):3–55.

Bergerud, A. T. 1974. Decline of Caribou in North America Following Settlement. J. Wildl. Manag. 38(4):757–770.

Bergerud, A. T. 1978. Caribou. P. 83–101 *in* Big game of North America : Ecology and Management. Schmidt, J.L., and D.L. Gilbert (eds.).Stackpole books, Harrisburg, Pa.

Bergerud, A. T. 1983. The natural population control of caribou. P. 14–61 *in* Symposium on natural regulation of wildlife populations. Forest Wildlife and Range Experimental Station, University of Idaho, Moscow,.

Bergerud, A. T. 1985. Antipredator strategies of caribou: dispersion along shorelines. Can. J. Zool. 63:1324–1329.

Bergerud, A. T. 1989. The Abundance, Distribution and Behaviour of Caribou in Pukaskwa National Park, 1972-1988. Bergerud and Associates, Fulford Harbour, B.C.

Bergerud, A. T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? Rangifer. 16(4):95–116

Bergerud, A. T., and J. P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. Can. J. Zool. 64(7):1515–1529.

Bergerud, A. T., and R. E. Page. 1987. Displacement and dispersion of parturient caribou at calving as antipredator tactics. Can. J. Zool. 65(7):1597–1606.

Bergerud, A. T., H. E. Butler, and D. R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. Can. J. Zool. 62(8):1566–1575.

Bergerud, A. T., W. J. Dalton, H. Butler, L. Camps, and R. Ferguson. 2007. Woodland caribou persistence and extirpation in relic populations on Lake Superior. Rangifer. 27(4):57–78.

Bergerud, A. T., B. E. McLaren, L. Krysl, K. Wade, and W. Wyett. 2014. Losing the predator - prey space race leads to extirpation of woodland caribou from Pukaskwa National Park. Ecoscience. 21(3–4):1–13.

Bergerud, A. T., B. E. McLaren, W. J. Dalton, L. Camps, H. Butler, and R. Ferguson. 2017. Functional Changes to the Slate Islands Provincial Park with Successive Arrival of Wolves, (*Canis lupis*), from the Lake Superior Coast. Can. field-nat (in press). 20 pp.

Bouchard, M., D. Kneeshaw, and Y. Bergeron. 2006. Forest dynamics after successive spruce budworm outbreaks in mixedwood forests. Ecology. 87(9):2319–2329.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecol. Model. 157(2):281–300.

Buechner, H. K., and C. V. Swanson. 1955. Increased natality resulting from lowered population density among elk in southeastern Washington. P. 560–567 *in* Transactions of the North American Wildlife and Natural Resources Conference.

Cringan, A. T. 1956. Some aspects of the biology of caribou and a study of the woodland caribou range of the Slate Islands, Lake Superior, Ontario. M.Sc. dissertation, Zoology, University of Toronto. 300pp.

Cringan, A. T. 1957. History, food habits and range requirements of the woodland caribou of continental North America. P. 485–501 *in* Transactions of the North American Wildlife and Natural Resources Conference.

Cumming, H. G. 1992. Woodland caribou: facts for forest managers. For. Chron. 68(4):481–491.

Cumming, H. G., and D. B. Beange. 1993. Survival of woodland caribou in commercial forests of northern Ontario. For. Chron. 69(5):579–588.

Davis, J. L., R. E. LeResche, and R. T. Shideler. 1978. Size, composition and productivity of the Fortymile caribou herd. Alaska Department of Fish and Game. Federal Aid *in* Wildlife Restoration. Research Final Report. Projects W-17-6 and W-17-7. Juneau, AK. 69 pp.

Davis, J. L., and P. Valkenburg. 1985. Qualitative and quantitative aspects of natural mortality of the Western Arctic Caribou Herd. Juneau, AK. 75 pp.

Dickie, M., R. Serrouya, R. S. McNay, S. Boutin, and J. Toit. 2016. Faster and farther: wolf movement on linear features and implications for hunting behaviour. J. Appl. Ecol. 54(1):253–263.

Drake, C. C., M. Manseau, C. F. C. Klutsch, P. J. Wilson, S. Kingston, and N. Carr. 2015. Genetic Similarities of Woodland Caribou (Rangifer tarandus caribou) in Pukaskwa National Park to the Lake Superior Coastal Range and Beyond. Pukaskwa National Park, Heron Bay, ON.

Drake, C. C., M. Manseau, C. F. C. Klütsch, P. Priadka, P. J. Wilson, S. Kingston, and N. Carr. 2018. Does connectivity exist for remnant boreal caribou (Rangifer tarandus caribou) along the Lake Superior Coastal Range? Options for landscape restoration. Rangifer. 38(1):13–26.

Dzus, E. 2001. Status of the Woodland Caribou (Rangifer tarandus caribou) in Alberta. Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Edmonton, Alberta 47 pp.

Elkie, P. C., A. Smiegielski, J. P. Elliot, R. Kushneriusk, and R. Rempel. 2013. Ontario's Landscape Tool: User's Manual. Ontario Ministry of Natural Resources. Policy Division, Forests Branch, Policy Section, Guides Unit.116 pp.

Elkie, P. C., K. Green, M. Racey, M. Gluck, J. P. Elliot, G. Hooper, R. Kushneriusk, and R. Rempel. 2014. Science and Information in support of Policies that address the Conservation of Woodland Caribou in Ontario: Occupancy, Habitat, Disturbance Models, Estimates of Natural Variation and Range Level Summaries. Ontario Ministry of Natural Resources, Forests Branch. 49 pp.

Environment Canada. 2012. Recovery Strategy for the Woodland Caribou (Rangifer tarandus caribou), Boreal population, in Canada. Ottawa, ON. 138 pp.

Ferguson, S. H. 1982. Why are caribou on Pic Island? M.Sc. dissertation, Biology, University of Victoria, Victoria, BC. 171 p.

Ferguson, S. H., A. T. Bergerud, and R. Ferguson. 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. Oecologia. 76(2):236–245.

Fortin D., R. Courtois, P. Etcheverry, C. Dussault, and A. Gingras. 2008. Winter selection of landscapes by woodland caribou: behavioural response to geographical gradients in habitat attributes. J. Appl. Ecol. 45(5):1392–1400.

Foster, R. F., and A. Harris. 2012. Environmental Assessment for the Stillwater Canada Inc. Marathon PGM-Cu Project - Supporting Information Document No. 26: Assessment of Impacts on Woodland Caribou. Thunder Bay, ON. 94 pp.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildl. Monogr. (84):1–50.

Grant, M. 1902. Moose. N. Y. Forest, Fish and Game Comm. New York, NY. 225-238.

Haber, G. C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Ph.D dissertation, Biology, University of British Columbia. Vancouver, B.C. 818 pp.

Hatler, D. F. 1986. Studies of radio-collared caribou in the Spatsizi Wilderness Park area, British Columbia, 1980-1984. Spatsizi Association for Biological Research, Smithers, BC. 44 pp.

Hobson, R. D. 1972. Surface roughness in topography: quantitative approach. P. 221–245 *in* Spatial Analysis in Geomorphology, Chorley, R.J. (ed.). Methuen, London, UK.

Hornseth, M. L., and R. S. Rempel. 2016. Seasonal resource selection of woodland caribou (Rangifer tarandus caribou) across a gradient of anthropogenic disturbance. Can. J. Zool. 94(2):79–93.

James, A. R. C., S. Boutin, D. M. Hebert, and A. B. Rippin. 2004. Spatial Separation of Caribou from Moose and Its Relation to Predation by Wolves. J. Wildl. Manag. 68(4):799.

Kelsall, J. P. 1968. The migratory barren-ground caribou of Canada. Canadian Wildlife Service Monography.

Kneeshaw, D. D., and Y. Bergeron. 1998. Canopy Gap Characteristics and Tree Replacement in the Southeastern Boreal Forest. Ecology. 79(3):783–794.

Leblond, M., J. Frair, D. Fortin, C. Dussault, J.-P. Ouellet, and R. Courtois. 2011. Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. Landsc. Ecol. 26(10):1433–1446.

McLaren, B. E., and R. A. Janke. 1996. Seedbed and canopy cover effects on balsam fir seedling establishment in Isle Royale National Park. Can. J. For. Res. 26(5):782–793.

Mercer, E., S. Mahoney, K. Curnew, and C. Finlay. 1985. Distribution and abundance of insular Newfoundland caribou and the effects of human activities. McGill Subarct. Res. Pap. 40:15–32.

Naylor, B., D. Kaminski, S. Bridge, P. C. Elkie, D. Ferguson, G. Lucking, and B. Watt. 1999. Ontario Wildlife Habitat Analysis Models: User's guide for OWHAM and OWHAM Tool. 44 pp.

Neale, G. 2000. Effects of snow depths on seasonal movements and homerange distributions of wolves, moose, and woodland caribou in and around Pukaskwa National Park, Ontario, Canada. M.Sc. Thesis, University of Montana, Bozeman, MT. 89 pp.

Nellemann, C., and M. G. Thomsen. 1994. Terrain Ruggedness and Caribou Forage Availability during Snowmelt on the Arctic Coastal Plain, Alaska. Arctic. 47(4):361–367.

Nellemann, C., and G. Fry. 1995. Quantitative Analysis of Terrain Ruggedness in Reindeer Winter Grounds. ARCTIC. 48(2):172–176.

Newmaster, S. G. 2010. Boreal Rainforests in Ontario? P. 162–163 *in* Ontario's Old-Growth Forests: A Guidebook Complete with History, Ecology and Maps. Fizhenry and Whitesand Limited, Markham, ON.

Newton, E. J., B. R. Patterson, M. L. Anderson, A. R. Rodgers, L. M. V. Vennen, and J. M. Fryxell. 2017. Compensatory selection for roads over natural linear features by wolves in northern Ontario: Implications for caribou conservation. PLOS ONE. 12(11):e0186525.

[OMNR] Ontario Ministry of Natural Resources 2005. Backgrounder on Wolf Conservation in Ontario.

[OMNRF] Ontario Ministry of Natural Resources and Forestry. 2009. Ontario`s Woodland Caribou Conservation Plan. Queen's Printer for Ontario, Toronto, ON. 24 pp.

[OMNRF] Ontario Ministry of Natural Resources and Forestry. 2014a. Delineation Report for Woodland Caribou Ranges in Ontario. Species at Risk Branch, Thunder Bay, ON. 55 pp.

[OMNRF] Ontario Ministry of Natural Resources and Forestry. 2014b. Forest Management Guide for Boreal Landscapes. Queen's Printer for Ontario, Toronto, ON. 114 pp.

[OMNRF] Ontario Ministry of Natural Resources and Forestry. 2014c. State of the Woodland Caribou Resource Report: Part Three. Species at Risk Branch, Thunder Bay, ON. 156 pp.

(OWCRT) Ontario Woodland Caribou Recovery Team. 2008a. Keeping Caribou in Ontario: Discussion Paper. Queen's Printer for Ontario. 41 pp.

(OWCRT) Ontario Woodland Caribou Recovery Team. 2008b. Recovery Strategy for the Woodland Caribou (Rangifer tarandus caribou) (Forest-dwelling, Boreal Population) in Ontario. Queen's Printer for Ontario. 96 pp.

Oswald, K. 1998. Moose Aerial Observation. Northeast Science & Technology Technical Report, Ontario Ministry of Natural Resources, Toronto, ON. 95 pp.

Patterson, L. D., C. C. Drake, M. L. Allen, and L. Parent. 2014. Detecting a population decline of woodland caribou (Rangifer tarandus caribou) from non-standardized monitoring data in Pukaskwa National Park, Ontario. Wildl. Soc. Bull. 38(2):348–357.

Peterson, R. L. 1955a. Distribution and Status of Moose in Ontario. P. 45–54 *in* North American moose, Canadian university paperbooks. University of Toronto Press, Toronto, ON.

Peterson, R. L. 1955b. Post-Glacial Dispersal of Moose in North America. P. 14–18 *in* North American Moose, University of Toronto Press, Toronto, ON.

Pimlott, D. H. 1959. Reproduction and Productivity of Newfoundland Moose. J. Wildl. Manag. 23(4):381–401.

Pinard, V., C., Dussault, J. P., Ouellet, D. Fortin, and R. Courtois. 2011. Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. J. Wildl. Manag. 76(1):189–199.

Racey, G., A. Harris, L. Gerrish, T. Armstrong, J. McNicol, and J. Baker. 1999. Forest Management Guidelines for the Conservation of Woodland Caribou: A Landscape Approach. Thunder Bay, ON. 69 pp.

Riley, S. J., S. D. DeGloria, and R. Elliot. 1999. A Terrain Ruggedness Index That Quantifies Topographic Hetergeneity. Intermt. J. Sci. 5(1–4):23–27.

Sappington, J. M., K. M. Longshore, and D. B. Thompson. 2007. Quantifying Landscape Ruggedness for Animal Habitat Analysis: A Case Study Using Bighorn Sheep in the Mojave Desert. J. Wildl. Manag. 71(5):1419–1426.

Shiras, G. I. 1912. The wild life of Lake Superior, past and present. Natl. Geogr. Mag. 24(7):113–204.

Shuter, J., N. C. Asselin, and A. R. Rodgers. 2016. Results of the 2016 Lake Superior Coast Range (LSCR) caribou (Rangifer tarandus caribou). Ontario Ministry of Natural Resources and Forestry, Centre for Northern Forest Ecosystem Research. Thunder Bay, ON. 35 pp.

Skoog, R. O. 1968. Ecology of the caribou (Rangifer tarandus granti) in Alaska. Ph. D. dissertation, University of California, Berkeley CA. 340 pp.

Taylor, A. R., and H. Y. H. Chen. 2011. Multiple successional pathways of boreal forest stands in central Canada. Ecography. 34(2):208–219.

Valkenburg, P., and J. L. Davis. 1985. Population status of the Fortymile caribou herd and identification of limiting factors. Alaska Department of Fish and Game. Federal Aid in Wildlife Restoration. Program Reports. W-22-3. Juneau, AK. 20 pp.

Verme, L. J. 1969. Reproductive Patterns of White-Tailed Deer Related to Nutritional Plane. J. Wildl. Manag. 33(4):881–887.

Wagenmakers, E.-J., and S. Farrell. 2004. AIC model selection using Akaike weights. Psychon. Bull. Rev. 11(1):192–196.

Whittington, J., M. Hebblewhite, N. J. DeCesare., L. Neufeld, M. Bradley, J. Wilmshurst, and M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. J. Appl. Ecol. 48(6):1535–1542.

Wilson, R. R., A. K. Prichard, L. S. Parrett, B. T. Person, G. M. Carroll, M. A. Smith, C. L. Rea, and D. A. Yokel. 2012. Summer resource selection and identification of important habitat prior to industrial development for the Teshekpuk Caribou Herd in northern Alaska. PloS One. 7(11):1-14.

Wittmer, H. U., A. R. E. Sinclair, and B. N. McLellan. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia. 144(2):257–267.

APPENDICES

APPENDIX I - OMNRF FOREST UNITS AND CARIBOU HABITAT MODELS

Table - OMNRF NW Regional Caribou refuge habitat model. Source: Elkie et al. (2014)

NW Regional Forest Unit	Winter Usable	Winter Preferred	Refuge
BfDom			61
ConMx			71
OCLow	51		always
SbDom	61		41
SbLow	41	101	always
SbMx1	61		41
PjDom	41	61	always
PjMx1	41	61	41

III

Table – Descriptions of OMNRF NW Regional Forest Units.

NW Regional Forest Unit		Description
Balsam Fir Dominated	BfDom	Stands with 70% or greater species composition of balsam fir.
White Birch Dominated	BwDom	Stands with 60% or greater species composition of white birch and at least 10% poplar.
Conifer Mixedwood	ConMx	Stands with 50% or greater species composition or any conifer species.
Hardwood Dominated	HrDom	Stands with 70% or greater species composition of any hardwood species.
Hardwood Mixedwood	HrdMw	Stands with 50% or greater species composition of any hardwood species.
Other Conifer Lowland	OCLow	Stands with 50% or greater species composition of any combination of cedar and larch.
Black Spruce Dominated	SbDom	Stands with 70% or greater species composition of black spruce and 20% or less species composition of any combination of white birch and poplar.
Spruce Lowland	SbLow	Organic black spruce ecosites (ES 34-38) whith 20% or less species composition of Pr + Pw + Pj + Sw + Bf).
Black Spruce Mixedwood	SbMx1	Stands with a 70% or greater species composition of a combination of red pine, black spruce, jack pine, white spruce and balsam fir, where the amount of balsam fir is not greater than 10%, and where the species composition of poplar and white birch is not greater than 20% and where there is more white and black spruce combined than there is black spruce.
Jack Pine Dominated	PjDom	Stands with 70% or greater species composition of jack pine and with 20% or less species composition of white birch and poplar combined.
Jack Pine Mixedwood	PjMx1	Stands with a 70% or greater species composition of a combination of red pine, black spruce, jack pine, white spruce and balsam fir, where the amount of balsam fir is not greater than 10%, and where the species composition of poplar and white birch is not greater than 20% and where there is more jack pine than there is white and black spruce combined
Poplar Dominated	PoDom	Stands with 70% or greater species composition of poplar.

APPENDIX II– SUPPORTING HABITAT MAPS

Legend

— Roads
—|— Railways
— Power Lines
Waterbodies
Study Area

Moose & Caribou habitat
BFDOM
CONMX

Moose habitat
BWDOM
HRDMX
HRDOM
PODOM

Caribou habitat
SBDOM
OCLOW
PJDOM
PJMX1
SBLOW
SBMX1

1:190,000

Lawson Island

Barclay
Islands

Pic Island

Slate Islands

Created by: Jack McClinchey
Faculty of Natural Resources Management
Lakehead University
UTM Zone 16N, NAD 83
March 26, 2018

0   5   10   20   30   40

Kilometers

N

Legend

— Roads

┝┼┼┤ Railways

— Power Lines

Waterbodies

Study Area

Moose habitat

BWDOM

HRDMX

HRDOM

PODOM

1:190,000

Lawson Island

Barclay Islands

Pic Island

Slate Islands

Created by: Jack McClinchey
Faculty of Natural Resources Management
Lakehead University
UTM Zone 16N, NAD 83
March 26, 2018

0	5	10	20	30	40

Kilometers

N

Legend

- —— Roads
- ┼┼┼ Railways
- —— Power Lines
- ▢ Waterbodies
- ▢ Study Area

Moose & Caribou habitat

- ▮ BFDOM
- ▮ CONMX

Lawson Island

Barclay Islands

Pic Island

Slate Islands
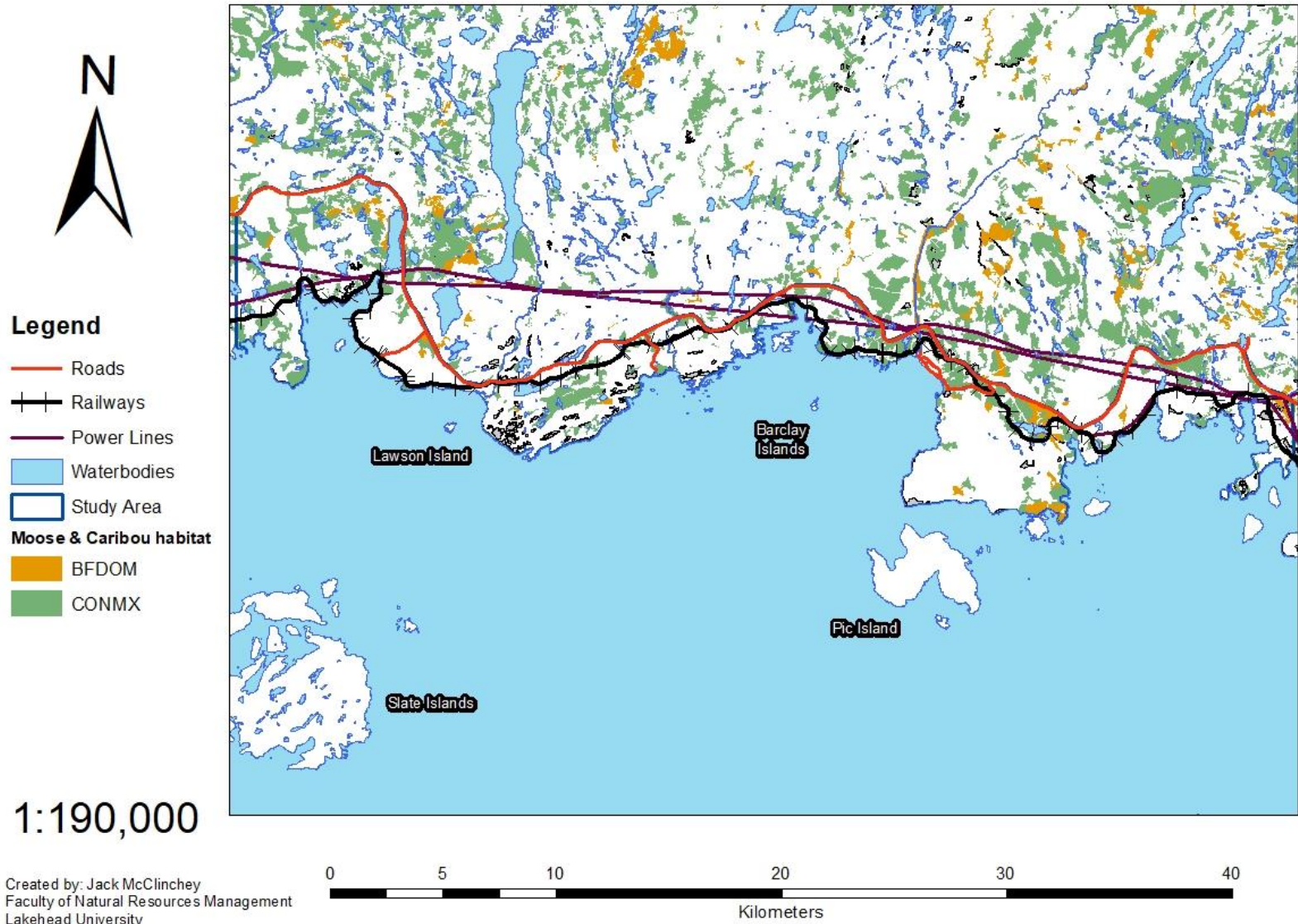
1:190,000

Created by: Jack McClinchey
Faculty of Natural Resources Management
Lakehead University
UTM Zone 16N, NAD 83
March 26, 2018

| 0 | 5 | 10 | 20 | 30 | 40 |

Kilometers

Legend

--- Roads

+–+ Railways

—— Power Lines

Waterbodies

Study Area

Caribou habitat

■ SBDOM

■ OCLOW

■ PJDOM

■ PJMX1

■ SBLOW

■ SBMX1

1:190,000

Created by: Jack McClinchey
Faculty of Natural Resources Management
Lakehead University
UTM Zone 16N, NAD 83
March 26, 2018

Lawson Island

Barclay Islands

Pic Island

Slate Islands

0   5   10   20   30   40

Kilometers