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# NUTRITIONAL VALUES OF HABITATS FOR WOODLAND CARIBOU DURING SUMMER

BY
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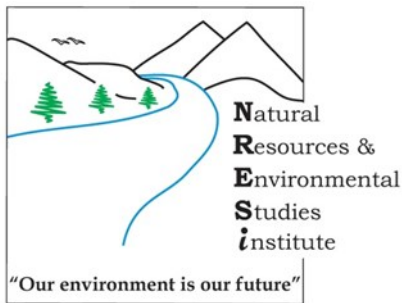
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Abstract

Many populations of woodland caribou (*Rangifer tarandus caribou*) in Canada are declining and may be at risk of extinction. Altered predator-prey dynamics are implicated in these declines, but nutrition is the foundation of population productivity and may place additional constraints on caribou. We used tame caribou (of three nutritional classes: lactating, non-lactating, yearling) as a habitat-assessment tool, at 135 sites across northeastern British Columbia, to ascertain the suitability of nutritional resources in alpine, montane, and boreal plant communities to support energy and protein requirements of caribou during summer. Caribou were highly selective foragers, avoiding more than half of understory vegetation biomass. Deciduous shrubs were the primary summer forage of caribou, and forbs, lichens, and mushrooms were secondary dietary items. Bite masses were largest on mushrooms and deciduous shrubs, and smallest on lichens and berries; larger bites allowed caribou to achieve higher intake rates. Caribou were most likely to meet energy and protein requirements in alpine willow communities and those forest communities with an abundance of accepted deciduous shrubs and forbs (e.g., early-seral). Nutritional deficiencies in many communities, particularly for reproductive caribou with higher nutritional demands associated with lactation, may make it even more challenging for caribou to make a living and reproduce on landscapes already impacted by anthropogenic disturbance and changing predator-prey dynamics.

Introduction

Woodland caribou (*Rangifer tarandus caribou*) are an iconic species of boreal and montane ecosystems across Canada. Alteration or elimination of over 40% of their historic habitat in British Columbia (BC) and associated changes in predator-prey dynamics have contributed to significant population declines (Spalding 2000, Wittmer et al. 2005). Increasing evidence suggests that nutritional resources during summer may place additional constraints on caribou (Crête and Huot 1993, Post and Klein 1999, Kerby and Post 2013), but the capacity of available nutritional resources to meet demands for survival, growth, and reproduction has not been quantified.

During summer, north-temperate ungulates experience elevated nutritional demands for lactation, growth, and the replenishment of body reserves needed for breeding in autumn and overwinter survival (McEwan and Whitehead 1970, Cook et al. 2004). For caribou, when nutritional condition of females is low, they may: delay breeding (and thus parturition) and (or) produce small neonates with lower probabilities of survival, in part due to increased susceptibility to predation (Rognmo et al. 1983, Skogland 1990); fail to breed or experience breeding pauses thus eliminating their ability to contribute to population recruitment in some years; or face reduced probability of overwinter survival and thus have no potential to contribute to the population thereafter (Allaye Chan-McLeod et al. 1994, Gerhart et al. 1997). These constraints on adults translate into limitations to calf performance (e.g., growth rates, body size and mass entering winter, and probability of overwinter survival; Reimers et al. 1983, Valkenburg et al. 2003, Dale et al. 2008). Animal performance is the product of complex interactions between both summer and winter nutritional deficiencies and physiological mechanisms used by ungulates in response to these deficiencies (Cook et al. 2013). Growing evidence from around the northern hemisphere, however, supports the hypothesis that nutrition on summer range, to a greater degree than nutrition on winter range, may drive productivity of free-ranging ungulates (Crête and Huot 1993, Cook et al. 2013, Kerby and Post 2013). Quantifying values of nutritional resources available to caribou during summer can help elucidate the role of nutrition in the conservation and recovery of declining caribou populations.

The goal of this research was to use tame caribou as a habitat assessment tool in northeastern BC, where boreal, central-mountain, and northern-mountain woodland caribou are designated as Threatened, Endangered, and Special Concern, respectively, by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2014a, b). Specifically, we worked to: (1) differentiate food (accepted) from non-food (avoided) vegetation biomass; (2) quantify accepted biomass in different plant communities available to caribou; (3) document foraging responses (e.g., intake rates, diet quality and composition) of caribou; and (4) identify the nutritional suitability of plant communities to meet energy and protein requirements for caribou during summer across alpine, montane, and boreal landscapes.

Methods

Study Area

Our study area encompassed potential natural vegetation (PNV) communities available to boreal, central-mountain, and northern-mountain caribou in northeastern BC (Fig. 1). Boreal caribou inhabit forests and wetland complexes in the boreal white (*Picea glauca*) and black spruce (*Picea mariana*) biogeoclimatic ecosystem classification (BEC) zone (Meidinger and Pojar 1991). We sampled boreal white spruce (BWS), boreal black spruce uplands, bogs and poor fens (BBS), and boreal treed rich fens (BTRF) in the boreal forest (see Denryter et al. 2017 for additional information on classification and description of plant communities). Boreal white spruce communities generally were upland stands with coniferous, deciduous, and mixed wood overstories at low elevations. Overstory species often included white spruce, trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*); open-canopied lodgepole pine (*Pinus contorta*) dominated on drier pine-lichen sites. The boreal black spruce (BBS) community encompassed both upland black spruce forests (typically with low understory productivity) and nutrient-poor treed muskegs (i.e., bogs and poor fens). Nutrient-poor muskegs — a type of BBS community — were characterized by stunted (<10 m tall) black spruce and tamarack (*Larix laricina*) on poorly drained sites with high ground cover of mosses (e.g., *Sphagnum* spp.) and evergreen shrubs. Boreal treed rich fens (BTRF) had higher understory productivity than BBS sites, and were dominated by black spruce <10 m tall, and dwarf birch or willows (<2 m tall).

Northern- and central-mountain caribou inhabit forests in the Sub-Boreal Spruce (*Picea* spp.) and Engelmann Spruce-Subalpine Fir (*P. glauca x engelmannii-Abies lasiocarpa*) BEC zones, as well as alpine plant communities. We sampled these spruce-fir forests at mid- (836–1,165 m; MidSF) to high-elevations (1,127–1,600 m; HighSF). Plant community composition of spruce-fir forests varied with physical geography, microclimate, and seral stage, but typically had subalpine fir, lodgepole pine or spruce as the dominant tree species. Among alpine plant communities (at >1,600 m), primary productivity varied across a moisture gradient of the sites we sampled from wet-productive types (willow-dominated; AWillow), to intermediate types (dwarf birch-dominated; ABirch), and dry types (lichen- or grass-dominated; ADry). Willow-dominated and birch-dominated alpine communities included plant communities in the Spruce-Willow-Birch (*Picea-Salix-Betula*) BEC zone and dry alpine communities included alpine tundra and alpine fellfields in the BEC classification system. Wetlands (W), such as willow- and sedge-dominated wet meadows, occurred sporadically throughout boreal and montane landscapes.

Foraging Studies

During the summers and early autumns of 2013–2015, we observed foraging by tame, female caribou of three nutritional classes — lactating, non-lactating, and yearling — in the predominant regional plant communities of northeastern BC (Fig. 1). Tame animals allow researchers to be in close proximity, which facilitates detailed quantification of forage and nutrient intakes, and they demonstrate what animals can achieve given available forage conditions (Trudell and White 1981; Parker et al. 1999). Tame animals also can be taken to areas not used by wild ungulates, which may provide insights into why wild ungulates do not use those areas (Cook et al. 2016). Food selection, diet composition, and foraging efficiencies of tame animals are representative of free-ranging animals when they are in similar habitats (Spalinger et al. 1997). Most of the tame caribou in our study were captured as calves from five mountain-dwelling caribou herds in Alaska, and hand-raised at the Robert G. White Large Animal Research Station, University of Alaska Fairbanks in 2009 (Parker and Barboza 2013). In 2013, these caribou were transferred to the National Council for Air and Stream
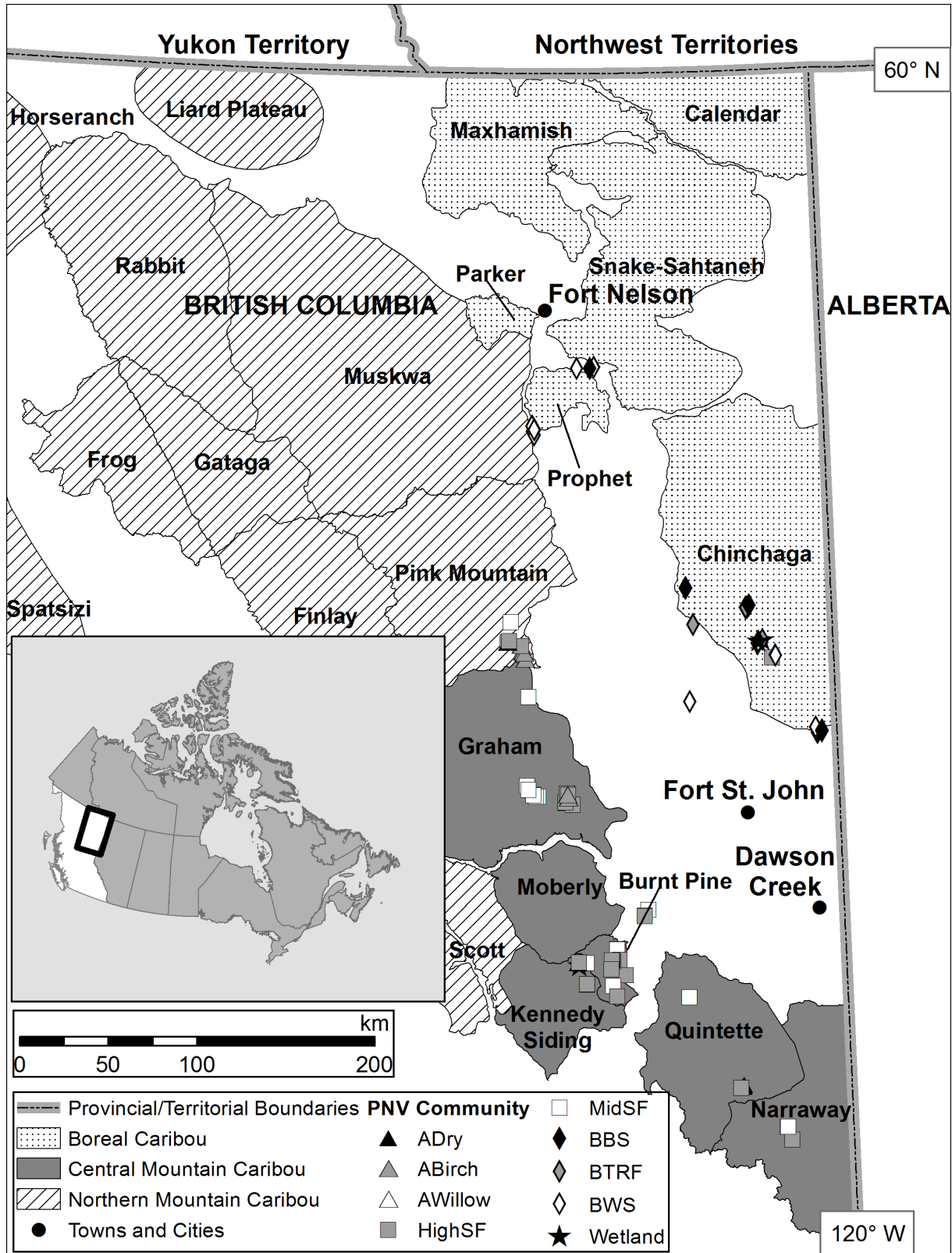
Figure 1. Locations of sites where foraging observations were collected on tame caribou during the summers and early autumns of 2013–2015 in northeastern British Columbia, relative to ranges of wild caribou herds (British Columbia Ministry of Environment - Ecosystems Branch 2015). Potential natural vegetation (PNV) communities included dry alpine (ADry); birch alpine (ABirch); willow alpine (AWillow); high-elevation spruce-fir forests (HighSF); mid-elevation spruce-fir forests (MidSF); boreal black spruce bogs, nutrient poor fens, and uplands (BBS); boreal treed rich fens (BTRF); boreal white spruce (BWS); and a variety of wetland sites (Wetland). For reference, the Alberta-British Columbia border runs north to south.

Improvement (NCASI) research facility near Fort St. John, BC; five dam-raised females born at the NCASI facility also were used in foraging studies. The University of Northern British Columbia Animal Care and Use Committee (Protocol Number 2013-9) approved all protocols used in this study.

During field trials, we estimated understory vegetation biomass using clipped plots (collecting aboveground biomass of current annual growth by plant species, as well as previous-year foliage for conifers and evergreens). We also collected data on stand characteristics (e.g., slope, aspect, canopy cover, tree density). Temporary animal enclosures (0.4–1.75 ha) with portable electric fencing equipment (Denryter et al. 2017) were then assembled and tame caribou were transported in a stock trailer to and from enclosures, where they were held for foraging observations for up to 48 h. Foraging data were collected between early July–late September or early October each year, with timing of vegetation green-up, calf size (for safe transport), insect harassment, and weather (e.g., snow) determining the duration of the sampling season. We observed foraging by three to four caribou (with their associated calves) at each site. For each caribou, we collected 75 min of foraging observations per day including two morning (0500–1100 h) and one evening (1700–2100 h) trial, which lasted 20 min each, and an additional 15-min trial at midday (1100–1600 h). During foraging trials, observers recorded each bite consumed, by species and following each trial, the observers collected bite mass samples based on direct observations of how caribou handled forage items. Observers collected 10 or 20 representative bites per plant species by mimicking the size of the bite taken and the plant part consumed (e.g., stripping leaves from a stem versus cropping a single leaf or cropping berries). We also collected activity data using accelerometers (Mini-Mitter® model AW64, Mini-Mitter Co., Bend, Oregon, USA), which were affixed to radio-collars on the caribou and recorded motion. Highest values resulted from activities with the highest movement: running > walking > foraging > standing > bedding.

To equate these values with specific behaviours and determine daily foraging time (and daily intake), we opportunistically collected direct observations of behaviour, continuously recording caribou behaviours at 1-min intervals.

Diet Composition, Diet Quality, and Nutrient Intake

To remove the effect of varying levels of moisture in different vegetation types, we dried the bite mass (and vegetation biomass) samples at $\geq$70 °C to a constant mass (dry matter). Hereafter, all biomass, bite mass, and intake (not specified as energy or protein) results are reported on a dry matter basis. We estimated mass of each plant species consumed within each enclosure and multiplied species-specific bite mass by the number of bites consumed of each species to obtain estimates of dry matter intake (Denryter et al. 2017). We calculated diet composition by forage class (i.e., deciduous shrubs, evergreen shrubs, forbs, graminoids [including horsetails], mushrooms, arboreal lichens, terrestrial lichens, and other [club mosses, ferns, conifers]) as the proportion of intake of each forage class (in g) divided by the total dry matter intake (in g) recorded during foraging trials. Proportion of available biomass of each forage class was calculated similarly.

We collected representative bites of plant species and parts in the proportions eaten by the caribou for simulated diets based on the species that comprised the top 90% of bites taken by each caribou at each site. Simulated diets were frozen immediately after collection and were transferred to the Wildlife Habitat and Nutrition Laboratory at Washington State University for nutritional analyses. Nutritional assays were completed to determine energy, fiber, protein, and tannin content of samples with bomb calorimetry, sequential fiber analysis, total elemental N, and tannin precipitation methods (Goering and Van Soest 1970, Martin and Martin 1983). Gross energy and crude protein values of diet samples were converted to digestible energy (DE) and digestible protein (DP) using

the equations of Robbins et al. (1987a, b) and Hanley et al. (1992). Daily DE and DP intakes were the products of an individual caribou's dry matter intake rate, foraging time, and dietary DE and DP.

Data Analysis

All data analyses were completed in Stata 14 (StataCorp LP, College Station, TX). To determine selection and hence, quantify food supplies, we assessed selection for each species that caribou encountered using Ivlev's electivity index, based on the proportion used (i.e., intake) and the proportion available (i.e., biomass) (Ivlev 1961). We used electivity results to quantify the amount of forage at each site as accepted (plant species eaten in proportion to (neutral) or proportionately greater than (selected) their availability) or avoided (plant species eaten proportionately less than their availability). To quantify relationships between foraging parameters and forage intake, we used linear and non-linear multilevel mixed-effects models (Skrondal and Rabe-Hesketh 2004) that allowed us to account for differences in nutritional classes of animals across years and to track individuals throughout the analyses.

We compared daily nutrient intakes obtained by caribou in different communities to reported nutritional requirements for caribou (National Research Council 2007) to evaluate the degree to which the communities may satisfy nutritional needs of caribou. For an average-sized 110 kg caribou, daily digestible energy requirements are reported to be 30,104 kJ • day^{-1} DE for maintenance of body mass when not lactating in summer and 50,534 kJ • day^{-1} DE during peak lactation. We approximated daily digestible protein requirements to be 94 g • day^{-1} DP for non-lactating caribou and 270 g • day^{-1} DP for lactating caribou at peak lactation (calculated as in Denryter 2017). Yearling caribou with continuing growth demands presumably have more similar requirements to lactating than non-lactating animals.

Results and Discussion

We collected ~942 h of foraging observations on the tame caribou, counted ~1.2 million bites, and collected ~1,296 bite mass samples and 517 diet quality samples at 135 sites across northeastern BC. Deciduous shrubs were the primary summer forage of caribou in our study (Fig. 2). Mushrooms, some forbs such as lilies (e.g., *Streptopus amplexifolius*) and peas (*Lathyrus* spp.), and some lichens were also important summer forages for caribou (Fig. 2).

Vegetation biomass varied more than 10-fold among communities, and on average <50% of available biomass was accepted by caribou as food (Fig. 3). Caribou were highly selective foragers, selecting only 28 of ~233 species encountered during our study; these 28 species accounted for ~78% of all intake. Deciduous shrubs, especially several species of willow (*Salix* spp.), birch (*Betula* spp.), blueberry (*Vaccinium* spp.), and green alder (*Alnus crispa*), were highly selected. Only four terrestrial lichens were selected by caribou (*Cetraria* spp., *Cladonia* spp., *Cladina* spp., and *Flavocetraria* spp.) and these accounted for 97% of all terrestrial lichens consumed. Two arboreal lichens, *Bryoria* spp. and *Alectoria* spp., also were selected by caribou. Caribou avoided two genera of terrestrial lichens (*Peltigera* and *Stereocaulon*) that were abundant throughout the study area, as well as two common evergreen shrubs (lingonberry leaves (*Vaccinium vitis-idaea*) and Labrador tea (*Ledum groenlandicum*)). Overall, avoided species (which included berries of evergreen shrubs) accounted for ~7% of caribou diets. A complete list of all species consumed by selection category is given in Denryter et al.
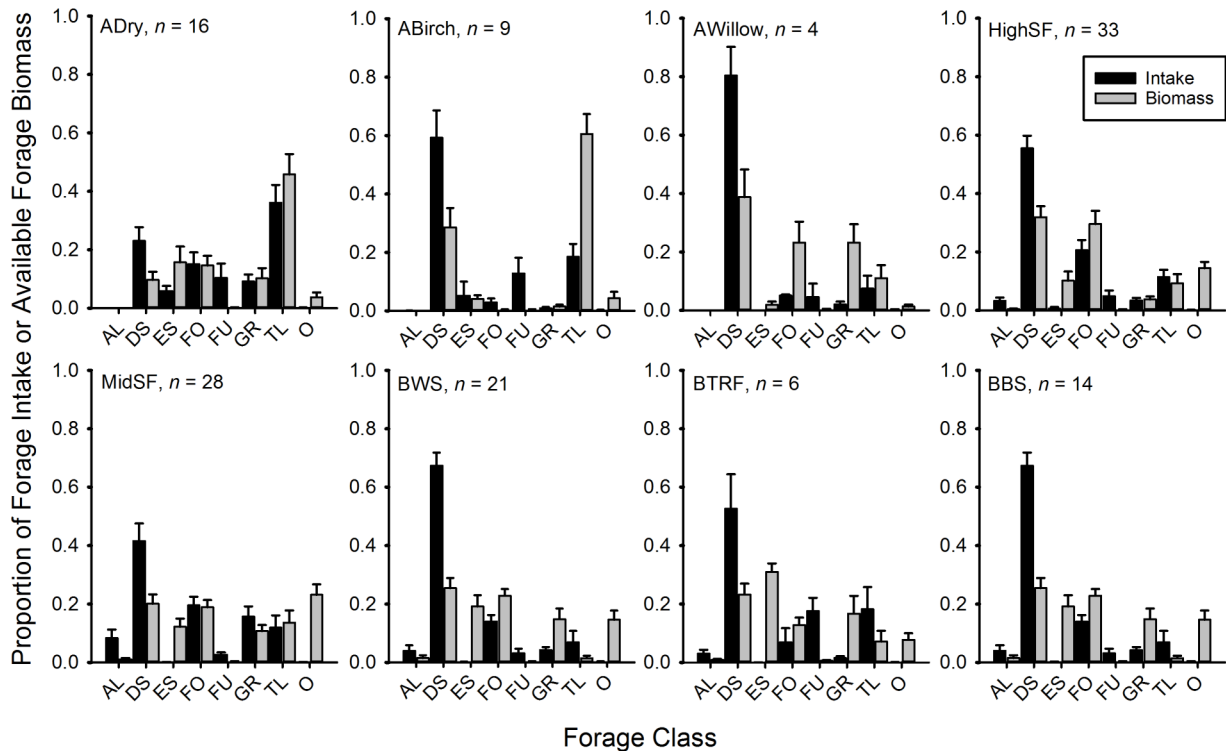
Figure 2. Mean (± SE) proportions of forage intake by tame caribou and available biomass of forage classes (AL = arboreal lichen, DS = deciduous shrub, ES = evergreen shrub, FO = forb, FU = fungi (primarily mushrooms), GR = graminoid, TL = terrestrial lichen, O = other) in potential natural vegetation (PNV) communities, which include dry alpine (ADry), birch alpine (ABirch), willow alpine (AWillow), high-elevation spruce-fir forest (HighSF), mid-elevation spruce-fir forest (MidSF), boreal white spruce (BWS), boreal treed rich fen (BTRF), and boreal black spruce (BBS), sampled during summer and early autumn of 2013–2015 in northeastern British Columbia. Numbers of unique sampling sites are given for each PNV community. Effects of stand characteristics (e.g., canopy cover, stand age, tree density, slope, aspect) are not accounted for in this figure.

(2017). Diet quality of the food consumed by caribou varied among plant communities and both DE and DP content of their diets declined across the summer season (Fig. 4).

Bite masses of species encountered by caribou varied within and among forage classes. Smallest bites were obtained on arboreal and terrestrial lichens, as well as the berries of evergreen shrubs (lingonberry and crowberry (*Empetrum nigrum*); Fig. 5A). Largest bites were obtained on mushrooms, but their availability varied across years. Deciduous shrub leaves (willow, alder, birch) also afforded caribou relatively large bites (50% larger than the small bites of lichens).

Caribou increased bite rates when bite sizes were smaller (Fig. 5B), but this foraging strategy was not able to compensate fully for decreasing bite size, as reflected in intake rates (Fig. 5C). Regardless of whether animals were lactating, non-lactating, or yearlings, intake rates increased with increasing bite size — as such, at small bite sizes (i.e., high bite rates), caribou were not able to achieve high per-minute intake rates (Fig. 5C). Daily intake rates, which have implications to the ability of an animal to satisfy daily nutritional requirements, were low when per-minute intake rates were low (Fig. 5D). Thus, if the acceptable vegetation available in a plant community afforded small bite sizes, caribou were compromised in achieving high enough intakes to meet summer nutritional requirements.

On average, caribou achieved daily digestible energy and digestible protein intakes that were at or above requirements to maintain body mass for non-lactating animals, except in dry alpine and boreal black spruce
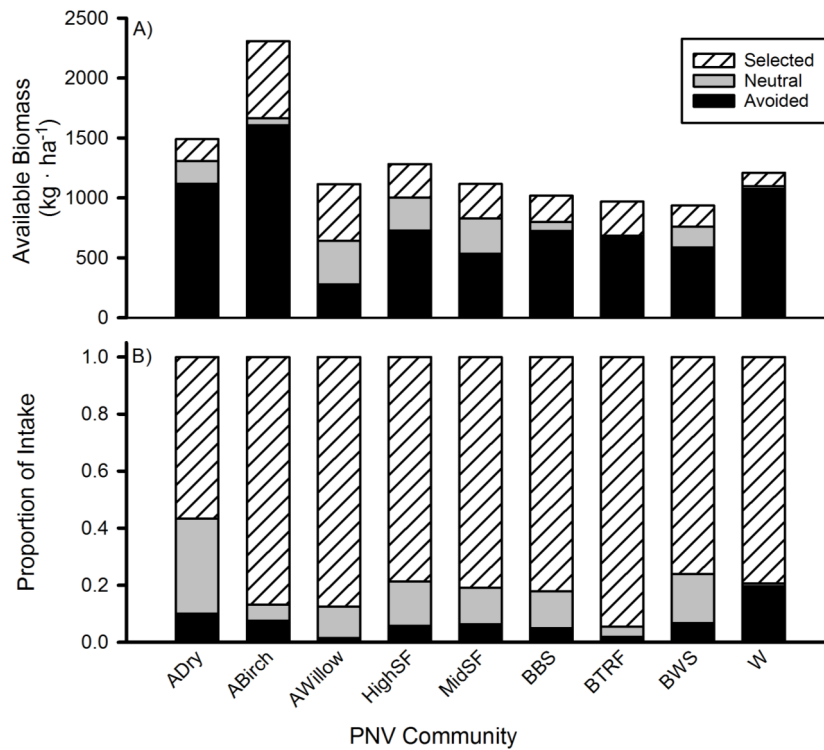
Figure 3. Total available biomass (kg ● ha-1) of understory vegetation (A) and mean proportion of intake (B) by tame caribou in potential natural vegetation (PNV) communities, which include dry alpine (ADry), birch alpine (ABirch), willow alpine (AWillow), high-elevation spruce-fir forest (HighSF), mid-elevation spruce-fir forest (MidSF), boreal white spruce (BWS), boreal treed rich fen (BTRF), boreal black spruce (BBS), and wetlands (W), sampled during summer and early autumn 2013–2015 in northeastern British Columbia. Sample sizes are given in Figure 2, except for wetlands (n = 4). For each, available biomass or intake of vegetation is presented for selected, neutral, and avoided species. Neutral and selected species represent forage accepted by caribou within these plant communities, compared to avoided species. Effects of stand characteristics (e.g., canopy cover, stand age, tree density, slope, aspect) are not accounted for in this figure.

communities (Fig. 6). In contrast, there were many plant communities where animals (on average) did not meet the requirements to support peak lactation, though willow-dominated alpine communities were an exception. In addition to natural vegetation communities, however, many site characteristics such as stand age, canopy cover, slope and aspect, as well as factors such as season and precipitation, influence plant communities and thus the nutritional responses of caribou (Cook et al. 2016). As such, when evaluating nutritional response variables of individual caribou at each site (rather than as averages for each vegetation community), it is apparent that caribou were able to meet or exceed daily energy and protein requirements at some sites (Fig. 7). Non-lactating caribou were able to meet requirements for DE in 55% of our foraging observations (per individual at

a site) and for DP in 59% of the observations. Lactating caribou, with higher nutritional requirements were more constrained; adequate daily intakes of DE and DP for peak lactation were documented in only 23% and 24% of foraging observations, respectively. Across all nutritional classes of animals and plant communities, caribou were most likely to meet requirements at willow alpine sites and in boreal white spruce communities with productive understories (typically mid- and early seral stands) (Fig. 6).

Caribou usually had the lowest nutrient intakes at windswept dry alpine sites and in boreal black spruce communities, where accepted biomass was comprised largely of lichens (small bite sizes and low intake rates). Caribou in these nutritionally inadequate plant communities must take advantage of adjacent or nearby abundant, higher-quality forage to
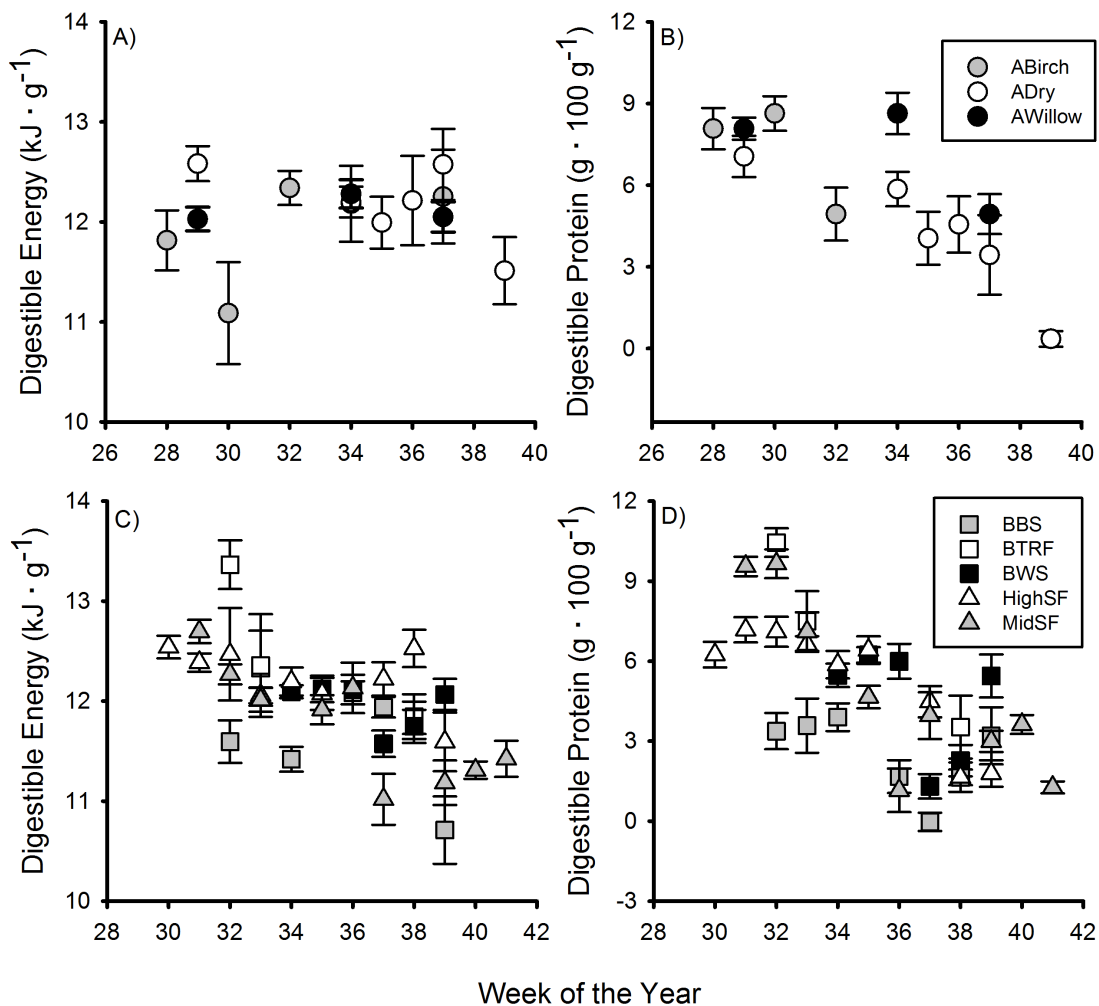
Figure 4. Average (x̄ ± SE) digestible energy and digestible protein contents in the diets of tame caribou foraging in alpine (A, B) and forest (C, D) communities, by week of the year (showing the influence of phenological changes, 2013–2015) in northeastern British Columbia. Alpine communities were dry alpine (ADry), birch alpine (ABirch), and willow alpine (AWillow). Forest communities were boreal black spruce (BBS), boreal treed rich fens (BTRF), boreal white spruce (BWS), high-elevation spruce-fir forests (HighSF), and mid-elevation spruce-fir forests (MidSF). Week 28 corresponds to 8–14 July and week 41 to 7–14 October. Effects of vegetation community, stand characteristics (e.g., canopy cover, stand age, tree density, slope, aspect), and precipitation are not accounted for in this figure.

satisfy nutritional demands. Understanding what factors (e.g., site characteristics, vegetation community, season, precipitation) explain this variation in nutritional responses across sites, and thus the ability for different plant communities to meet nutritional requirements, will be critical for understanding how landscapes can be managed most effectively for caribou.

Conclusions and Recommendations

Caribou have been considered lichen specialists (e.g., Thomas et al. 1996, Terry et al. 1996), but based on our work with tame caribou, it is evident that the role of lichens in the nutritional ecology of caribou has been oversimplified. Lichens alone, because of small bite sizes and low protein content, are inadequate to support nutritional demands of caribou during summer and caribou must use other forages or face negative nutritional balance (Boertje 1990). As such, deciduous shrubs and some large-leaved forbs, which are highly selected, afford relatively large bite masses, and are of relatively high-quality
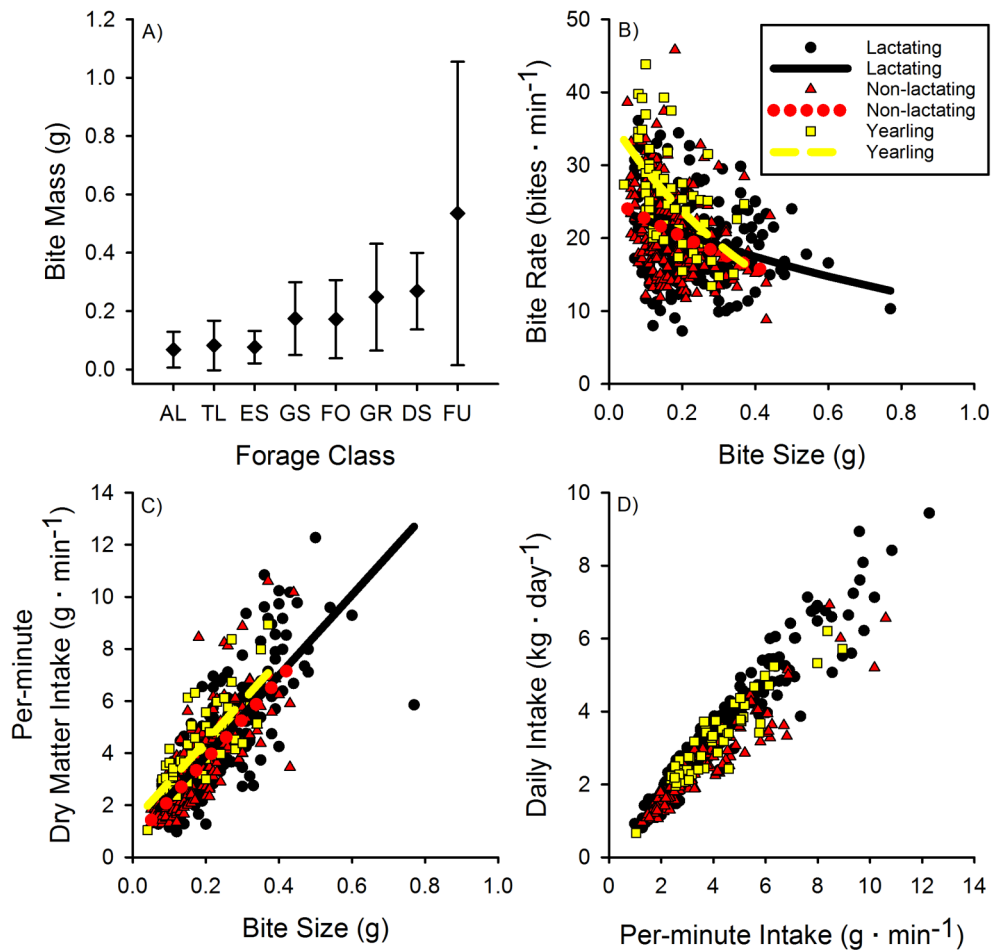
Figure 5. Relationships among foraging parameters and intake rates for caribou: A) mean bite mass (± SE) by forage class; B) bite rate relative to bite size (mean bite mass of caribou at a given site); C) per-minute intake rates in relation to bite size; and D) daily intake rates for caribou estimated from per-minute intake and daily foraging time. Forage classes: AL = arboreal lichen, TL = terrestrial lichen, ES = evergreen shrub, GS = grasses, FO = forb, GR = graminoid non-grasses – sedges, rushes, horsetails, DS = deciduous shrub, FU = fungi (primarily mushrooms).

during summer, are more important for caribou than previously thought.

Our results indicate that caribou inhabiting alpine, montane, and boreal ecosystems in northeastern BC can most easily meet requirements in willow-dominated communities in the alpine and early-seral, spruce-fir and white spruce forests because these communities offer an abundance of accepted plant species that allow caribou to obtain high-quality diets, large bite masses, and high intake rates. The extent of energy

and protein limitations for boreal, central-mountain, and northern-mountain caribou ultimately depends on the abundance and distribution of plant communities across the landscape and how caribou select for nutritional resources.

Caribou that have additional nutritional demands, especially during peak lactation, and are without access to productive plant communities with an abundance of accepted deciduous shrubs and forbs during summer are unlikely to satisfy nutritional
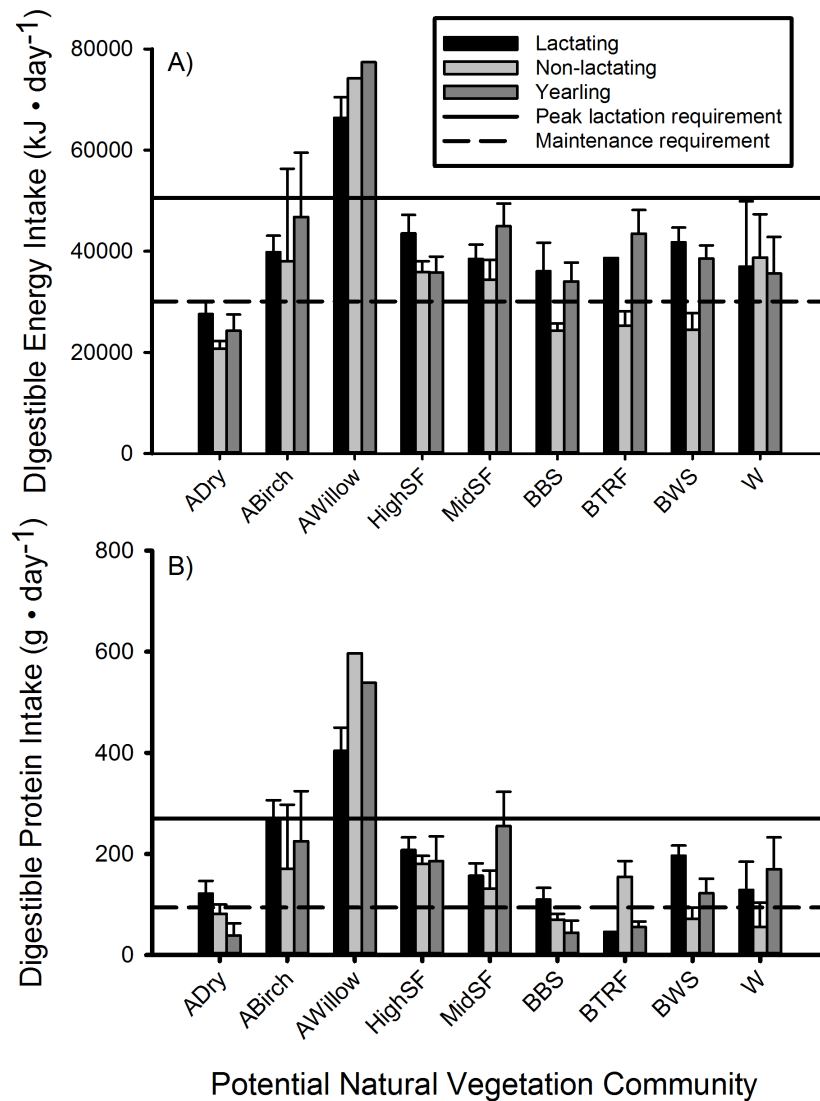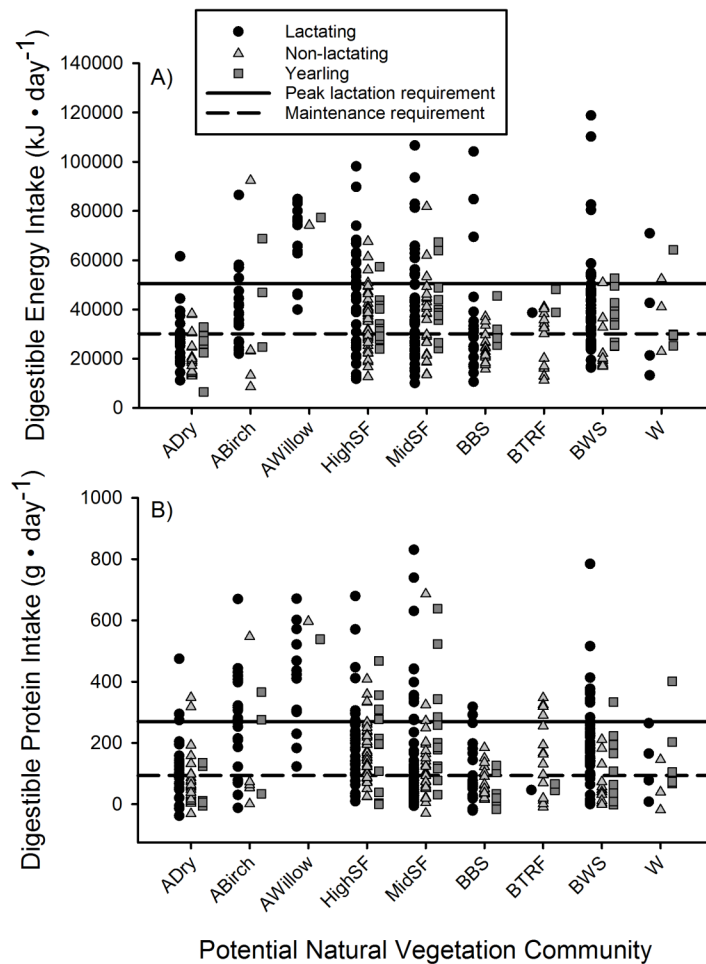
Figure 6. Average (x̄ ± SE) daily digestible energy (A) and digestible protein (B) intakes by tame caribou in potential natural vegetation (PNV) communities in northeastern British Columbia. Sample sizes for lactating, non-lactating, and yearling caribou observations by PNV community were: dry alpine (ADry; n = 22, 25, 7), birch alpine (ABirch; n = 21, 4, 3), willow alpine (AWillow; n = 13, 1, 1), high-elevation spruce-fir forests (HighSF; n = 35, 34, 10), mid-elevation spruce-fir forests (MidSF; n = 55, 19, 8), boreal black spruce (BBS; n = 19, 18, 6), boreal treed rich fens (BTRF; n = 1, 12, 2), boreal white spruce (BWS; n = 49, 11, 13), and wetlands (W; n = 4, 3, 5). Solid lines represent daily intake requirements at peak lactation; however, these requirements decline over summer. Dashed lines are daily intake requirements for maintenance (at constant body mass) of non-lactating adults, as per the National Research Council (2007). Effects of stand characteristics (e.g., canopy cover, stand age, tree density, slope, aspect) and precipitation are not accounted for in this figure.

requirements, with consequences to population growth rates. The capacity of lactating caribou to compensate for nutritional deficiencies in the wild likely is variable and highly dependent on time of year and the balance between their requirements and the nutritional resources available to them. Between spring and autumn, food quality declines, as do lactation requirements when calves are being weaned. Caribou, however, must increase

body reserves of energy and protein that were depleted during the previous winter and during the high energetic demands of lactation if they are to successfully breed in autumn and increase the odds of survival in winter. Our data show that lactating and non-lactating caribou may be unable to attain enough daily energy or protein from forage intake to gain mass in many plant communities in northeastern BC during late summer and early

Figure 7. Daily digestible energy (A) and digestible protein (B) intakes by tame caribou in potential natural vegetation (PNV) communities in northeastern British Columbia. Communities were dry alpine (ADry), birch alpine (ABirch), willow alpine (AWillow), high-elevation spruce-fir forests (HighSF), mid-elevation spruce-fir forests (MidSF), boreal black spruce (BBS), boreal treed rich fens (BTRF), boreal white spruce (BWS), and wetlands (W). Sample sizes for lactating, non-lactating, and yearling caribou are given in Figure 6. Negative protein values indicate that more protein was lost during digestive processes than gained from the forage. Solid lines represent daily intake requirements at peak lactation; however, these requirements decline over summer. Dashed lines are daily intake requirements for maintenance (at constant body mass) of non-lactating adults, as per the National Research Council (2007). Effects of stand characteristics (e.g., canopy cover, stand age, tree density, slope, aspect) and precipitation are not accounted for in this figure.

autumn. Additional work is needed to understand how the distribution of nutritional resources across the landscape influences caribou movements and the annual fat and protein dynamics of caribou as they relate to reproduction and survival.

Even with access to productive communities, caribou must contend with insect harassment, predation risk, disturbance, and other impediments to foraging. How plant communities are distributed on the landscape also influences their use relative to foraging currencies and trade-offs. The plant communities where tame caribou achieved highest nutrient intakes typically had higher abundance of deciduous shrubs with large bite masses. The trade-off for free-ranging caribou foraging exclusively in those communities may be higher predation risk if those plant communities also are important for other ungulates (e.g., moose *Alces alces*, white-tailed deer *Odocoileus virginianus*) and their associated predators (Bowman et al. 2010, Latham et al. 2011). Both windswept dry alpine areas and black spruce bogs-poor fens (peatlands) are postulated to serve as

refugia from predators (Rettie and Messier 2000, Gustine et al. 2006), but it is not likely that caribou in these areas can simultaneously satisfy nutritional demands and avoid predators. Dry alpine sites were among the most nutritionally inadequate plant communities we sampled. Alpine-dwelling caribou without access to productive willow communities may have to make short, altitudinal movements to productive subalpine parklands and forests to access better nutritional resources if they are to satisfy nutritional requirements during summer. Among forest communities, boreal black spruce forests typically were characterized by low quantities of deciduous shrubs, and most of the accepted understory forage species did not afford large bites, result in high intake rates, or provide adequate digestible energy and protein intakes. Boreal caribou presumably must move between black spruce bogs-poor fens and nutritionally superior treed rich fens and white spruce forests with abundant, high-quality forage.

Implications to the conservation and management of caribou are the following:

i. Food and non-food plants must be distinguished and only species accepted by caribou should be used to evaluate useable forage quantity and quality. Although lichens are a primary winter forage of caribou, select deciduous shrubs are the primary summer forage and should be considered in evaluations of quality of summer ranges for caribou.

ii. Diet and forage quality typically decline from a peak in spring-summer through autumn. Because our study was conducted in mid-July to early October, additional studies should consider assessing forage quality and quantity from vegetation green-up to mid-summer to better understand nutritional values of habitats during the calving and insect seasons.

iii. Foodscapes of digestible energy and digestible protein, based on those attributes that most influence the plant community and thus nutrition of caribou (e.g., vegetation community, successional stage, topography, season, climate) should be developed to spatially characterize the nutritional landscape for caribou. Careful consideration should be given to the accuracy and resolution of spatial datasets used to generate these foodscapes.

iv. Given the role of predation in caribou ecology and the inadequacy of nutritional resources in some plant communities, future research should specifically assess nutrition-predation interactions to better understand the trade-offs for caribou inhabiting montane and boreal landscapes. For example, changing predator-prey dynamics and increased predator densities may preclude caribou from using high-quality habitats; as such, predators may have a role in influencing the nutritional status of populations.

For resource managers, it is important to recognize that conservation of caribou habitats needs to encompass a variety of plant communities across ecological and successional gradients to provide caribou with a diversity of foraging options during summer. Caribou are highly selective foragers. To meet nutritional demands, particularly for lactating animals and growing calves, they must forage in communities with relatively high quantities of accepted food and species that enable high intake rates. Large landscapes allow caribou to move at low densities over large spatial scales and high-grade forage from within and among available plant communities.

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