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Straight from the caribou’s mouth: detailed observations of tame caribou reveal new insights into summer-autumn diets

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Abstract

High-quality habitats for caribou (*Rangifer tarandus*, L., 1758) are associated primarily with lichens, but lichens alone fail to satisfy summer nutritional requirements. To evaluate the summer forage value of plant communities across northeastern British Columbia (BC), where populations of northern and boreal ecotypes of caribou are declining, we observed foraging by tame, female caribou. We compared diet composition to forage abundance to determine forage selection and to quantify forage availability. Deciduous shrubs, not lichens, largely dominated summer diets. Caribou were highly selective foragers, with 28 species comprising 78% of diets. Caribou avoided ≥ 50% of understory vegetation in all communities, especially conifers, evergreen shrubs, mosses, and two genera of terrestrial lichens. Availability of accepted forage (species not avoided) was strongly heterogeneous across landscapes. Alpine shrub areas and mid-elevation spruce-fir stands in the mountains, and treed rich fens and white spruce communities in the boreal forests provided the greatest quantities of accepted forage for caribou. Dry alpine sites and unproductive black spruce communities provided the least accepted forage. Our work has direct implications to caribou conservation by contributing to a greater understanding of the forage value of summer habitats, with implications to habitat selection, seasonal movements, and distribution ecology.

Keywords: *Rangifer tarandus caribou*, woodland caribou, diet composition, alpine, boreal forest, food selection, foraging.
Introduction

Synchronous population declines of caribou (*Rangifer tarandus*, L., 1758) across their circumpolar range suggest that caribou populations are sensitive to numerous limiting factors (Vors and Boyce 2009). At regional scales, development and extraction of natural resources exert pressures on caribou by modifying local habitats and altering predator-prey dynamics (Seip 1992; reviewed by Festa-Bianchet et al. 2011). At a larger scale, climate change may contribute to increases in calf mortality and declines in herd productivity due to changes in phenology of forages (Post and Forchhammer 2008; Kerby and Post 2013). Climate change also is expected to interact with and exacerbate the effects of other limiting factors to influence habitat use, foraging, and demography of caribou populations in the future (Sharma et al. 2009; Festa-Bianchet et al. 2011). Regardless of the proximate limiting factor, many caribou populations in British Columbia (BC) are declining. All three ecotypes of woodland caribou (*Rangifer tarandus caribou*; Gmelin, 1788) in BC are designated by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as endangered (mountain caribou), threatened (boreal caribou), or of special concern (northern caribou; Committee on the Status of Endangered Wildlife in Canada 2002). Despite COSEWIC designations and recovery measures, many caribou populations continue to decline and since 2002, at least three caribou populations have been extirpated from BC (Committee on the Status of Endangered Wildlife in Canada 2014).

Forage resources (i.e., vegetation consumed by herbivores) are a fundamental driver of ungulate ecology, influencing distributions, habitat use, and seasonal migrations within populations (Albon and Langvatn 1992; Mahoney and Schaefer 2002; Pettorelli et al. 2007; Owen-Smith et al. 2010; Babin et al. 2011). For individuals, assimilation of nutrients from high-quality nutritional resources in summer is essential for the accretion of fat and protein reserves.
for pregnancy and overwinter survival (Cook et al. 2004, 2013; Dale et al. 2008; Parker et al. 2009; Hurley et al. 2014). Parturient caribou face elevated nutritional demands during summer for lactation and calf-rearing (McEwan and Whitehead 1970; Post et al. 2003; Parker et al. 2009). Through nutritional pathways, summer forage resources influence productivity of caribou herds in Alaska (Post and Klein 1999), Quebec (Crête et al. 1990), Greenland (Post and Forchhammer 2008; Kerby and Post 2013), and Norway (Reimers et al. 1983). Despite the importance of summer forage resources, almost no data on summer forage availability and quality or food habits of caribou in BC are available to assess the potential for nutritional limitations of caribou summer ranges (Brown et al. 2007).

General assumptions about what caribou eat may be oversimplified because of limited available datasets and because classic food habits studies of caribou occurred predominantly during winter (Thompson and McCourt 1981; Rominger and Oldemeyer 1989; Russell et al. 1993; Ihl and Klein 2001). Thus differences in diet composition among seasons, particularly from winter to summer, may be underappreciated. Although lichens are the predominant winter forage for caribou, there is growing recognition that lichens alone are inadequate to satisfy nutritional requirements of caribou. Recently it was suggested that high year-round use of lichens may even be a bottom-up limiting factor for caribou populations in the boreal forest (Thompson et al. 2015) because of low protein (nitrogen) content (Boertje 1990; Storeheier et al. 2002). In addition to dietary protein limitations, low lichen availability can limit caribou, preventing them from achieving per-minute intake rates necessary to satisfy daily intake requirements (Rominger et al. 1996).

Another important limitation of food habits studies for caribou is that such studies have mostly been restricted to post-ingestion techniques. Fecal microhistology (Thompson and
McCourt 1981; Boertje 1984; Russell and Nixon 1990), rumen content analysis (Edwards and Ritcey 1960; Bergerud 1972; Thomas and Edmonds 1983), and post-hoc investigation of feeding craters (Thomas et al. 1996; Johnson et al. 2000) provide a general index of species consumed by caribou. Post-ingestion techniques, however, may not provide accurate diet composition due to their biases and limitations (Bergerud and Russell 1964). Recent use of video collars on free-ranging caribou increased seasonal dietary information for caribou in Ontario’s boreal forest (Thompson et al. 2015), but this new technique also may have limitations (e.g., camera angle).

Tame animals, representing their wild counterparts, tolerate observers in close proximity, affording a level of detail unmatched by other observation methods (Bergerud and Nolan 1970; Trudell and White 1981; Wickstrom et al. 1984; Rominger and Oldemeyer 1989; Parker et al. 1999). The development of typical foraging behaviours in tamed cervids apparently does not require the same experiential learning as in domesticated ruminants that learn what to eat by watching other animals (reviewed by Provenza and Balph 1987). Comparative studies indicate that diet selection and foraging dynamics of tame cervids are indistinguishable from wild cervids (Bergerud and Nolan 1970; Wallmo and Neff 1970; Bergerud 1972; Olsen-Rutz and Urness 1987; Spalinger et al. 1997). ‘Naïve’ animals, exposed to novel environments in separate trials from their ‘experienced’ counterparts, exhibited the same forage preferences as ‘experienced’ animals under identical foraging conditions (Spalinger et al. 1997). Additional comparisons between tame and wild animals showed they had equivalent forage preferences and foraging efficiencies (Spalinger et al. 1997). Earlier work with tame caribou during winter in southeastern BC established the plausibility of using tame caribou as a habitat assessment tool (Rominger et al. 1996). However, late autumn and winter foraging studies of caribou probably are not representative of selection from a more abundant and variable forage base during summer.
Additionally, plant communities in northern BC differ from those in southern BC, limiting the generalization of earlier work across the range of caribou habitats in BC.

In northeastern BC, caribou live in alpine and forest habitats of the northern Rocky Mountains and in the forests and wetland complexes of the boreal flats east of the Rockies. We studied the summer food habits and diet selection of tame caribou in northeastern BC to gain a better understanding of how summer forage may influence free-ranging northern and boreal caribou. As part of a large endeavor to assess the nutritional value of summer habitats for caribou in the plant communities of the mountains and boreal forests of northeastern BC, our objectives here were to: (1) quantify food habits of caribou during summer and early autumn, (2) evaluate selection among plant species, and (3) provide estimates of the amount of forage resources available to caribou in these communities. By documenting food habits, determining selectivity, and quantifying availability of forage resources, these data provide novel insights into the forage value of caribou summer habitats, which may help advance the conservation of caribou.

**Materials and Methods**

During the summers and early autumns of 2013-2015, we observed foraging of hand-reared, female caribou in the predominant regional plant communities of northeastern BC (Fig. 1). We used lactating adult caribou whenever possible, but also used dam-raised yearlings in 2014 and non-lactating adults in 2014 and 2015. The adult caribou were captured as calves from mountain-dwelling herds (Delta, Hodzana, Macomb, Ray Mountain, White Mountain) 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 Improvement (NCASI) research facility near Fort St. John,
In addition to the adults raised in Alaska, we used five dam-raised females born at the NCASI facility. The University of Northern British Columbia Animal Care and Use Committee (Protocol Number 2013-9) approved all protocols used in this study.

During their time in captivity (after weaning), the caribou used in our study were maintained on a pelleted ration formulated specifically for caribou (Parker and Barboza 2013). While in Alaska, the animals had access to native forages including shrubs, trees, lichens, mushrooms, and grasses in their enclosure, similar to forages available to wild caribou (Parker and Barboza 2013). Preliminary foraging studies in captivity exposed these caribou to dwarf birch (*Betula glandulosa* Michx.) and feltleaf willow (*Salix alaxensis* (Andersson) Coville; Thompson and Barboza 2014), which are common across caribou ranges. At the NCASI facility, caribou diets primarily consisted of the pelleted ration, alfalfa hay (*Medicago sativa* L.), clover (*Trifolium* spp. L.), dandelion (*Taraxacum* spp. Wigg) and grass (*Poa pratensis* L., *Phleum pratense* L., *Bromus* spp. L.) in the pasture, but we supplemented caribou with willows (*Salix* spp. L.), aspen (*Populus tremuloides* L.), and lichens (primarily *Cladina* spp. Nyl. and *Cladonia* spp. Evans). Caribou exhibited a natural affinity for native forages.

We selected foraging sites across potential natural vegetation (PNV) communities available to free-ranging caribou in boreal, montane, and alpine ecosystems of northeastern BC (Table 1). Boreal ecosystems, inhabited by boreal caribou, included black spruce (*Picea mariana* Kuntze) and white spruce (*P. glauca* Voss) communities in the Boreal White and Black Spruce (BWBS) biogeoclimatic ecological classification (BEC) zone (Meidinger and Pojar 1991; Table 1). Northern ecotype caribou inhabit both forested montane and alpine ecosystems. In montane ecosystems, we sampled boreal white and black spruce (BWBS) communities in the montane valleys, and mid- (836 – 1 165 m) and high-elevation (1 127 – 1 600 m) spruce (*Picea*
spp.) communities in the Sub-Boreal Spruce (SBS) and Engelmann Spruce-Subalpine Fir (ESSF; *P. glauca x engelmannii* Engelm.-Abies lasiocarpa Endl.) zones. Mid- and high-elevation spruce forests in the mountains were distinguished by plant community composition (Table 1). Along mountaintops, we included a variety of subalpine shrub and alpine communities in the Spruce-Willow-Birch (*Picea-Salix-Betula*; SWB) zone and Alpine Groups (Table 1). We opportunistically sampled a few wetlands in boreal and montane landscapes. Sampling encompassed variation (as described in Table 1) in PNV communities, with a focus on sampling forests at early, mid, and late-successional stages, and on sampling alpine areas with varying levels of primary productivity associated with moisture gradients. Our goal was to capture as much variation in foraging and diet composition as possible within and among PNV communities.

Vegetation sampling occurred between late June and early October. At each site we laid out a linear baseline transect on a random bearing with four perpendicular transects, spaced at equal intervals (generally 20 – 40 m). Baseline and transect lengths varied to include only the vegetation representative of a single type of plant community, such that ecotones with more than one type of PNV community were excluded. Equally spaced along each perpendicular transect we placed two 2-m² circular vegetation plots. Within each plot, we clipped all aboveground biomass of current annual growth by plant species. For conifers and evergreens, we also clipped previous year foliage. Clubmosses (*Lycopodium* spp. L.) and lichens (arboreal and terrestrial) were clipped in their entirety. Except for mosses and a few *Parmeliaceae* family lichens, we collected all vegetation biomass from ground level to 2-m height, representing the biomass available to (within reach of) caribou. We visually estimated percent cover of mosses at each
We separated plant samples by species and oven-dried them at \( \geq 70^\circ \text{C} \) to a constant mass to estimate available biomass of each species at each site.

After collecting vegetation biomass, we assembled temporary electric fencing to create an animal enclosure within the PNV community, beginning along the baseline transect laid out for vegetation sampling. Enclosures generally ranged in size from 0.4 – 1.75 ha, with larger sizes for plant communities having lower total biomass and for longer duration of occupancy (up to 48 h, plus habituation time). Larger enclosures in low-biomass settings helped to ensure enough forage existed to avoid impacts on foraging patterns of caribou. Caribou were held in enclosures < 48 h where forage was very low or when large predators were detected nearby. Of the 135 enclosures we sampled with caribou, we used 13 for \( \leq 24 \) h, 51 for 24 – 48 h, and 72 for 48 h.

We transported tame caribou by stock trailer to enclosures between early July – late September/early October each year. Duration of sampling depended on factors such as timing of vegetation green-up, calf size (for safe transport), insect harassment, and weather (e.g., snow). Once on site, we initially allowed caribou 10 – 16 h to habituate to their new environment prior to collecting data on diet composition. As the study progressed, animals learned the routine and exposure to new plants became less common, allowing us to decrease habituation time. Ultimately, caribou began foraging normally almost immediately upon release into enclosures. Caribou subsisted exclusively on native vegetation during their time in enclosures and we did not provide additional food supplementation, except a small pellet reward for loading into the stock trailer.

We usually observed four caribou within each enclosure, but due to a shortage of tractable animals, we observed only three caribou in 19 of 45 enclosures in 2014 and in four of 45 enclosures in 2015. We observed the animals during four foraging trials spaced throughout
the day from dawn until dusk, for a total of 75 min per day per caribou or 5 h total per day per enclosure (3.75 h • day\(^{-1}\) for three caribou). We collected two morning trials (0500 – 1100 h), one midday trial (1100 – 1600 h), and one evening trial (1700 – 2100 h). Morning and evening trials lasted 20 min each, while midday trials were 15 min. During foraging trials, observers recorded the species of each bite that focal caribou consumed. Representative bite masses were collected based on direct observations of foraging (Wallmo and Neff 1970; Boertje 1984; Rominger et al. 1996), which included cropping, stripping, and single-leaf bites. We dried the bite mass samples at ≥ 70°C to a constant mass to estimate average dry matter content of each species consumed within each enclosure. We summed the products of bite mass (g) and bite rate (bites/trial) for each species consumed during foraging trials to estimate dry matter intake (g) during each trial. We then summed the dry matter intakes from the foraging trials of all animals per enclosure to determine diet composition and selection for that community.

For each enclosure, we calculated percent of intake of each species as the species-specific dry matter intake (g) divided by the total dry matter intake (g) recorded during foraging trials. Percent of available biomass for each species was calculated similarly. We treated each enclosure in which a species was present as an independent sample. We grouped individual plant species into forage classes (deciduous shrubs, evergreen shrubs, forbs, graminoids [including horsetails], mushrooms, arboreal lichens, terrestrial lichens, and other [club mosses, ferns, conifers]) for comparisons of diet composition among PNV communities. For conifers and evergreen shrubs, we combined current and previous year’s annual growth for dry matter intake and biomass. We did not separate berries from new growth (leaves and stems) of evergreen shrubs.

For each species, we assessed selection using Ivlev’s electivity index (Eq. 1):
\[(1) \quad E = (U - A)/(U + A)\]

where \((E)\) is the electivity score, \((U)\) is the proportion used (i.e., intake) and \((A)\) is the proportion available (i.e., biomass; Ivlev 1961). When positive identification to species was not possible and/or to meet minimum sample size requirements for statistical analyses, we combined some plant species to genus (e.g., *Aster* spp. L.) and others to forage class (e.g., mushroom; Table A1).

We present the mean Ivlev score for each species or taxon (across all enclosures where the species was present) consumed by caribou in this study (Table A1). We chose Ivlev’s electivity index (with use-availability proportions) for ease of interpretation: scores near -1 indicate strong avoidance, near zero indicate random use, and near +1 indicate strong selection. In a few cases, we observed intake of a species by caribou, but we did not record any biomass of that species in the sample vegetation plots. Due to inherent error associated with any measure of biomass (availability, \(A\)), there will be times when highly selected but rare species occur in diets (use, \(U\)), but not in biomass. However, if \(U > 0\), then \(A\) also, by definition, must be \(> 0\). For such cases, we substituted the quantity of intake (\(g\)) of that species for the zero value of biomass (\(kg \cdot ha^{-1}\)), as we knew that quantity was the minimum biomass of that species in that enclosure. Removing these species would have introduced a biological and mathematic bias into our calculation of selection. Moreover, if we had instead deleted those cases, highly selected but rare species would have been categorized as strongly (and incorrectly) avoided using the Ivlev calculation.

For electivity scores by species, we used a Wilcoxon signed-rank test to test for difference from zero \((\alpha = 0.05)\) because the data could not be normalized (Lechowicz 1982). Normal distributions are not expected with Ivlev’s electivity index for a given species with multiple observations, as data are commonly skewed toward +1 or -1. Species that had electivity scores significantly \(> 0\) were categorized as selected, significantly \(< 0\) were avoided, and not
significantly different than 0 were neutral. We used electivity results to quantify the amount of forage at each site as accepted (sum of selected and neutral species) or unaccepted (avoided species). Sample sizes (i.e., the number of enclosures in which caribou encountered a given species) by plant species, and the PNV communities in which caribou consumed them, are given in Appendix A (Table A1).

To ensure that our estimates of accepted and avoided forage reflected relatively consistent selectivity of caribou, we assessed whether selection of species was consistent across PNV communities and across time. We compared electivity scores of species using the following PNV groups for increased statistical power: 1) alpine (dry and shrub alpine); 2) boreal (boreal black spruce [bogs, fens, uplands], boreal treed rich fens, and boreal white spruce); and 3) montane (mid- and high-elevation spruce). Wetland communities were excluded from this analysis due to small sample size \((n = 4)\). We used Kruskal-Wallis tests for non-parametric data (again due to skewness in the dataset) to compare Ivlev scores for each plant species within each PNV group. When main effects of group were significant \((\alpha = 0.05)\), we used the kwallis2 add-in in Stata 11.2 (StataCorp 2009) for post-hoc group comparisons. For PNV comparisons of selection, we set a minimum sample size of \(n \geq 10\) per PNV group to test for differences in Ivlev scores. In preliminary data exploration, we determined that sample sizes < 10 in non-parametric tests often had insufficient power to provide meaningful results because electivity scores could be highly variable. For example, each observation of each species has an Ivlev score calculated individually, but together these scores were used to determine if the mean electivity score was significantly different from zero. For a species where \(n = 6\), and five observations were selected and one was avoided, the Wilcoxon signed-rank test on all six scores would return an insignificant result \((P > 0.05)\). Insignificance in the signed-rank test means the species would be
categorized as neutral, even though a majority of the individual observations had positive Ivlev scores (indicative of selection). We had adequate sample size \((n \geq 10)\) to test for differences in diet selection for 40 species that occurred in two PNV groups and 11 species that were in three PNV groups. We also categorized three seasonal sampling periods to reflect changes in diet quality, which could affect forage selection. From diet quality results (unpublished data), we identified a high-quality season from 1 July – 15 August, an early senescence season when leaves begin changing colors from 15 August – 15 September, and a late senescence season when leaf drop and declines in quality are greatest from 16 September – 10 October. Dates were consistent across all three years. Of the plant species assessed for selection, we had adequate sample sizes \((n \geq 10); \text{ as in PNV comparisons}\) for testing 30 species in two of the sampling periods and 30 species in all three sampling periods.

**Results**

*Diet composition*

We observed foraging by tame, female caribou at 135 sites where we recorded 1,193,461 bites on forages during 3,016 foraging trials totaling nearly 942 h of foraging observations. Of the more than 282 species of understory vegetation that caribou encountered during the three years of this study, they consumed at least one bite of 233 distinct species. From July – October each year, we observed caribou foraging at alpine (shrub, \(n = 13\); dry, \(n = 16\)), montane spruce forests (mid-elevation, \(n = 28\); high-elevation, \(n = 33\)), boreal black spruce (bogs and treed poor fens, \(n = 12\); treed rich fens, \(n = 6\); uplands, \(n = 2\)), boreal white spruce (\(n = 21\)), and wetland (\(n = 4\)) communities. Individuals within the same enclosure were remarkably consistent in the species and the proportions of each species they consumed. Diet breadth, based on number of species consumed, was on average greatest in boreal white spruce communities \((31 \pm 9; \bar{x} \pm SD)\)
and lowest in wetlands (15 ± 1). The maximum number of species consumed was 54 (in a high-elevation spruce forest) and the minimum was 10 (in a boreal treed rich fen). Caribou consumed deciduous shrubs, terrestrial lichens, forbs, graminoids, mushrooms, and arboreal lichens (Figs. 2, 3; Table 2). Despite high abundance in many enclosures, evergreen shrubs, conifers, mosses, clubmosses, and the terrestrial lichens Stereocaulon paschale L. and Peltigera spp. Nyl. accounted for <1% of all recorded intake (Figs. 2, 3; Table 2).

Deciduous shrubs dominated the summer and early autumn diets of caribou in all plant communities sampled (Figs. 2, 3; Table 2). At shrub alpine and boreal white spruce sites, deciduous shrubs comprised two-thirds of the diet and > 50% of diets at high-elevation spruce and boreal treed rich fen sites (Figs. 2, 3; Table 2). Lowest mean contributions of deciduous shrubs to caribou diets occurred in boreal upland black spruce (7 ± 3%, \( \bar{x} \pm SE \)) sites and in boreal black spruce bogs (25 ± 7%). The percent of deciduous shrubs in the diets of caribou averaged two times the percent of their available biomass, except in high-elevation spruce forests (where percent intake was 1.8 times percent biomass; Figs. 2, 3). From deciduous shrubs, caribou primarily ingested leaves and berries during summer and early autumn.

Highest consumption of terrestrial and arboreal lichens (45 ± 8% of caribou diets) by caribou occurred in unproductive boreal black spruce communities, particularly bogs and poor fens, followed by dry alpine sites where there was relatively little other accepted forage (Figs. 2, 3; Table 2). At more productive boreal (rich fens, boreal white spruce) and alpine (shrub) communities, lichens contributed much less to caribou diets – as low as 7% (Figs. 2, 3; Table 2).

There were high inter-annual differences in the contribution of mushrooms to caribou diets, corresponding with differences in their abundance related to precipitation and PNV community. Mean dietary proportion of mushrooms was greatest during 2015 (9 ± 2%, \( \bar{x} \pm SE \))
and least in 2014 (0.3 ± 0.1%). Dietary mushroom contributions ranged from 0 – 76% of individual caribou diets (Table 2) during our wettest summer (2013: 282 mm precipitation reported for Fort St. John, BC from 15 June to 10 October, compared to 104 mm in 2014 and 160 mm in 2015; The Weather Network 2016). In dry alpine communities in 2013, mushrooms made notable contributions to caribou diets, averaging 20% of the diet (Fig. 2). In contrast, mushrooms comprised only 1 – 3% of caribou diets among all the PNV communities in our driest year (2014) due to limited availability. Species composition and availability of forbs and graminoids varied among PNV communities (Figs. 2, 3), with concomitant variation in use. Caribou consumed at least 87 species of forbs (Table A1) and forb consumption on average was greatest in montane spruce forests (approximately 20% of the diet) and least at shrub alpine sites (4 ± 1%; Fig. 2, Table 2). Graminoids on average were used most by caribou in mid-elevation montane spruce communities (Fig. 2, Table 2), but typically contributed little to diets.

Selection and Avoidance

Some of the ~282 species caribou encountered in our study were not collected for biomass estimates or were not identifiable to species (Table A1), resulting in 234 forages assessed for selection. For some species with small sample sizes or for which we did not have biomass estimates within caribou enclosures, we inferred selection based on how caribou used similar taxa and/or mean electivity scores if available (Table A1). Caribou avoided 115 species, displayed neutral use of 91 species, and selected 28 species (Table A1). Selection patterns were generally consistent across the seasonal gradient and among PNV communities. No species changed from avoided to selected or vice versa across the summer-autumn sampling periods (all $P > 0.017$, Bonferroni adjustment). Three species that were neutral early in summer were avoided in later sampling periods (i.e., mid-season: *Equisetum sylvaticum* L., *Hierochloe alpina*
(Sw. ex Willd) Roem. and Schult.; late season: *Epilobium angustifolium* L.). Among PNV communities, only one species (*Vaccinium vitis-idaea* L.) changed selection category (for all other species, *P* > 0.017 [Bonferroni adjustment] and the mean Ivlev score was similar among PNV types). In alpine communities, caribou consumed the berries of *V. vitis-idaea* (neutral) and *Empetrum nigrum* L. (selected) particularly late in the season, but in general avoided the leaves and stems of these (and all) evergreen shrubs. Across all PNV communities, caribou diets averaged 78 ± 2 % selected species, 15 ± 1 % neutral species, and 7 ± 1 % avoided species (Fig. 4C).

Although we observed consumption of over 200 species, caribou were highly selective among plant taxa (Table A1). Strongest selection was for deciduous shrubs, forbs, lichens, and mushrooms. Among deciduous shrubs, caribou exhibited highest selection for *Betula papyrifera* Marshall, *Salix* spp., *Vaccinium* spp. L. (deciduous species), and *Alnus crispa* Pursh (Table A1). Among forbs, they selected various *Aster* spp., as well as several species in the lily (*Clintonia uniflora* Kunth, *Streptopus amplexifolius* (L.) DC.) and pea (*Lathyrus* spp. L.) families (Table A1). Caribou selected some (*Alectoria* Ach., *Bryoria* (Gyeln.) Brodo and Hawkshaw), but not all arboreal lichens and only five of the 14 species of terrestrial lichens encountered (Table A1). *Cetraria* L., *Flavocetraria* (Bellardi) Kärnefelt and Thell, *Cladina*, and *Cladonia* spp. accounted for 97% of all terrestrial lichen intake. Caribou also selected among available mushrooms, but we were unable to identify mushrooms to species. The only selected graminoid species was the grass *Elymus innovatus* Beal.

Caribou avoided non-deciduous, non-lichen plant groups, especially evergreen shrubs, conifers, ferns, clubmosses, mosses, and some terrestrial lichens (Table A1). They avoided several highly abundant species including evergreen Labrador tea (*Ledum [Rhododendron]*
groenlandicum Retz.), deciduous white-flowered rhododendron (Rhododendron albiflorum Hook.), and the terrestrial lichen Stereocaulon paschale. Even when S. paschale accounted for nearly half of the available biomass, it contributed to <1% of all intake (Table A1). Based on our percent cover estimates, mosses were abundant in most enclosures, but never comprised >0.05% of any caribou diets, indicating strong avoidance.

Accepted Biomass

Available biomass, and the proportion accepted or avoided by caribou, varied among PNV communities (Fig. 4 A, B). Except for shrub alpine communities, accepted biomass comprised less than half of the available understory vegetation in all PNV communities where we observed foraging caribou (Fig. 4B). Accepted biomass was highest in shrub alpine communities (742 ± 81 kg \( \cdot \) ha\(^{-1} \); Fig. 4A; Table 3) and lowest in upland black spruce communities (42 ± 31 kg \( \cdot \) ha\(^{-1} \), \( n = 2 \); Fig. 4A; Table 3). Overall, boreal communities had less total and accepted biomass than shrub alpine communities or spruce forests in the mountains (Fig. 4; Table 3). Deciduous shrubs largely accounted for the high levels of accepted biomass within many plant communities, specifically Salix spp., Betula spp., and Alnus crispa. Avoided biomass, dominated by the terrestrial lichen Stereocaulon paschale and evergreen shrubs, was greatest in shrub (1 198 ± 308 kg \( \cdot \) ha\(^{-1} \); Fig. 4A) and dry (1 118 ± 241 kg \( \cdot \) ha\(^{-1} \); Fig. 4A) alpine communities.

Discussion

With over 940 hours of direct observation, we provide the most comprehensive data on diet composition and selection for caribou in the boreal forests and mountains of western Canada. We conducted this study exclusively during summer and early autumn because it is during these seasons that caribou experience their highest nutritional demands of the year. Few
studies have assessed how nutrition during summer may affect caribou populations in western Canada (but see Russell et al. 2005) despite the importance of summer nutrition to other northern ungulate species (e.g., Cook et al. 2004, 2013; McArt et al. 2009).

We assessed the forage base from a caribou perspective, linking diet composition to specific plant communities and, therefore, bypassing assumptions of intake, removal, and differential digestibility associated with microhistological (i.e., fecal and rumen analyses) or feeding-site assessments (Bergerud and Russell 1964; Bergerud 1972). Our close proximity to foraging caribou allowed us to document nuances in foraging behaviour such as false bites, introral sorting, changing search images, and variation in bite mass, as reported elsewhere (Trudell and White 1981; Parker et al. 1999; Thompson and Barboza 2014). Such fine-scale foraging decisions can have multiplier effects on dietary assessments (White 1983).

During the growing season, caribou consume diverse diets of relatively high quality through selective foraging (Bergerud 1972; Thompson and McCourt 1981; Boertje 1984; Russell et al. 1993, Thomas et al. 1996; Thompson et al. 2015). We found caribou to be highly selective foragers, selecting only 28 species (~10% of those encountered; Table A1), almost half of which were deciduous shrubs. Deciduous shrubs were the primary summer forage of caribou in our study, and for woodland caribou (R. t. caribou) in Newfoundland (Bergerud 1972), and barren-ground caribou (R. t. granti [Allen 1902]) in Alaska (Thompson and McCourt 1981; Boertje 1984) and Greenland (R. t. groenlandicus [Borowski 1780]; Thing 1984). Use of deciduous shrubs was always greater than the proportion of those species available. In contrast, caribou in Ontario evidently consumed few (~1%) deciduous shrubs during summer (Thompson et al. 2015), which may be indicative of habitats with different species composition and perhaps low availability of accepted shrub species. Deciduous shrub leaves offer large bite masses – a
primary driver of intake rate (Shipley and Spalinger 1992) – and they are a relatively high source of energy and protein (Klein 1990; Thompson and Barboza 2014), making them an advantageous choice for caribou, especially when nutritional requirements are elevated.

Caribou selected some forbs and mushrooms (Table A1), which had important, but variable, contributions to caribou diets. Large-leaved forb species (e.g., Clintonia uniflora, Smilacina racemosa Desf., Streptopus amplexifolius) were some of the most highly preferred of all plant species. Although prevalent at some sites, caribou consumed relatively little fireweed (Epilobium angustifolium), which was surprising given its apparent selection and high use by other cervids (Irwin and Peek 1983; Merrill et al. 1995; Parker et al. 1999; Ulappa 2015).

Mushrooms were also highly selected in our study, but their biomass was quite variable. As a result mushrooms made variable contributions to caribou diets, either dominating them (Skoog 1968; Roby and Thing 1985) or being absent altogether (summer 2014; this study). Although we did not identify mushrooms to species, mushrooms consumed by caribou include Boletus, Lactarius Pers., and Russula spp. Pers. (Skoog 1968; Launchbaugh and Urness 1970; Boertje 1984).

Arboreal and terrestrial lichens are primary winter forages for caribou in BC (Edwards et al. 1960; Kinley et al. 2007) and terrestrial lichens are a primary summer forage in Ontario (Thompson et al. 2015). However, neither arboreal nor terrestrial lichens were the primary summer forage of caribou in our study. Our caribou consumed more lichens when availability of accepted lichens was relatively high, but consumption declined when accepted vascular plants were abundant. Our results support Bergerud’s (1972) hypothesis that lichen use is a function of availability rather than an obligate foraging strategy. Lichens contribute significantly to caribou diets in some ecosystems and seasons, but alone they are inadequate to satisfy summer
nutritional requirements of caribou (Boertje 1984, 1990; reviewed by Miller 1996). Protein levels in lichens are generally too low (2-6% crude protein; Bergerud 1972; Person et al. 1980; Storeheier et al. 2002) to restore body reserves of protein and caribou spend most of the year in a negative protein balance (Gerhart et al. 1996). Caribou can exploit protein-rich vascular plants during summer to store body reserves, allowing them to withstand periods of negative protein balance (Gerhart et al. 1996), including during winter when diets are dominated by lichens (e.g., Terry et al. 2000) and for fetal growth in late spring (Parker et al. 2005).

Evergreen shrubs (e.g., Ledum spp.), conifers (e.g., Abies and Picea spp.), and mosses provide few readily accessible nutrients because of plant defensive compounds and low digestibility (Bergerud and Russell 1964; Bryant et al. 1991; Sauvé and Côté 2006) and such low-quality plants are often avoided (Klein 1970; Bryant et al. 1983; White 1983; Sauvé and Côté 2006). Consumption of low-quality forages reduces the ability of ruminant species to satisfy longer-term intake rates (reviewed by Allen 1996), which may explain the highly selective behaviour of caribou. Even when the availability of accepted species was low, caribou consistently avoided such low-quality plants (Boertje 1984; Thompson et al. 2015; this study). Nitrogen-fixing lichen genera Peltigera and Stereocaulon produce toxins (Huss-Danell 1977; Kallio and Kallio 1978; Kytöviita and Crittenden 2007) rendering them unpalatable to reindeer (Rangifer tarandus tarandus L.; Storeheier et al. 2002; Kaasalainen et al. 2013) and caribou (Hollemann and Luick 1977; this study). Caribou used careful, highly selective foraging and intra-oral sorting to separate selected terrestrial lichens from dense mats of Stereocaulon. Intra-oral sorting also was used to separate berries from leaves and stems of evergreen shrubs (E. nigrum, V. vitis-idaea) as reported elsewhere (Boertje 1984; Thing 1984). Unpalatable items in
caribou diets may reflect incidental intake during intra-oral sorting or poor range quality (Bergerud and Russell 1964; Boertje 1984).

Although selection indices do not indicate true forage preference (which may only be determined through cafeteria-style foraging trials where abundance of all items is equal), they are informative and widely used (e.g., Cook et al. in press; Holleman and Luick 1977; Thompson and Barboza 2014). An apparent limitation of selection studies is the difficulty in determining selection for rare species, which we also documented. *Smilacina racemosa* and *Cetraria islandica* were classified as neutral, but are most likely selected based on our observations (they were consumed by caribou whenever encountered). Rare species, because of their inherently small contribution to biomass and/or diet composition (<1%), did not have a strong influence on our overall inferences, especially in quantifying accepted biomass within plant communities. Moreover, results from selection indices corroborated our observations of the highly selective foraging behaviours of caribou and as such were useful in quantifying forage values of different plant communities.

Forage availability and distribution have strong implications for how highly mobile species, such as caribou, interact with their habitats, especially if animals spatially disperse to exploit relatively few selected species. Accepted biomass is a biologically sensitive metric that reflects the selectivity of caribou and as such, offers novel insights into understanding differences in food supplies across northeastern BC. In all PNV communities sampled, caribou accepted ≤ 50% of the available biomass as food. Shrub-dominated alpine communities, particularly willow-dominated (rather than birch-dominated) sites, were the most valuable summer habitats, based on availability of accepted biomass. Willow-dominated alpine sites were uncommon in our study area, so free-ranging caribou must move between alpine-subalpine
habitats and productive mid- to high-elevation spruce forests for the best foraging opportunities in the mountains. Such movement patterns would allow caribou to use dry alpine, windswept sites of relatively low summer forage value for calving (Gustine et al. 2006) and relief from insects, and to access a more productive forage base in nearby habitats. Multiscale habitat selection by northern ecotype caribou presumably allows caribou to balance nutritional demands and predation risk (Gustine and Parker 2008). The success of this strategy ultimately depends on the distribution and abundance of high-quality foraging habitats and habitats offering low risk of predation.

Boreal PNV communities on average were less productive than alpine or montane communities. Upland boreal black spruce sites were the least productive communities we sampled, with very low levels of total and accepted biomass. Bog-fen black spruce communities had greater available biomass of terrestrial lichens and these sites often had low quantities of other accepted forages. Rich fens and white spruce communities provided more deciduous shrubs and accepted biomass than other boreal communities. Free-ranging boreal caribou select unproductive habitats (i.e., black spruce types) and habitats close to productive forests (i.e., white spruce types), presumably using the former primarily as refugia from predators and the latter for foraging (Demars et al. 2012; Wilson and Demars 2015). Our measures of accepted biomass support the assumptions of Wilson and Demars (2015) regarding the relative forage values of these different habitats. As in the mountains, caribou in the boreal likely must move among plant communities to balance nutritional demands and predation risk, but further assessment of forage-predation interactions in both ecosystems is needed.

We transported the tame caribou to PNV communities available to wild caribou with the intention of quantifying and comparing foraging values of summer habitats. We were limited to
areas with road access, but these sites were representative of alpine, montane, and boreal plant communities in northeastern BC. The data would have been inherently biased and unable to provide the detail necessary to understand how accepted forage availability differs among habitat types had we excluded areas thought to be avoided by wild caribou (e.g., clearcuts; Chubbs et al. 1993). The tame caribou exhibited remarkably consistent selection patterns within and among PNV communities, despite marked variation in plant composition and despite using animals with varying nutritional requirements (e.g., lactating females versus non-lactating females). Though encounter rate of novel plants may have been high at the start of the study, our caribou quickly gained experience with native forages equating to thousands of hours of foraging experience over the three years of this research. Had they not been knowledgeable about their food choices, we would not have been able to identify consistent selection and avoidance of species because electivity scores would have been highly variable.

Given the consistency among individuals and between wild and tame animals foraging on similar landscapes (Bergerud and Nolan 1970; Olson-Rutz and Urness 1987; Spalinger et al. 1997), the data presented here provide an index of the foods that wild caribou select within the primary PNV communities of northeastern BC. While diet composition data alone cannot be used to evaluate the nutritional value of a habitat or landscape to foraging caribou, understanding what portion of the available biomass can be considered ‘food’ provides the necessary first step. The tame caribou defined what is accepted as ‘food’ in each plant community sampled, allowing us to assess variability in the forage base. Accepted biomass and similar forager-defined metrics have the potential to generate biologically informative caribou-habitat relationships, as they have been related to intake rates and to diet quality in multiple ungulate species (White and Trudell 1980; Wickstrom et al. 1984; Rominger et al. 1996; Cook et al. in press). These studies, along
with our own, demonstrate the need for biologically sensitive indicators to assess suitability of
habitats for foraging (Searle et al. 2007). Measurements of total forage or use of surrogate
forage variables, such as stem density, per-capita old growth forest, land-cover type, or lichen
availability (Rettie and Messier 2000; Wittmer et al. 2005; Metsaranta and Mallory 2007; Pinard
et al. 2012; McLellan et al. 2012), are not able to discriminate between accepted and avoided
forage biomass.

Our findings show that habitats with an abundance of palatable deciduous shrubs and a
diverse understory of selected forbs, lichens, and mushrooms provide optimal summer foraging
opportunities for caribou. In documenting the summer forage base, our research additionally
generates novel opportunities to examine animal-habitat relationships in future research. Future
work may be able to link animal behaviour to changes in the summer forage base. Further, these
data set the stage to examine tradeoffs in habitat selection, when caribou must balance
acquisition of food with predation, insect harassment, and other impediments to foraging.

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Table 1. Characteristics and sample size ($n$) of potential natural vegetation (PNV) communities sampled for both understory vegetation biomass and forage consumption by caribou (*Rangifer tarandus* L., 1758) in northeastern British Columbia, with corresponding Biogeoclimatic Ecosystem Classification (BEC) classes in bold.

<table>
<thead>
<tr>
<th>PNV $^*$</th>
<th>Ecological Characteristics</th>
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<tbody>
<tr>
<td>Boreal black spruce bog and/or poor fen (BBSbf)</td>
<td>Extensive nutrient-poor muskegs with overstories dominated (&gt;25 – 60% cover) by stunted (&lt;10 m tall) black spruce (<em>Picea mariana</em>) and occasionally sparse tamarack (<em>Larix laricina</em>) on poorly drained sites in the northern boreal lowlands. Understory typically dominated by <em>Ledum groenlandicum, Chamaedaphne calyculata, Empetrum nigrum, Andromeda polifolia</em>, with <em>Vaccinium vitis-idaea</em> often present. <em>Sphagnum</em> mosses cover &gt;20% of the area. Poor fens are distinguished from bogs in part by the presence of tamarack and can have dwarf birch (<em>Betula glandulosa</em>) and willows (<em>Salix</em> spp.) sparsely present. ($n = 12$). BEC classes: <strong>BWBSmw, BWBSmk</strong>.</td>
</tr>
<tr>
<td>Boreal black spruce upland (BBSupl)</td>
<td>Upland stands dominated by black spruce &gt;10 m tall. Sites have closed forest canopies and minimal understory productivity. Ground cover is primarily mosses with sparse lichens (e.g., <em>Cladina</em> spp., <em>Cladonia</em> spp.) and dwarf shrubs (&lt;0.2 m; <em>Ledum groenlandicum, Empetrum nigrum, Vaccinium myrtilloides, Vaccinium vitis-idaea</em>) available. ($n = 2$). BEC classes: <strong>BWBSmw, BWBSmk</strong>†.</td>
</tr>
<tr>
<td>PNV</td>
<td>Ecological Characteristics</td>
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<tr>
<td>Boreal treed rich fen (BTRF)</td>
<td>Nutrient-rich peatlands at low elevations in the boreal forest, dominated (&gt;25–60 % cover; &lt;10 m tall) by black spruce and &gt;5% tamarack. Species-rich sites with bog birch, sweet gale (<em>Myrica gale</em>), and willows &lt;2 m tall. <em>Sphagnum</em> mosses cover &lt;20% of area. (<em>n</em> = 6). BEC classes: <strong>Wetland fens (Wf)</strong> in <strong>BWBSmw, BWBSmk†</strong>.</td>
</tr>
<tr>
<td>Boreal white spruce (BWS)</td>
<td>Upland stands with overstories of conifers and deciduous species at low elevations in the boreal forest. At more mesic and well-drained sites in the Alberta Plateau, overstory species include white spruce (<em>P. glauca</em>), trembling aspen (<em>Populus tremuloides</em>), and balsam poplar (<em>Populus balsamifera</em>). Open-canopied lodgepole pine (<em>Pinus contorta</em>) dominates on drier sites where pine-lichen forests occur on coarse-textured soils. (<em>n</em> = 21). BEC classes: <strong>BWBSmk, BWBSmw</strong>.</td>
</tr>
<tr>
<td>Mid-elevation spruce forest (MidSF)</td>
<td>Montane forests at mid elevations (e.g., 836 – 1 165 m) supporting subalpine fir (<em>Abies lasiocarpa</em>), lodgepole pine, and <em>Picea</em> spp. Sites vary depending on physical geography and climate. Understory species include <em>Vaccinium membranaceum, V. vitis-idaea, Rosa acicularis, Linnaea borealis,</em></td>
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<tr>
<td>Ecological Characteristics</td>
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</table>
| *Viburnum edule, Elymus innovatus,* and/or *Equisetum* spp., depending on elevation and location.  
\( n = 28 \). BEC classes: **BWBSwk2** in the north; **BWBSwk1** and **SBSwk2** from the Peace Arm of the Williston Reservoir to the Alberta border. |

| High-elevation spruce forest (HighSF) | Montane forests at high elevations (e.g., 1 127 – 1 600 m) with subalpine fir, spruce (*Picea* spp.), and lodgepole pine. Shrub layer usually dominated by *Betula glandulosa* (SWBmk) or *Rhododendron albilorum* (ESSFmv). Common understory shrub species may also include *Salix* spp., *Vaccinium membranaceum*, and *Alnus crispa*.  
\( n = 33 \). BEC classes: **ESSFmv4** and **SWBmk** north of the Peace Arm of the Williston Reservoir; **ESSFmv2** from the Peace Arm of Williston Reservoir to Alberta border. |

| Dry alpine (ADry) | Dry sites supporting low-growing, sparse vegetation at high-elevation (e.g., 1 447 – 1 859 m); trees absent except for krummholz patches at timberline including spruce (*Picea* spp.), subalpine fir and lodgepole pine. Sites may be dominated by exposed gravel, rock, and/or mineral soil and may be interspersed with mat-forming forbs, graminoids (e.g., *Festuca* spp.), and/or lichens (e.g., *Stereocaulon* |

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PNV* Ecological Characteristics

Erect shrubs largely absent, but dwarf shrubs (<0.2 m tall) including *Empetrum nigrum*, *Vaccinium vitis-idaea*, *Arctostaphylos alpina*, and *Salix reticulata* may be common. \( n = 16 \). BEC classes: **Alpine Fellfield (Af)**, **Alpine Grasslands (Ag)**, **Alpine Heath (Ah)**.

**Shrub alpine (AShrub)** Subalpine shrub groups at high-elevation (e.g., 1 413 – 1 750 m) indicated by the presence (>10% cover) and abundance of erect (>0.2 m) deciduous shrubs. Relatively mesic to wet sites are dominated by willows and/or co-dominated by dwarf birch, with dwarf birch dominant on drier sites. Trees are absent except for krummholz patches at timberline. \( n = 13 \). BEC classes: **SWBmk** and **Sc** (subalpine shrubland class).

**Wetlands (W)** Broad class of wetland sites inundated with water during much of the year with soils that are wet year-round and generally lacking coniferous or deciduous tree species. This type includes willow- and sedge-dominated wet meadows at mid- to high elevations in the mountains, and shrubby rich fens (willow-dominated) and graminoid-rich fens (sedge-dominated) in the boreal forest. Some forbs (i.e., *Aster* spp., *Senecio* spp.) can be common in the mountain wetland meadows. Primary species in the
PNV  *  Ecological Characteristics

Boreal wetlands include *Betula glandulosa* and/or *Myrica gale* (indicator species for shrubby rich fens).

\((n = 4)\). BEC classes: **Wm (wetland marshes), Wf (wetland fens)** in BWBS and ESSF.

\*Adapted from British Columbia BEC Classification (Delong et al. 1994, 2011; Mackenzie 2012) and Boreal Wetland Classification (Ducks Unlimited Canada 2014).

† Included in this PNV type, but not sampled with caribou.
Table 2: Mean (± SE, minimum – maximum) proportion of intake by forage class (arboreal lichens [AL], deciduous shrubs [DS],
evergreen shrubs [ES], forbs [FO], fungi [FU], graminoids [grasses, sedges, rushes, horsetails; GR], terrestrial lichens [TL], and other
[O] which includes conifers, clubmosses, ferns, and mosses) for tame caribou (*Rangifer tarandus* L., 1758) within potential natural

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<th>Forage Class</th>
<th>Potential Natural Vegetation (PNV)*</th>
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<tr>
<td></td>
<td>BBSbf</td>
</tr>
<tr>
<td>AL</td>
<td>0.11 ± 0.06</td>
</tr>
<tr>
<td></td>
<td>0 – 0.63</td>
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<tr>
<td>DS</td>
<td>0.25 ± 0.07</td>
</tr>
<tr>
<td></td>
<td>0.02 – 0.87</td>
</tr>
<tr>
<td>ES</td>
<td>0.01 ± 0</td>
</tr>
<tr>
<td></td>
<td>0 – 0.03</td>
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<tr>
<td>FO</td>
<td>0.08 ± 0.02</td>
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<td></td>
<td>0.01 – 0.21</td>
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<tr>
<td>FU</td>
<td>0.05 ± 0.01</td>
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<td>0 – 0.14</td>
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<th></th>
<th>0.06 ± 0.03</th>
<th>0.02 ± 0.02</th>
<th>0.01 ± 0.01</th>
<th>0.04 ± 0.01</th>
<th>0.16 ± 0.02</th>
<th>0.03 ± 0.01</th>
<th>0.09 ± 0.02</th>
<th>0.01 ± 0.04</th>
<th>0.16 ± 0.11</th>
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<tr>
<td>GR</td>
<td>0 – 0.36</td>
<td>0 – 0.04</td>
<td>0 – 0.04</td>
<td>0 – 0.15</td>
<td>0 – 0.28</td>
<td>0 – 0.23</td>
<td>0 – 0.28</td>
<td>0 – 0.04</td>
<td>0.02 – 0.47</td>
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<tr>
<td>TL</td>
<td>0.45 ± 0.08</td>
<td>0.79 ± 0.02</td>
<td>0.18 ± 0.07</td>
<td>0.07 ± 0.04</td>
<td>0.12 ± 0.06</td>
<td>0.11 ± 0.02</td>
<td>0.30 ± 0.06</td>
<td>0.14 ± 0.04</td>
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<td>O</td>
<td>0 ± 0</td>
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<td>0 ± 0</td>
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<td>0 ± 0</td>
<td>0.06 ± 0</td>
<td>0.01 ± 0</td>
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<td>0 – 0</td>
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<td>0 – 0.01</td>
<td>0 – 0.01</td>
<td>0 – 0.01</td>
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</table>

PNV communities are boreal black spruce bogs and fens (BBSbf), boreal treed rich fens (BTRF), boreal white spruce (BWS), boreal black spruce uplands (BBSupl), mid elevation spruce forests (MidSF), high elevation spruce forests (HighSF), dry alpine (ADry), shrub alpine (AShrub), and wetlands (W).
Table 3: Mean (± SE, min – max) available biomass (kg • ha\(^{-1}\)) by forage class (arboreal lichens [AL], conifers [CO], clubmosses [CM], deciduous shrubs [DS], evergreen shrubs [ES], forbs [FO], ferns [FE], fungi [FU], grasses [GS], graminoid non-grasses [GR], mosses [MO], and terrestrial lichens [TL]) within potential natural vegetation (PNV) communities of northeastern British Columbia.

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<th>Forage class</th>
<th>Potential Natural Vegetation (PNV)*</th>
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<td></td>
<td>BBSbf</td>
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<tr>
<td>AL</td>
<td>7 ± 4</td>
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<td></td>
<td>0 – 46</td>
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<tr>
<td>CO</td>
<td>159 ± 41</td>
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<tr>
<td></td>
<td>0 – 528</td>
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<tr>
<td>CM</td>
<td>0 ± 0</td>
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<tr>
<td></td>
<td>0 – 0</td>
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<tr>
<td>DS</td>
<td>19 ± 8</td>
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<td></td>
<td>0 – 91</td>
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<tr>
<td>ES</td>
<td>575 ± 92</td>
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<tr>
<td></td>
<td>116 – 1 075</td>
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<td></td>
<td>FO</td>
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<td></td>
<td>63 ± 16</td>
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<td>5 – 195</td>
<td>3-Jan</td>
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<td>0 ± 0</td>
<td>0 ± 0</td>
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<tr>
<td>0 – 0</td>
<td>0 – 0</td>
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<tr>
<td>2 ± 1</td>
<td>0 ± 0</td>
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<td>0 – 5</td>
<td>0 – 0</td>
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<tr>
<td>14 ± 14</td>
<td>0 ± 0</td>
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<tr>
<td>0 – 163</td>
<td>0 – 0</td>
</tr>
<tr>
<td>92 ± 38</td>
<td>15 ± 15</td>
</tr>
<tr>
<td>0 – 473</td>
<td>0 – 30</td>
</tr>
<tr>
<td>77 ± 8</td>
<td>100 –</td>
</tr>
<tr>
<td>16 – 100</td>
<td>100 –</td>
</tr>
<tr>
<td>237 ± 89</td>
<td>23 ± 17</td>
</tr>
<tr>
<td>5 – 828</td>
<td>7 – 40</td>
</tr>
</tbody>
</table>

PNV communities (with sample size in parentheses) are boreal black spruce bogs and fens (BBSbf), boreal treed rich fens (BTRF), boreal white spruce (BWS), boreal black spruce uplands (BBSupl), mid elevation spruce forests (MidSF), high elevation spruce forests (HighSF), dry alpine (ADry), shrub alpine (ASHrub), and wetlands (W).
Measurements for mosses represent visual estimates of percent ground cover as we did not collect biomass of mosses.
Figure captions:

Figure 1. Locations of direct observations of tame caribou (Rangifer tarandus L., 1758) foraging within boreal black spruce bogs and fens (BBSbf), boreal black spruce uplands (BBSupl), boreal treed rich fens (BTRF), boreal white spruce (BWS), mid-elevation spruce forests (MidSF), high-elevation spruce forest (HighSF), dry alpine (ADry), shrub alpine (ASHrub), and wetlands (W) potential natural vegetation (PNV) communities in relation to free-ranging caribou herds in northeastern British Columbia, Canada (inset).

Figure 2. Mean (+ SE) proportion of forage intake by tame caribou (Rangifer tarandus L., 1758) and available biomass of forage classes in potential natural vegetation (PNV) communities of montane and alpine ecosystems (MidSF = mid-elevation spruce, HighSF = high-elevation spruce, ADry = dry alpine, AShrub = shrub alpine) sampled during summer and early autumn of 2013–2015 in northeastern British Columbia.

Figure 3. Mean (+ SE) proportion of forage intake by tame caribou (Rangifer tarandus L., 1758) and available biomass of forage classes in potential natural vegetation (PNV) communities of boreal ecosystems (BBSbf = boreal black spruce bog and fen, BBSupl = boreal black spruce upland, BTRF = boreal treed rich fen, BWS = boreal white spruce) sampled during summer and early autumn of 2013–2015 in northeastern British Columbia.

Figure 4. Total available biomass (kg • ha\(^{-1}\)) of understory vegetation (A), proportion of available biomass (B), and mean proportion of intake (C) by tame caribou (Rangifer tarandus L., 1758) in potential natural vegetation (PNV) communities sampled during summer and early autumn 2013–2015 in northeastern British Columbia. For each, available biomass 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.
BBSbf = boreal black spruce bogs and poor fens, BTRF = boreal treed rich fens, BWS = boreal white spruce forests, BBSupl = boreal black spruce uplands, MidSF = montane mid-elevation spruce forests, HighSF = montane high-elevation spruce forests, ADry = dry alpine, AShrub = shrub alpine, W = wetlands.
Figure 1. Locations of direct observations of tame caribou caribou (Rangifer tarandus L., 1758) foraging within boreal black spruce bogs and fens (BBSbf), boreal black spruce uplands (BBSupl), boreal treed rich fens (BTRF), boreal white spruce (BWS), mid-elevation spruce forests (MidSF), high-elevation spruce forest (HighSF), dry alpine (ADry), shrub alpine (AShrub), and wetlands (W) potential natural vegetation (PNV) communities in relation to free-ranging caribou herds in northeastern British Columbia, Canada (inset).

233x306mm (300 x 300 DPI)
Figure 2. Mean (+ SE) proportion of forage intake by tame caribou (Rangifer tarandus L., 1758) and available biomass of forage classes in potential natural vegetation (PNV) communities of montane and alpine ecosystems (MidSF = mid-elevation spruce, HighSF = high-elevation spruce, ADry = dry alpine, AShrub = shrub alpine) sampled during summer and early autumn of 2013-2015 in northeastern British Columbia.

237x185mm (300 x 300 DPI)
Figure 3. Mean (+ SE) proportion of forage intake by tame caribou (Rangifer tarandus L., 1758) and available biomass of forage classes in potential natural vegetation (PNV) communities of boreal ecosystems (BBSbf = boreal black spruce bog and fen, BBSupl = boreal black spruce upland, BTRF = boreal treed rich fen, BWS = boreal white spruce) sampled during summer and early autumn of 2013-2015 in northeastern British Columbia.

Fig. 3
236x184mm (300 x 300 DPI)
Figure 4. Total available biomass (kg • ha⁻¹) of understory vegetation (A), proportion of available biomass (B), and mean proportion of intake (C) by tame caribou (Rangifer tarandus L., 1758) in potential natural vegetation (PNV) communities sampled during summer and early autumn 2013–2015 in northeastern British Columbia. For each, available biomass 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. BBSbf = boreal black spruce bogs and poor fens, BTRF = boreal treed rich fens, BWS = boreal white spruce forests, BBSupl = boreal black spruce uplands, MidSF = montane mid-elevation spruce forests, HighSF = montane high-elevation spruce forests, ADry = dry alpine, AShrub = shrub alpine, W = wetlands.