Bottom-up and Top-down Forces Shaping Caribou Forage Availability on the Lake
Superior Coast

by

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ABSTRACT

Woodland caribou (*Rangifer tarandus*) occupying the Lake Superior Coastal distribution, Ontario, exist in three subpopulations with distinct ranges and demographics. In this study, three ranges are analyzed in terms of summer forage density from bites available to caribou at Pukaskwa National Park, on Michipicoten Island, and on the Slate islands in an attempt to identify whether bottom-up (plant habitat driven) or top-down (herbivore driven) effects are driving the density (g per m^2) of 18 coarsely grouped and locally important forage taxa. Crude protein of the 18 taxa was also assessed as a measure of forage quality. Effects on forage density were explored with multiple models, notably sets of predictions comparing dominant overstory taxon, elevation, shrub density, and overstory cover (bottom-up factors), *versus* slope (accessibility to caribou) and occupation of areas of higher herbivore density on predator refuge islands (top-down factors) as estimators of forage density. At Pukaskwa National Park, lichen, a year-round food source, was highest in density under open jack pine (*Pinus banksiana*) canopies (β = 892, S.E. = 74), but was lower in density where gentle slopes occurred on refuge islands (β = -50.6, S.E. = 23.9). On Michipicoten Island, forage density in the shrub layer was higher with increasing elevation (β = -46.8, S.E. = 44.4) and lower on gentle slopes (β = -108, S.E. = 0); meanwhile, lichen density was highest under black spruce (*Picea mariana*) canopies (β = 0.262, S.E. = 0.113). Density of forage plants in the herb layer on the Slate islands was positively correlated with the forage density of the shrub layer (β = 0.176, S.E. = 0.016). Thus, a mixture of top-down and bottom-up effects was the

general model supported by the forage survey at each location. Terrestrial lichen, arboreal lichen, and Canada yew (*Taxus canadensis*) were of lowest quality as represented by crude protein. Current foraging conditions along the Lake Superior Coastal distribution are discussed.

TABLE OF CONTENTS

ACKNOWLEDGMENTS

INTRODUCTION

Animals can have profound effects on their habitats and play critical roles in shaping their environments (Naiman 1988). The relationships between ungulate herbivores and their plant environments are among the best studied (Caughley 1976, Hobbs 1996). Free-ranging ungulates alter vegetation structure and composition all over the world, having shaped the landscapes of northern Europe (Emanuelsson 2009), altered bogs (Pellerin et al. 2006) and forests (McInnes et al. 1992) in North America, and created the African rangelands (Augustine and McNaughton 2004). The range of effects of such interactions on the carrying capacity and population dynamics of the herbivores spans a continuum from positive (Fryxell 1991) to catastrophic (Klein 1969), while negative effects on vegetation are most likely when predators are missing (Oksanen 1992).

Many studies in this arena focus on relationships between a specific ungulate herbivore and an individual forage plant. For example, Edwards (1985) provided insight into the relationship between moose (*Alces alces*) and wild sarsasparilla (*Aralia nudicaulis*), which was more vulnerable to moose browsing in higher density patches and at some threshold failed to reproduce. Similar threshold relationships exist between white-tailed deer (*Odocoileus virginianus*) and Canada yew (*Taxus canadensis*), in this case where extirpation of the mixedwood forest shrub begins at specific deer densities. Chouinard and Filion (2001) investigated white-tailed deer and balsam fir (*Abies balsamea*) on Anticosti Island, Québec, finding that hyperabundant deer reduced or eliminated balsam fir recruitment, altering boreal forest stand characteristics toward open black spruce (*Picea mariana*), while Balgooyen and Waller (1995) found that deer

browsing affected the abundance and height of blue bead-lily (*Clintonia borealis*) and recommended this plant for use as an indicator of white-tailed deer hyperabundance. Studies involving caribou (*Rangifer tarandus*) have focused either on lichen as a taxonomic group (e.g., Crête et al. 2001), or in one case, on the Ungava peninsula of Québec and Labrador, on dwarf birch (*Betula nana*), heavily suppressed on the summer range of the George River caribou population (Crête and Doucet 1998).

Woodland caribou (*R. t. caribou*), although often referred to as specialists (e.g., Thomas et al. 1996), are actually generalist herbivores and their relationship to their foraging environments must be considered at the community level. They occupy a large fundamental niche that sometimes relies on a large complement of forage taxa (see review by Brown and Mallory 2007). In spring, caribou generally consume the new growth of vascular plants and consume little lichen. During spring and summer, caribou largely consume the leaves of herbs and shrubs. As seasons progress into autumn, woodland caribou consume more terrestrial lichen, and then transition to arboreal lichen as snow cover prohibits access to terrestrial forage. Thus, at different times of the year, herb, shrub, and lichen densities are all important considerations in defining caribou habitat. Often, summer forage is not considered a limit to caribou and many studies only address lichen and winter habitat. However, a growing number of authors suggest that more attention be paid to summer conditions in explaining the limits on northern ungulate populations (Hjeljord and Histol 1999, Cook et al. 2004, Stewart et al. 2005, Herfindal et al. 2006, McArt et al. 2006). The context of the study described by this study is the foraging environment of Lake Superior caribou across a variety of taxa, stratified roughly into three vegetation layers: shrubs, herbs, and lichens.

When community-level studies of the effects of herbivores are conducted, they often rely on data from exclosures, fenced areas that exclude herbivores and create an "unbrowsed" or "ungrazed" treatment area to compare to the "browsed" or "grazed" area outside the fence. The usefulness of such data is often limited and they do not provide an holistic picture of the effects of the herbivore at various densities and across various plant communities (Hester et al. 2000). For example, modeling by Jorritsma et al. (1999) illustrated threshold and non-linear effects of ungulate browsing on forest development, while white-tailed deer enclosures on Anticosti Island confirmed non-linear effects with deer density in a boreal forest ecosystem (Tremblay et al. 2006). Such non-linear effects will not be detected in the binary design implied by exclosures, so exclosure studies are limited in their inference space.

Instead of using exclosures, in this study I sampled vegetation subject to free-ranging herbivores to better assess the forage available to caribou at three sites along their discontinuous Lake Superior coastal distribution. A multiple-model approach valuing simplicity and well-supported predictions over model fit (Ginzburg and Jensen 2004) is used to gain general insight across the system by this assessment of forage density (the mass of forage easily available for consumption by caribou on the landscape, measured in g per m^2, and on the question of whether summer forage is significantly suppressed by ungulate herbivores, a phenomenon already partially documented on the Slate islands, near Terrace Bay, Ontario (Bergerud et al. 2007). The objectives are thus two-fold: 1) to provide a snapshot of available summer forage in the habitats of each of three subpopulations of Lake Superior caribou, including the Slate islands, and 2) to test expected relationships between forage density and abiotic

variables on the Lake Superior coast. The second objective will be accomplished using *a priori* predictions based in literature describing forest systems and ungulate foraging. With specific predictions supporting either bottom-up effects (plant habitat based drivers) explaining forage distribution or top-down (caribou driven) control of vegetation, including association of forage density with Pukaskwa's mainland or its nearshore islands (Table 1), support for the notion that Lake Superior herbivores, notably caribou, are shaping their own summer forage availability will be tested.

The investigation of caribou habitat is nowhere more important than for the Lake Superior coastal population. Within this population, listed along with the more northerly and continuous Ontario population as threatened (Environment Canada 2011*a*, OMNR 2011), there exist three distinct subpopulations. These subpopulations all occupy the ecotone of the boreal and the Great Lakes-St. Lawrence forests, are separated geographically, and occupy a unique habitat relative to the population of the continuous distribution. One of these subpopulations has apparently occurred in what is currently Pukaskwa National Park since the Ontario population became discontinuous, sometime around 1880 (de Vos and Peterson 1951, Schaefer 2003). Here caribou spend a disproportionate amount of time during summer on a few small islands, which effectively support a much higher ecological density of caribou in "refuge" habitat (away from the threat of wolves, *Canis lupus*, in calving and post-calving periods) than does the Lake Superior coastal area (Bergerud 1985). Michipicoten Island, near Wawa, Ontario, and the Slate islands, both currently Ontario provincial parks, occur at considerably longer distances offshore in Lake Superior than the Pukaskwa coastal islands, and support closed and predator-free subpopulations of woodland caribou.

Assessing conditions for each subpopulation is important for management, because the

Lake Superior system is not a metapopulation and there is little to no likelihood of

natural repopulation of the distant offshore islands via dispersal.

Table 1. Sampling locations, forage groups and predicted models for caribou forage density including factors associated with the bottom-up (plant habitat driven) and factors associated with the top-down (herbivore driven) hypotheses explaining forage distribution at Pukaskwa National Park, on Michipicoten Island and on the Slate islands, Ontario. "Island" refers to whether samples estimating forage density occurred on the mainland of Pukaskwa (at Spruce Harbour) or offshore on One Lake and Otter islands.

Sampling locations and forage groups	Factors associated with the bottom-up hypothesis	Factors associated with the top-down hypothesis
Pukaskwa National Park		
Shrub layer	Forest overstory	Slope, island
Herb layer	Forest overstory, forage density in the shrub layer	Slope, island
Lichen layer	Dominant overstory taxon, forest overstory	Slope, island
Michipicoten Island Provincial Park		
Shrub layer	Forest overstory, elevation	Slope
Herb layer	Forest overstory, elevation, forage density in the shrub layer	Slope
Lichen layer	Dominant overstory taxon, forest overstory	Slope
Slate Islands Provicnial Park		
Shrub layer	Forest overstory	Slope
Herb layer	Forest overstory, forage density in the shrub layer	Slope
Lichen layer	Dominant oversotry taxon, forest overstory	Slope

PREDICTIONS ON CARIBOU FORAGE DISTRIBUTION IN THE LAKE SUPERIOR COASTAL AREA

In the absence of browsing, density of shrubs and herbs should be negatively

correlated with the canopy cover in a forest overstory (Pastor et al. 1993), as forest

understory biomass, and thus density, increases with solar radiation generally

(Zavitkovski 1976). As solar radiation in an understory is positively correlated with

distance from the forest floor (Messier et al. 1998), density of herbs should also be

negatively related to shrub density. For vegetation communities on the Lake Superior

islands, forest composition changes rapidly with elevation above the lake (Linn 1957, 1962, Jordan et al. 2000, Kuchta 2010 unpubl.), also leading to differences in expected forest understory densities (Rutkowski and Stottlemyer 1993). Finally, dominant overstory taxa should be a predictor of both arboreal and terrestrial lichen density (Brown et al. 2006), while under more open overstory canopies terrestrial lichen density should be higher (Schaefer 1996, Bergerud et al. 2007).

The relationships between forage density and plant habitats, as above, should be broken as foraging options are reduced by browsing. As herbivores increasingly rely on fewer resources, a positive feedback in the effects of browsing can lead to "overbrowsing" (van de Koppel et al. 2002). One area where such negative effects of browsing may occur is on the refuge islands at Pukaskwa National Park where forage densities may be reduced over the mainland (Ferguson et al. 1988). Furthermore, ungulates, and specifically caribou, prefer to travel and forage on level ground (LeResche and Linderman 1975, Terry et al. 1996, Armleder et al. 1999, Terry et al. 2000), which could lead to lower forage densities on gentle slopes if these areas have been "overbrowsed."

These sets of predictions, when combined (Table 1), act as a mechanism to achieve Objective 2. If woodland caribou forage conditions in their Lake Superior distribution are largely driven by bottom-up processes, relationships between selected plant habitat variables should explain forage density. If conditions are driven by the herbivores, then less support should occur for expected relationships with forest overstory and elevation, and heavily sloped areas and islands should be significant predictors of forage density. If caribou browsing largely drives foraging conditions (i.e.,

"overbrowsing" has occurred), then all predicted relationships should fail, as even slope should not be a good predictor of variation in forage density.

METHODS

STUDY AREAS

This study was conducted at three locations across northeastern Lake Superior and within the Lake Superior Coastal range for woodland caribou (Fig. 1). All locations share similar cool summer climates. The two nearest weather stations are in Wawa and Terrace Bay, Ontario (Environment Canada 2011*b*). Wawa experiences 727.4 mm of rain and 328.6 cm of snow annually. Summer temperatures peak in July and average 14.9 ºC, while January temperatures average -14.8 ºC. Mean annual temperature is 1.7 ºC. Terrace Bay experiences about 599.2 mm of rain and 210.2 cm of snow annually. Summer temperatures peak in July and average about 14.5 ºC, while January temperatures average about -14.7 ºC. Mean annual temperature is 1.5 ºC.

In addition to caribou, all locations support populations of snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*) and red fox (*Vulpes vulpes*). Wolves, lynx (*Lynx canadensis*), black bear (*Ursus americanus*) and white-tailed deer in very low numbers occur only in Pukaskwa National Park, although wolves have made very occasional excursions onto the Slate islands. Pukaskwa is the only location accessible to moose, which are estimated at below 0.1 per km^2 (Vance et al. 2008, unpubl.).
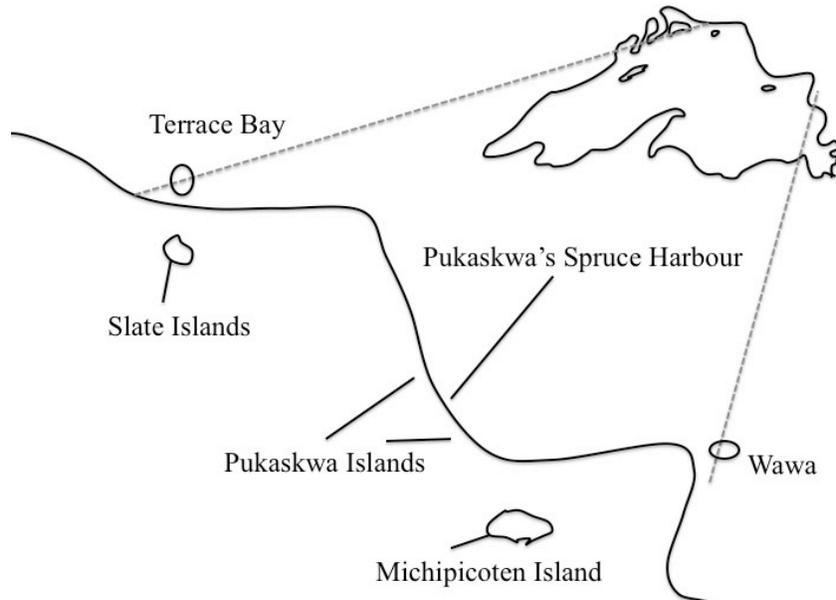
Figure 1. Study locations on Michipicoten Island, Pukaskwa National Park's Spruce Harbour, two Pukaskwa coastal islands, and the Slate islands, all within the Lake Superior Coastal range of woodland caribou. Also shown are the locations of the Terrace Bay and Wawa weather stations.

 Michipicoten Island

Michipicoten Island is the third largest island in Lake Superior, located in the northeastern part of the lake, 16 km offshore at its nearest point (Fig. 1). Most of the area, 36,740 ha, is a provincial park (OMNR 2004). Michipicoten Island is largely (87 %) forested and is dominated by white birch (*Betula papyrifera*) and red maple (*Acer rubrum*), occurring in mixed and coniferous forest types (OMNR 2004). Dominant conifers include balsam fir, white spruce (*Picea glauca*) and black spruce. Disturbance intervals are long and there is abundant old-growth forest on the island. Woodland caribou, previously considered extirpated in the 1880s (although one male was observed on the island in 1981), were repatriated in 1982 with a translocation from the Slate islands (OMNR 2004). Since that time, the caribou subpopulation has increased from 8

to about 200 in 2001 (λ=1.18; Bergerud et al. 2007). Newer estimates place the

subpopulation between 328 and 875 in 2011 (λ=1.12; Kuchta, Lakehead University,

unpubl.; Appendix 1). Caribou on Michipicoten Island are increasing.

Pukaskwa National Park

Pukaskwa National Park is located along the northeastern Lake Superior

shoreline and encloses an area of 187,800 ha and approximately 83 km of shoreline (Fig.

1). The coastal zone, where this study was conducted, accounts for about 22 % of the

area of the park (Vance et al. 2008, unpubl.). About 94 % of the park is forested and

coastal islands account for 0.1 % (171 ha). Spruce Harbour, the sampling area along the

mainland, as well as One Lake and Otter islands, the two nearshore islands sampled, is

dominated by two forest types, black spruce coniferous forest, and white birch-balsam fir

mixedwood forest (Vance et al. 2008, unpubl). Woodland caribou occur at low density

and primarily along the shoreline adjacent to nearshore islands (Bergerud 1985). The

caribou subpopulation is in slow decline (Bergerud et al. 2007, Patterson et al. unpubl.).

Densities in refuge areas are likely much higher than elsewhere in the park, and strong

competition for food is possible on refuge islands; e.g., 63.9 % of caribou locations

within the park are on a few small islands, while use of nearshore islands and the most

adjacent mainland areas has proportionately increased since 2000 (Bergerud, unpubl.,

Patterson et al. unpubl.). Moose also frequent both the islands and the mainland area

included in the sampling in this study. For this study, the mainland forests at Spruce

Harbour will be referred to as Pukaskwa's Spruce Harbour, while the more heavily used

One Lake (approximately 23 ha and about 60 m from the mainland) and Otter

(approximately 170 ha and about 600 m from the mainland) islands will be referred to as

the Pukaskwa islands.

The Slate Islands

The Slate islands form a large archipelago of eight islands and several smaller islets south of Terrace Bay in Lake Superior, 9 km from its shoreline at their nearest point (Fig. 1). The archipelago is a provincial park with an area of 6,570 ha, and is approximately 8 km in diameter (OMNR 2004). The Slate islands are almost entirely classed into two forest types, white birch mixedwoods and coniferous. Disturbance intervals are long, although the islands were subject to logging prior to around 1940. Woodland caribou, previously absent from the islands, have been present for over 100 years with a peak of about 650 in 1984; the subpopulation is currently estimated at around 100 (Bergerud et al. 2007, Carr et al. in press). The subpopulation has been subject to large oscillations, as would be expected under density dependence, with late-winter mortality being the primary natural demographic control (Bergerud et al. 2007). Caribou are assumed to be fluctuating around carrying capacity with strong competition for food a result.

DATA COLLECTION

Bite-count plots were established in June and July of 2011 on Michipicoten Island, at Pukaskwa's Spruce Harbour, on One Lake Island and Otter Island (Pukaskwa islands), and on the Slate islands. In this sequence, sampling was actually staggered over 5- to 12-day periods during a total of six weeks, determined by limited access. Pukaskwa plots were located on randomly assigned compass declinations and had a minimum spatial separation of 50 m. Because of harsher terrain, logistical constraints, and remote

locations, plots on Michipicoten and the Slate islands were assigned without *a priori* knowledge of the plot location and in proximity to accessible coastal drop-off points. Plots ranged from a minimum of 50 m to a maximum of 2 km from the shoreline of Lake Superior. Elevation of plots ranged from lake level (183 m) to 292 m on Michipicoten Island, 233 m at Pukaskwa Spruce Harbour, 259 m on the Pukaskwa islands, and 227 m on the Slate islands. Sampling up to an elevation of 233 m is sufficient to reach all forest communities on Lake Superior islands (Linn 1957, 1962).

For each plot, dominant overstory taxon was determined by the dominant tree as in the Ontario Forest Resource Inventory maps (FRI; OMNR 2007). Forest canopy cover (forest overstory) was estimated in percent as the mean of four readings from a spherical densiometer. Each plot was also assessed as to slope, estimated over the length of the transect. For Pukaskwa, sites were classed as island (Pukaskwa islands) or not island (Spruce Harbour).

Eighteen regionally significant summer caribou forage taxa were identified *a priori* from local literature (Ferguson et al. 1980, 1988); this list includes the following shrubs: mountain maple (*Acer spicatum*), white birch, dogwoods (*Cornus* spp. other than *C. canadensis*), aspen (*Populus* spp.), cherries (*Prunus* spp.), currants (*Ribes* spp.), roses (*Rosa* spp.), thimbleberry (*Rubus parviflorus*), blackberries and dewberries (other *Rubus* spp.), mountain ash (*Sorbus* spp.), Canada yew, and cranberries (*Viburnum* spp.); herbs: wild sarsasparilla, asters (*Aster* spp.), bunchberry (*Cornus canadensis*), and wood fern (*Dryopteris austriaca*); terrestrial lichens (fruticose lichens dominated by *Cladonia* spp.); and arboreal lichens (*Alectoria* spp., *Usnea* spp., and others). Bites of this list of forage taxa were counted as follows: for the shrubs, in 2 m x 20 m x 2 m high plots, as this is

the area easily reached by a foraging caribou (Terry et al. 2001); and for the herbs and lichens, in ten smaller, 1 m x 1 m plots, located every second meter within the larger plots. A bite was counted as each portion of a plant that could be consumed by an adult caribou in one bite, following the methods of Ferguson et al. (1980). Bites for lichen were counted as each 7 cm x 7 cm patch. In the cases of mountain maple, white birch and Canada yew on Michipicoten Island, the high volume of forage made counting bites individually impractical, thus bites were calculated as:

$$B = MB \times S$$

where B = bites on the landscape, MB = mean number of bites per stem < 7 mm in diameter, calculated from a minimum of 30 randomly chosen stems, and S = number of stems counted in each transect.

Green biomass of potential bites of each plant taxon was collected daily as available on Michipicoten Island (over a 12 day period in June), in Pukaskwa (onshore islands and mainland combined, over 12-days in two periods in June and July), and on the Slate islands (over a 4-day period in July). Biomass was weighed by bite to the nearest 0.01 g with an electronic scale at the end of each day (Ohaus model SP202). A green biomass subsample of each taxon was then air dried and retained after the field season; its dry mass was estimated after oven-drying at 65 °C for 48 h. Regression equations were used to predict oven-dry mass for the remaining bites for each taxon at each location. A mean oven-dry mass per bite for each forage taxon was estimated separately for Michipicoten Island, Pukaskwa (Spruce Harbour and offshore islands combined), and the Slate islands.

At each location, additional random samples of each forage taxon were frozen on dry ice within 2 h of collection for later chemical analysis. Samples of a minimum of five plants collected from different areas within each location were pooled to reduce the confounding effects of differences in forage quality between individual plants and their habitats (Albon and Langvatn 1992). Pooled samples were oven-dried and ground through a 1-mm mesh, then analyzed for nitrogen and carbon content using a CNS-2000 (LECO Instruments, Mississauga, ON) at Lakehead University. Values for nitrogen were then multiplied by 6.25 (Robbins 1993) to obtain crude protein for each taxon, a representation of available protein (Servello et al. 2005). Carbon-nitrogen ratios were also calculated as a coarse measure of forage quality, where higher ratios indicate reduced digestibility (Mattson 1980). Crude protein and carbon-nitrogen ratios were later found to be highly negatively correlated ($r = 0.99$; Appendix 2), so only crude protein is reported here.

DATA ANALYSIS

Forage density was estimated for each taxon at each location by multiplying the mean oven-dry mass per bite, estimated in g, by the number of bites of that taxon estimated for a 1 m^2 x 2 m tall area from the mean number of bites in all plots divided by plot size (estimated in m^2). Because logistical, weather and time constraints compromised the intended sample size and design, variance in the estimates was explored by plotting the coefficients of variation in forage density (g per m^2) separately for the shrub, herb and lichen layers and over the sequence and number of plots sampled. As sampling on Pukaskwa and the Slate islands still proved to be effectively random for shrubs, herbs and lichens, a simple mean was used to determine the total forage density

in each of these groups. On Michipicoten Island, sampling did not span the entire island, so to reduce variance, a weighted mean based on forest stand maps (OMNR 2004) was used to estimate forage density for each taxon. Weighted means followed the formula:

$$\text{Mean} = \sum (A \times D)$$

where: A = the proportion of forest of each of three types (coniferous forest 5.5 %, mixed forest 1.1 %, and deciduous forest 93.3 %) and D = the mean forage density estimated from plots of each type of forest for each plant taxon.

The effects of forest overstory, dominant overstory taxon, elevation and, for Pukaskwa, whether the forage was sampled at Spruce Harbour or on an island were investigated using maximum likelihood generalized linear models (GLM). Models were compared using Akaike's information criterion (AIC) corrected for small sample sizes, except on the Slate islands, where the correction could not be calculated and an uncorrected AIC was used. AIC values were used to calculate a "weighting," which is a proportion by which model outputs may be averaged to produce a "multimodel" and a more stabilized estimate (Burnham and Anderson 2002). Tukey's post-hoc tests were used to assess homogeneous subsets for forage quality based on crude protein. All estimates are presented as a range plus and minus one standard error (± S.E.) of the mean and $\alpha = 0.05$. All statistical tests were carried out using Statistical Package for Social Sciences (SPSS), version 18.

RESULTS

Terrestrial lichens were the dominant forage group at Pukaskwa National Park, both on the offshore islands and at Spruce Harbour (Fig. 2, forage density by individual

taxa in Appendix 3). Shrubs, notably Canada yew, were the dominant forage group on Michipicoten Island. Arboreal lichens were dominant on the Slate islands. Quality as crude protein varied considerably across the forage taxa ($F_{17, 38} = 8.04$, $p < 0.01$), but did not vary significantly with location ($F_{22, 38} = 1.88$, $p = 0.85$) or date of sampling ($F_{1, 38} = 0.04$, $p = 0.17$; Appendix 4). Lichens were lowest in crude protein, and Canada yew was the lowest-quality vascular plant included among the caribou forage taxa.
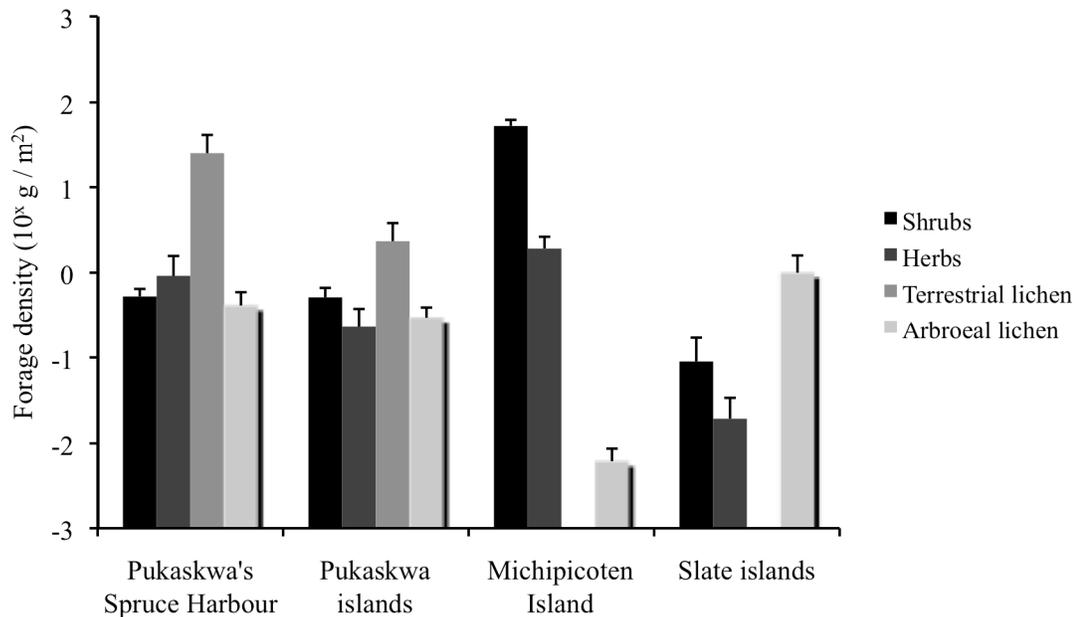
Figure 2. Mean forage density by taxon group for Pukaskwa's Spruce Harbour, the Pukaskwa islands, Michipicoten Island, and the Slate islands. Error bars represent one standard error of the mean.

Forage density in the shrub and herb layers at Pukaskwa National Park was not well explained by bottom-up or top-down model factors, although a model including "slope" and "island" did approach significance for forage density in the herb layer (Table 2). Lichen density was best explained by a model including

dominant overstory taxon and forest overstory (Appendix 5). At Pukaskwa, stands

dominated by Jack pine (*Pinus banksiana*) had higher densities of lichen (β = 892 ±

74), but this effect was reduced as canopy cover in the forest overstory increased

(β = -9.75 ± 0.90). A second model including "slope" and "island" showed that the

mainland location (Spruce Harbour) had higher lichen densities (β = 62.6 ± S.E. =

18.8), while gentle slopes supported lower lichen densities, but only on the

nearshore refuge islands (β = -50.6 ± 23.9).

Table 2. Sampling locations, forage groups and predicted model results for caribou forage density at Pukaskwa National Park, on Michipicoten Island and on the Slate islands, Ontario. AICc is Akaike's information criterion adjusted for small sample sizes, except for on the Slate Islands, where AIC is Akaike's information criterion. "Model weighting" is the proportion by which estimates from significant models should be multiplied and summed to create a stabilized estimate of forage density. "Appendix" shows the appendix in which more detail can be found.

Location, forage group, and factors tested	Appendix	Model weighting in multimodel	p	AICc
Pukaskwa National Park				
Shrubs				
Forest overstory	-	-	0.63	55.90
Slope	-	-	0.15	55.09
Island	-	-	0.88	56.11
Slope + island	-	-	0.95	61.62
Herbs				
Forest overstory	-	-	0.13	88.38
Shrubs	-	-	0.49	90.18
Forest overstory + shrubs	-	-	0.44	93.78
Slope	-	-	0.31	91.11
Islands	-	-	0.09	87.88
Slope + island	-	-	0.07	91.15
Lichen				
Dominant overstory taxon	-	0.000	0.00	253.42
Forest overstory	-	0.000	0.02	267.11
Dominant overstory taxon + forest overstory	5	1.000	0.00	223.53
Slope	-	-	0.17	271.70
Island	-	0.000	0.01	266.06
Slope + island	-	0.000	0.01	268.34

Table 2. Continued.

Location, forage group, and factors tested	Appendix	Model weighting in multimodel	p	AICc
Michipicoten Island				
Shrubs				
Forest overstory	-	-	0.31	222.35
Elevation	6	0.088	0.05	219.54
Forest overstory + elevation	-	-	0.21	225.47
Slope	6	1.000	0.00	214.67
Herbs				
Elevation	-	-	0.65	113.38
Shrubs	-	-	0.32	112.60
Forest overstory	-	-	0.50	113.14
Forest overstory + elevation	-	-	0.86	119.42
Elevation + shrubs	-	-	0.46	117.58
Forest overstory + shrubs	-	-	0.41	117.31
Forest overstory + elevation + shrubs	-	-	0.52	120.92
Slope	-	-	0.12	112.44
Lichen				
Dominant overstory taxon	7	1.000	0.01	-20.16
Forest overstory	-	-	0.47	-17.89
Dominant overstory taxon + forest overstory	7	0.027	0.00	-12.95
Slope	-	-	0.88	-17.03
Slate Islands Provincial Park			p	AIC
Shrubs				
No models (insufficient replication)			-	-
Herbs				
Forest overstory	-	-	0.50	-18.59
Shrubs	9	1.000	0.00	-36.23
Forest overstory + shrubs	9	0.530	0.00	-34.96
Slope	-	-	0.35	-18.22
Lichen				
Dominant overstory taxon	-	-	0.44	25.77
Forest overstory	-	-	0.95	26.37
Dominant overstory taxon + Forest overstory	-	-	0.50	28.03
Slope	-	-	0.30	25.98

Shrub forage density on Michipicoten Island was explained by a model including slope or by a model including elevation (Table 2; Appendix 6). Shrub forage density was lower on gentle slopes (β = -108 ± 0) and higher with increasing elevation (β = 0.386 ± 0.187). No model explained forage density in the herb layer on Michipicoten Island. Two of the tested model variants were significant in

explaining lichen density on Michipicoten Island, but these models shared terms. Thus, no multimodel was appropriate, and the most parsimonious model including dominant overstory taxon was selected (Appendix 7). Stands dominated by black spruce had higher lichen densities (β = 0.406 ± 0.081), while higher canopy cover in the forest overstory reduced this effect (β = -0.004 ± 0.002).

Replication was insufficient to explore models for forage density of the shrub layer and forage density of the lichen layer on the Slate islands (Appendix 8), but two of the tested models yielded significant results for forage density in the herb layer at this location: a model including forage density of the shrub layer and a model including forage density of the shrub layer and forest overstory (Table 2; Appendix 9). The model with forage density of the shrub layer was the best fit (β = 0.004 ± 0.016; Appendix 8).

DISCUSSION

The occurrence of terrestrial and arboreal lichens, a year-round food source for caribou in northern Ontario (Brown and Mallory 2007, I. D. Thompson, Canadian Forest Service, personal communication), is predicted by habitat, i.e. bottom-up factors, at two locations in the Lake Superior coastal distribution of caribou: Pukaskwa National Park and Michipicoten Island. Lichen occurrence is explained by dominant overstory taxon and canopy cover in the forest overstory. Different overstory taxa also support varying densities of lichen, matching expectations in literature (Schaefer 1996, Bergerud et al. 2007). Terrestrial lichen is abundant at Pukaskwa, but is entirely absent from Michipicoten Island, where arboreal lichens dominate (Bergerud et al. 2007; Appendix

3). Top-down effects also appear to influence lichen distribution at Pukaskwa National Park, where gentle slopes mean lower forage density in the lichen layers, but only on islands.

Further evidence of top-down moderation of bottom-up effects comes from Michipicoten Island, were forage density in the shrub layer is higher with increasing elevation and lower on gentle slopes. This effect was not consistent for the other two forage groups. If caribou were limited by lichen, for example, the high current densities of caribou on Michipicoten Island would have eliminated heterogeneity in lichen on Michipicoten Island. Bergerud et al. (2007) suggest that, prior to caribou translocations to Michipicoten Island, lichen densities were already very low.

Earlier observations of the Slate islands by Cringan (1956) and Bergerud et al. (2007), and now the results of this study, support the idea that on this archipelago vegetation is affected by browsing to the point of extirpation or near extirpation of forage plants such as sarsaparilla and thimbleberry. The lack of an effect of slope in describing forage density in the herb layer on the Slate islands also supports the idea of overbrowsing of the vegetation layers most accessible to caribou. However, while it was predicted that forage density in the herb and shrub layers should be negatively correlated, the positive correlation found is perhaps related to the ability of some forage taxa to flourish under specific conditions. A similar situation was observed for birch and balsam fir on Anticosti Island, where fertile soil conditions fostered growth impeded elsewhere by browsing (Dufresne et al. 2011). Presumably caribou on the Slate islands are able to thoroughly influence forage availability at multiple layers simultaneously.

Forces shaping forage communities in the Lake Superior coastal caribou distribution appear to be mixed (Table 3). One of the implications of describing top-down effects is the acknowledged weakening of bottom-up relationships explaining the distribution of forage taxa. However, herbivore effects on vegetation are apparent in each of the three locations within the distribution and, although there is no evidence to suggest that these effects are affecting caribou demographics at Pukaskwa or on Michipicoten Island, progressive deterioration of the range is possible and should be considered by managers. As observed in winter deer yards (Brown and Doucet 1991) and in moose via "cafeteria" studies (Renecker and Hudson 1986), progressive deterioration of range leads to increased diet breadth (Cowie 1977) and ever mounting pressure on forage resources (van de Koppel et al. 2002). Heavy use of the Lake Superior coastal range can cause a failure in reproduction and recruitment of certain forage taxa, as shown previously for caribou on the Slate islands (Bergerud et al. 2007), in areas of high white-tailed deer density in mixed Great Lakes-St. Lawrence forests (Rooney and Waller 2003), and on Isle Royale, where moose have often been hyperabundant (Janke et al. 1978, Edwards 1985). Caughley (1976) suggested that ungulates respond to poor foraging conditions in three ways: first, by delaying age of first reproduction; second, by reducing pregnancy rates; and third by reducing mean litter size; all predictions are supported by literature. For example, white-tailed deer fed low-nutrition diets experience lower fecundity (Verme 1965) while pregnancy, ovulation, and twinning rates in domestic sheep (*Ovis aries*) are highly affected by nutrition (Coop 1966). When food resources are drastically reduced, mortality may be the largest factor affecting a population (Caughley 1970). Bergerud et al. (2007) documented exactly this situation of large starvation events on the Slate islands.

The demographic effects of forage limitation are not addressed in this study and, thus, the usefulness of the data is limited in a management context unless future research highlighting caribou nutritional needs and exploring the mixed diets of the Lake Superior populations occurs. Although values for forage densities of various forage taxa and groups are presented here, and data was collected in such a way as to be directly applicable to caribou foraging, extrapolations to caribou demographics are far outside the scope of this study. Additionally, this study treated all taxa as equally palatable to caribou. However, other studies have found differences in palatability among taxa (Ferguson et al. 1980) so further exploration of diet preference may lead to a greater understanding of the system.

Table 3. Models describing forage densities in shrub, herb and lichen layers in Pukaskwa National Park, on Michipicoten Island, and at Slate Islands Provincial Park, with corresponding conclusions about plant habitat and herbivore effects.

Location and forage group	Primary model	Additional models	Explanation	Conclusion
Pukaskwa National Park				
Shrub layer	-	-	Slope and island effects top-down, but bottom-up effects explain lichen	Effects of browsing likely for lichen on islands
Herb layer	-	-		
Lichen layer	Dominant overstory taxon	Slope + island		
Michipicoten Island				
Shrub layer	Slope	Elevation	Slope effect top-down, but bottom-up effects explain shrubs and lichen	Effects of browsing evident for shrubs, but not lichen
Herb layer	-	-		
Lichen layer	Dominant overstory taxon	-		
Slate Islands Provincial Park				
Shrub layer	Insufficient data	-	Forest overstory cover effect bottom-up, but effect of shrub layer is top-down; slope has no effect	Probable bottom-up still evident under heavy browsing
Herb layer	Shrub density	-		
Lichen layer	-	-		

Shifts in forage preference toward less palatable taxa by abundant herbivores may

be the most useful indicator of declining range condition (Augustine and de Calesta 2003). Declines in Canada yew, a forage plant that can be depleted quickly in response to heavy browsing (Windels and Flaspohler 2011), would be an excellent indicator of a high degree of browsing on Michipicoten Island, due to this plant's low preference by caribou, its high density, the ease of measurement of its patches, and the established link between deer density and the abundance of Canada yew (Balgooyen and Waller 1995, Windels and Flaspohler 2011). This study provides excellent baseline data for monitoring or future study of the shrub on Michipicoten Island. Unfortunately, the presence of moose at Pukaskwa makes monitoring Canada yew less useful, as the shrub is highly sought after by moose (Krefting 1974). Currently an exclosure study is being conducted on the Slate islands by Ontario Parks (Steve Kingston, Ontario Parks, personal communication), but thought should be given to monitoring all locations in the Lake Superior coastal distribution. This study suggests that foraging herbivores are having effects on vegetation communities across the three ranges, both on summer vascular forage and on winter lichen. It may be beneficial to standardize methodology and monitor subpopulations to estimate summer forage in such a way as to identify actual demographic limitation of the subpopulations and the degree to which summer forage availability affects overwintering by caribou on Michipicoten Island in the absence of lichen.

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Appendix 1. Background, methods, results and discussion for the 2011 population estimate on Michipicoten Island.

Introduction

Woodland caribou (*Rangifer tarandus caribou*) are threatened in Ontario and their range has receded northward (Schaefer 2003). The result of this hasty retreat north has been the stranding of relic herds along the coast of Lake Superior. These caribou exist in distinct geographies, with some dispersed along the Pukaskwa coast north to Pic Island and the Caldwell Peninsula, and others on the predator-free Slate Islands (Bergerud et al. 2007).

In 1982 the Ontario Ministry of Natural Resources translocated caribou from the Slate islands to re-populate other parts of their southern distribution. Releases took place on Montreal Island in 1984, and on Bowman Island in 1985 (Bergerud and Mercer, 1989), but neither population persisted due to predation (Fig. I). An additional release of eight individuals on predator-free Michipicoten Island were added to the lone male observed there in 1981 (Bergerud 1985, Bergerud et al. 2007). Michipicoten Island had originally supported a population of caribou but they were functionally extirpated by miners in the 1880s (OMNR 2004). After caribou were repatriated to the island, two flight surveys were conducted. The population reached 26, indicating $\lambda=1.22$ for the first six years (Bergerud and Mercer 1989). It was then estimated at 200 in 2001, indicating $\lambda=1.40$ over the next the next 13 years (Bergerud et al. 2007). This rate of population growth is among the fastest ever recorded for caribou, even surpassing the growth rates recorded in the classic ungulate eruption cases of St. Matthews Island, Alaska, ($\lambda=1.32$; Klein 1968) and Southampton Island, NWT, ($\lambda=1.28$; Heard and Ouellet 1994).

As Michipicoten Island is a closed system and there is no chance of dispersal, such a high growth rate is clearly unsustainable and fits the profile of an eruption (McCullough 1997). It is reasonable to expect that population growth will likely continue and exceed carrying capacity before it wanes in accordance with density-dependent population regulation. Population size and density are among the most fundamental information required for management and tracking of population trends, but population assessments have not been conducted on Michipicoten Island since the aerial survey in 2001, and there are no current plans to begin regular assessments. Population estimates by pellet-group counts used to be standard in wildlife management and produced viable, yet imprecise, population estimates (Eberbardt and Van Etten 1956, Bailey and Putman 1981, and others). Michipicoten Island represents an ideal case for their use because the system lacks many of the sources of error which cause trouble with the method. The high animal density, closed system and lack of similar species with which caribou pellets could be confused should allow for a reasonable estimate using the method (Neff 1968). The purpose of this note is two fold: 1) to produce a reasonable estimate of current caribou population on Michipicoten Island with pellet counts, and 2) to provide a baseline set of pellet-count data for comparison by future researchers.

Methods

Michipicoten Island is the third largest island in Lake Superior. It is located in the northeastern part of the lake and is 16 km offshore at its nearest point (Fig. I). Michipicoten Island is 87% forested. I classified forests using raster models overlaid on vegetation maps and segregated the forest into three types: birch forests and maple forests (deciduous), mixed forests, and conifer forests. These three types accounted for

about 89.5% of the island area (OMNR 2004). Forest cells which were not classified as above were classified as 'other' and treated as an average of the three dominant forest types.
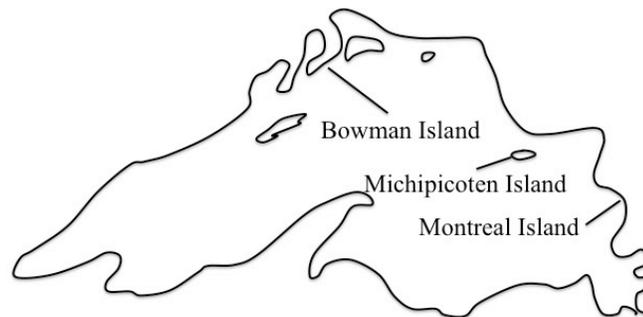

Figure I. Lake Superior map showing Michipicoten Island.

Caribou scat density data were collected during July 2011 at 22 locations on Michipicoten Island, 8 in conifer forests, 7 in deciduous forests, and 7 in mixed forests. Pellet groups were defined as more than 12 pellets in a cluster with a minimum spatial separation of > 0.5m between clusters. Loosely scattered or individual pellets were not counted. Pellet groups were counted by two observers based on experience and, for the most part, intuition of two observers matched when classifying groups. Both estimates are based on a value garnered from overwinter defecation rates of captive Slate islands caribou, 23 pellet groups per day (Bergerud et al. 2007), and a visibility of one year for pellets. Observable pellet time was based on the fact that leaf litter covers winter pellets each autumn over the majority of the island and leaf litter was not moved during

sampling. This assumption is consistent with timelines published for visibility of moose

pellets in Sweeden (Persson 2003).

Distances to the nearest neighbour were measured from one to the next of the

seven nearest pellet groups beginning from the center of a randomly placed transect.

Pellet-group densities were estimated using the mean distance and 95% confidence

intervals to each of the seven nearest neighbours for each forest type following Barbour

et al. (1999). Distances were converted to population estimates by multiplying by the

area of each of the forest types using this equation.

$$P = \sum d \times a / e$$

where P = population estimate, d = pellet density per forest type, a = area of forest type,

and e = elimination rate of 8,395 pellet groups per caribou / year.

Results and discussion

Pellet-group densities were highest in coniferous forests, followed by deciduous

and mixed forests (Table I). The calculated estimate for caribou density was 680 (Table

II). Population growth on Michipicoten Island was reported by Bergerud et al. (2007) as

$\lambda=1.18$ for the period of 1982 to 2001, when the population was estimated at 200. This

estimate places the rate of increase from 2001 to 680 individuals in 2011 at $\lambda=1.12$, a

reasonable figure for an expanding caribou population (Fig. II).

Table I: Mean pellet groups per forest type and the area of each forest type on Michipicoten Island.

Forest type	Pellet groups / ha	S.E.	Area (ha)
Conifer	3173	913	650
Deciduous	146	19	10987
Mixed	359	267	139
Other	1436	516	1387

Table II: Population estimates and 95% confidence limits (CI) for Michipicoten Island using the nearest neighbour method.

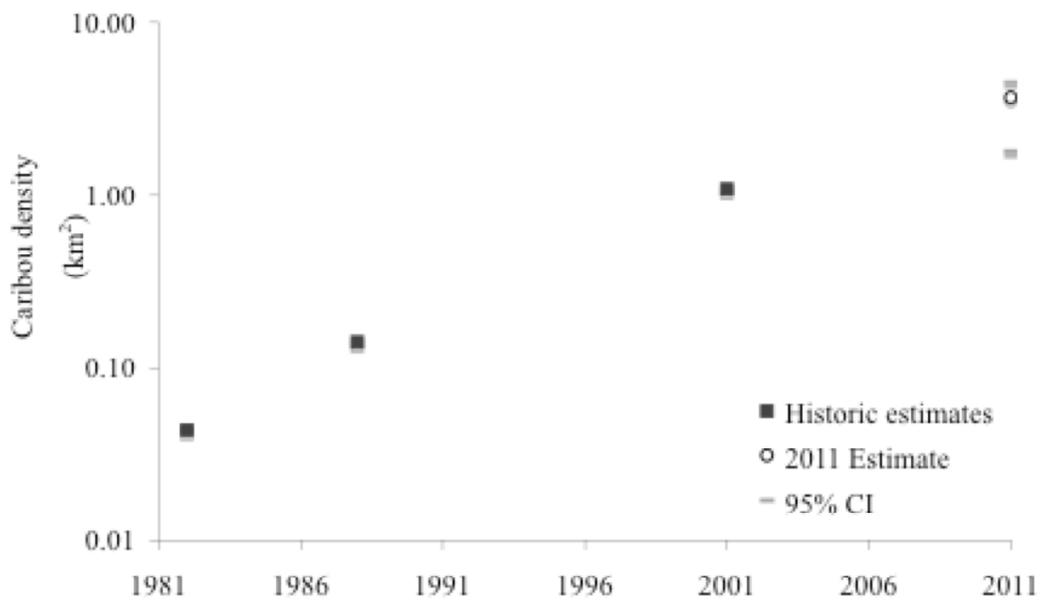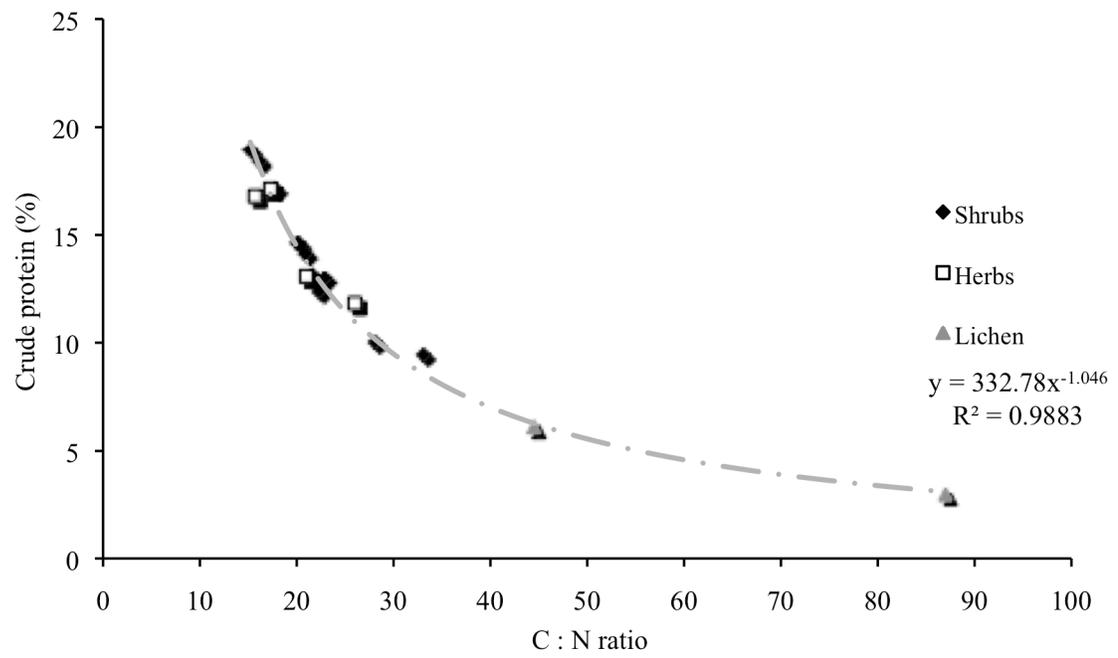|	Michipicoten Island
Population estimate	680
Lower 95% CI	328
Upper 95% CI	875

Figure II: Caribou density on Michipicoten Island since 1981.

Although wide confidence intervals span a difference of nearly 550 animals, even lower limits represent continuing population growth on the Island since 2001. The upper confidence limit of the estimate represents a higher density, but this is still a biological possibility as it proposes a density only about half of the peak density observed on the nearby Slate Islands (4.8 caribou / km^2 vs. 9.7 caribou / km^2 on the Slate Islands; Bergerud et al. 2007). That population densities remain below those historically seen on the Slate Islands suggest the estimate is reliable (Bergerud et al. 2007, Carr et al. 2012 in press). The estimate of between 328 and 875 caribou on Michipicoten Island provides a range of values not exceeding growth rates of other caribou and reindeer populations (Klein 1956, Heard and Ouellet 1994).

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Appendix 2. Crude protein and carbon : nitrogen (C:N) ratio of forage taxa on the Lake Superior caribou range.

y = 332.78x$^{-1.046}$
R^2 = 0.9883

Appendix 3. Forage density by individual taxa comprising the shrub and herb layers for Pukaskwa's Spruce Harbour, the Pukaskwa Islands, Michipicoten Island, and the Slate islands.

Shrubs

Herbs
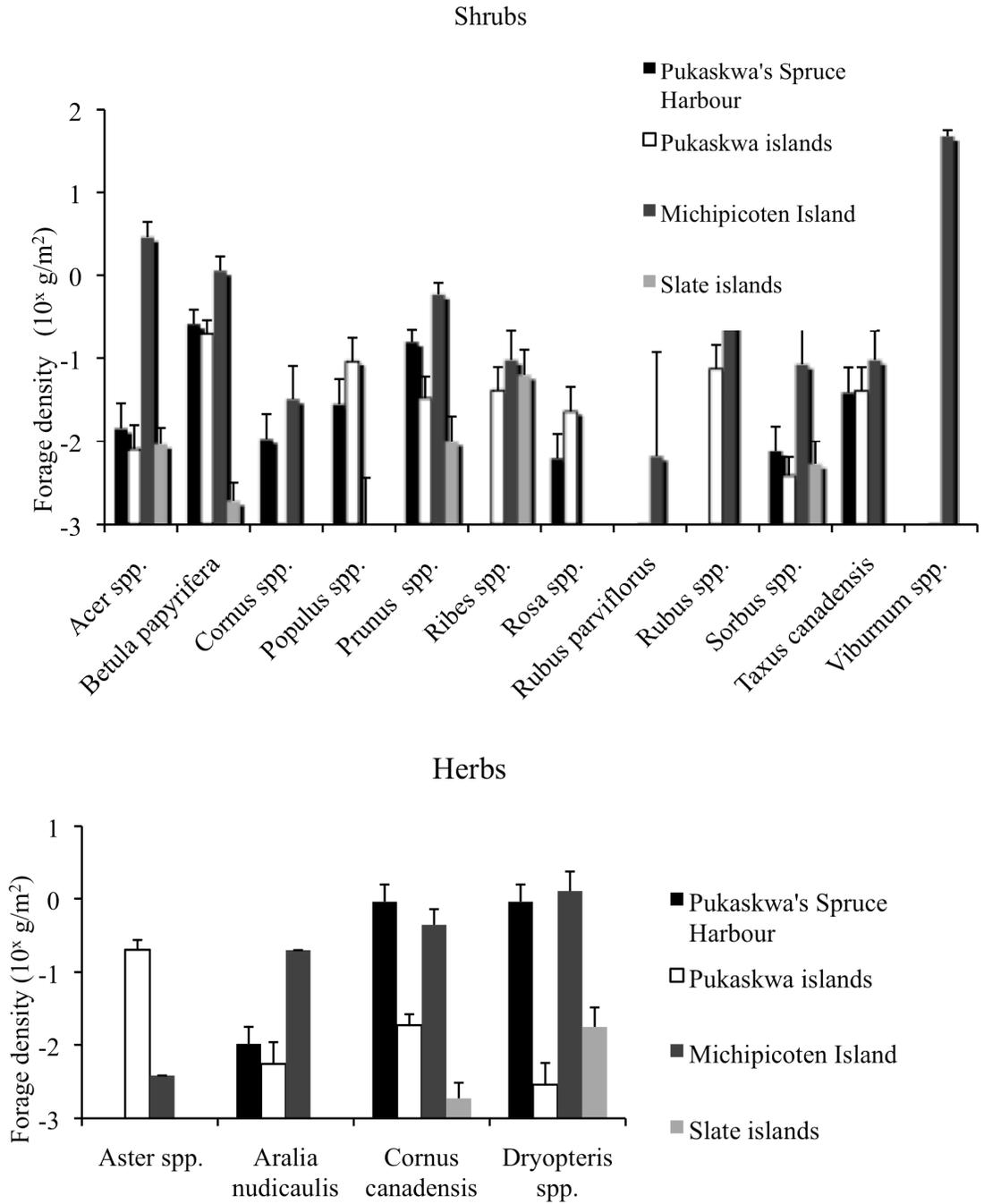
Appendix 4. Homogenious subsets from Tukey HSD post-hoc tests for forage quality of caribou forage taxa on the Lake Superior coastal range.

Tukey HSD		Homogeneous subsets			
Taxa	*n*	1	2	3	4
Cladonia spp.	2	2.99			
Alectoria spp. *& Usnea* spp.	4	6.11	6.11		
Taxus canadensis	3		9.44	9.44	
Ribes spp.	3		10.02	10.02	
Dryopteris spp.	4			11.86	11.86
Rubus spp.	3			12.39	12.39
Cornus spp.	2			12.82	12.82
Viburnum spp.	4			13.02	13.02
Conrus canadensis	5			13.1	13.1
Sorbus spp.	4			13.15	13.15
Betula papyrifera	4			14.14	14.14
Acer spp.	4			14.29	14.29
Prunus spp.	4			14.59	14.59
Aster spp.	3				16.78
Aralia nudicaulis	3				17.11
Rubus parviflorus	3				17.11

Source	df	*F*	*p*
Model	22	14.13	0.00
Intercept	1	2448.66	0.00
Taxa	17	8.04	0.00
Days after June 1	2	1.88	0.17
Location	1	0.04	0.85
Error	38		

Appendix 5. Model of factors associated with bottom-up (forest overstory and dominant canopy taxon) and top-down (island and slope) regulation of forage density in the lichen layer at Pukaskwa National Park, where: BF = balsam fir (*Abies balsamea*), JP = jack pine (*Pinus banksiana*), PB = paper birch (*Betula papyrifera*), SB = black spruce (*Picea mariana*), SM = maple (*Acer* spp.), and TA = trembling aspen (*Populus tremuloides*).

Model Term	p		
Model weighting	1.000		
Intercept	0.00		
Forest overstory	0.00		
Dominant canopy taxa	0.00		
Forest overstory + dominant canopy taxa	0.00		
	p	β	S.E.
Intercept	0.58	2.12	3.79
Forest overstory	0.32	0.076	0.0754
BF	0.77	-2.06	7.03
JP	0.00	892	74
PB	0.46	-4.24	5.70
SB	Reference	0.00	-
BF + forest overstory	0.99	-0.029	1.870
JP + forest overstory	0.00	-9.75	0.90
PB + forest overstory	0.33	0.235	0.243
SB + forest overstory	Reference	0.00	-

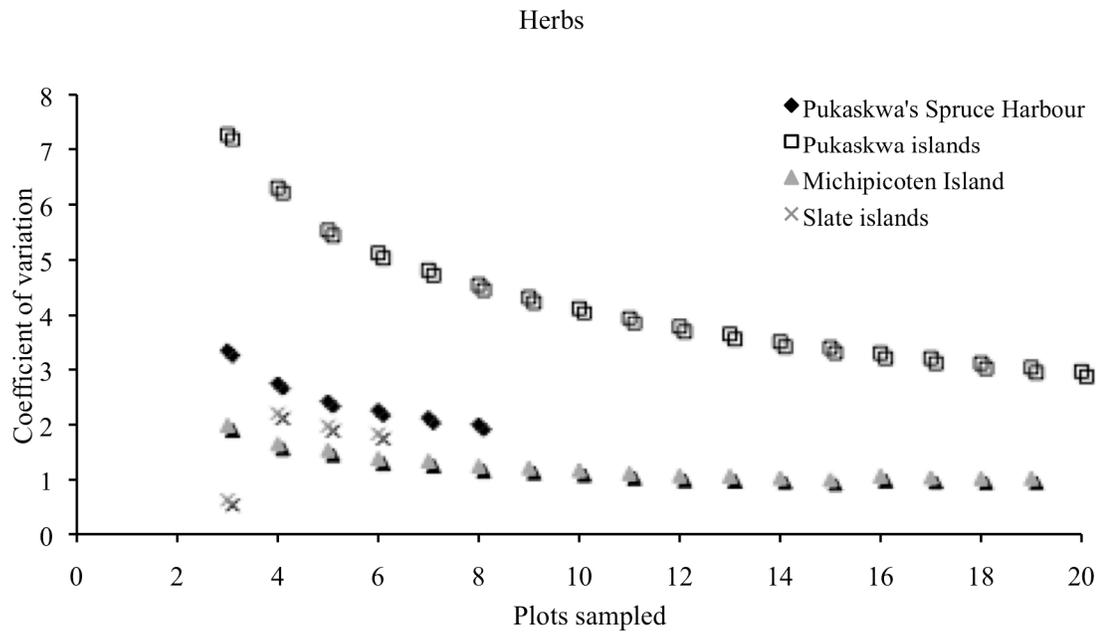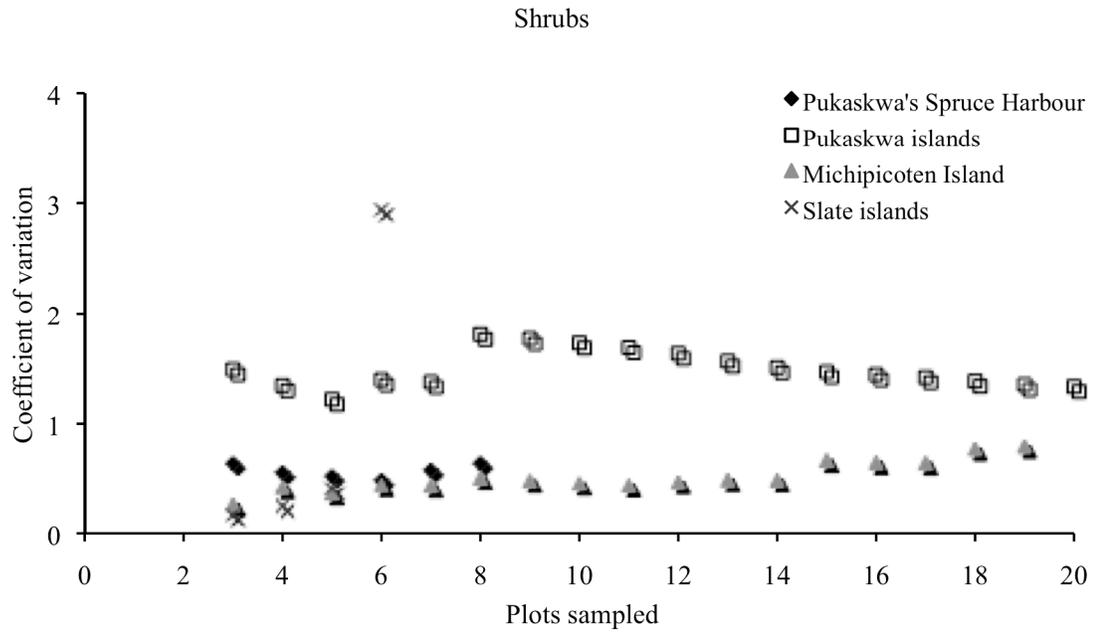| Model Term	p		
Model weighting	0.000		
Intercept	0.01		
Island	0.00		
Slope	0.05		
Island + Slope	0.03		
	p	β	S.E.
Intercept	0.99	0.155	18.244
Island yes	0.00	62.7	18.8
Island no	Reference	0.00	-
Slope gentle	0.00	19.6	74.2
Slope intermediate	0.46	4.35	21.93
Slope steep	Reference	0.00	-
Island no + slope gentle	0.03	-50.6	23.9
Island no + slope intermediate	-	-	-
Island yes + slope gentle	-	-	-
Islnad yes + slope intermediate	-	-	-
Island yes + slope intermediate	Reference	-	-

Appendix 6. Model factors associated with bottom-up (elevation) and top-down (slope) regulation of forage density in the shrub layer on Michipicoten Island.

Model Term	p		
Model weighting	1.000	β	S.E.
Intercept	0.29	-46.8	44.4
Elevation	0.04	0.386	0.187
Model weighting	0.027		
Intercept	0.00		
Slope	0.00		
	p	β	S.E.
Intercept	0.00	143	4
Gentle	0.00	-108	0
Intermediate	0.42	-35.3	7.0
Steep	Reference	0.00	-

Appendix 7. Model of factors associated with top-down (dominant overstory taxon and forest overstory) regulation of forage density in the lichen layer on Michipicoten Island. Taxa names as in appendix 5.

Model Term	p	β	S.E.
Model weighting	1.000		
Intercept	0.96	0.008	0.098
BF	0.95	0.007	0.104
PB	0.98	-0.003	0.107
SB	0.02	0.262	0.113
SM	0.92	-0.008	0.107
TA	Reference	0.000	-
Model weighting	0.027		
Intercept	0.00		
Dominant canopy taxa	0.00		
Forest overstory	0.17		
Dominant canopy taxa + forest overstory	0.01		
	p	β	S.E.
Intercept	0.91	0.008	0.065
BF	0.93	0.007	0.072
PB	0.97	-0.003	0.077
SB	0.00	0.406	0.081
SM	0.92	-0.008	0.073
TA	Reference	0.000	-
Forest overstory	1.00	0.000	0.002
BF + forest overstory	0.99	0.000	0.002
PB + forest overstory	1.00	0.000	0.002
SB + forest overstory	0.01	-0.004	0.002
SM + forest overstory	Reference	0.000	-
TA + forest overstory	Data insufficient		

Appendix 8. Coefficient of variation in forage density of the shrub, herb and lichen layers at various sample sizes for the Pukaskwa islands, Pukaskwa's Spruce Harbour, Michipicoten Island, and at Slate Islands Provincial Park.

Shrubs

Herbs

Lichen
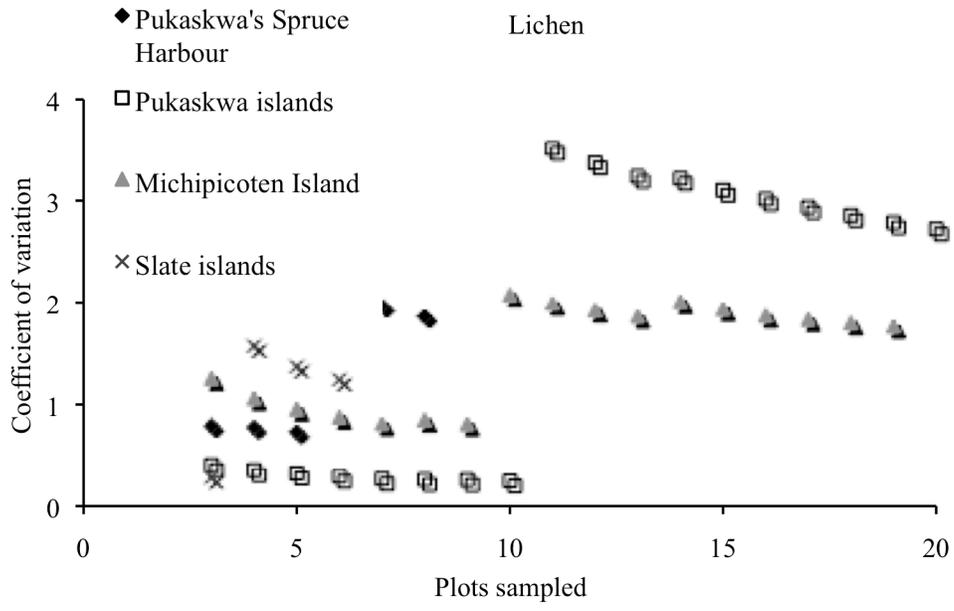
Appendix 9. Model of factors associated with bottom-up regulation of forage density in the herb layer at Slate Islands Provincial Park.

Model Term	p	β	S.E.
Model weighting	1.000		
Intercept	0.27	0.004	0.003
Shrub density	0.00	0.176	0.016