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Animal-defined resources reveal nutritional inadequacies for woodland caribou during summer–autumn

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Abstract

Populations of woodland caribou (*Rangifer tarandus caribou*) are declining throughout their range and many are at risk of extirpation, yet the role of nutrition in these declines remains poorly understood, in part owing to a lack of information about available nutritional resources during summer. We quantified rates of intake of digestible protein and digestible energy by tame caribou foraging in temporary enclosures in the predominant plant communities of northeastern British Columbia, Canada, during summer–autumn and compared intake rates to daily requirements for protein and energy during lactation. We tested hypotheses related to the nutritional adequacy of the environment to support nutritional requirements during lactation (with and without replenishment of body reserves) and simulated scenarios of foraging by caribou in these plant communities to better understand how wild caribou could meet nutritional demands on these landscapes. Nutritional resources varied among plant communities across seasonal, ecological, and successional gradients; digestible energy intake per minute and per day were significantly greater in younger than older forests; dietary digestible energy and per-minute and daily intake of digestible protein were greater, though not significantly so, in younger than older forests; and dietary digestible protein was greater in older than younger forests,

though differences were not significant. Tame caribou were unable to satisfy protein and energy requirements during lactation, even without replenishment of body reserves, at most sites sampled. Further, foraging simulations suggested widespread nutritional inadequacies on ranges of wild caribou. Selection for habitats offering the best nutrition may mitigate some nutritional inadequacies, but given low availability of vegetation communities with high nutritional value, performance (e.g., calf production, growth, replenishment of body fat and protein) of caribou may be depressed at levels of nutrition documented herein. Our results, coupled with recent measurements of body fat of wild caribou in northeastern British Columbia, refute the hypothesis that the nutritional environment available to caribou during summer in northeastern British Columbia is adequate to fully support nutritional demands of lactating caribou, which has implications to productivity of caribou populations, recovery, and conservation.

Earth is amid a sixth mass-extinction event (Barnosky et al. 2011, Ceballos et al. 2015) and caribou (*Rangifer tarandus*) may be one of the casualties. Most populations of caribou are declining across their circumpolar and boreal ranges (Vors and Boyce 2009, Festa-Bianchet et al. 2011, Russell et al. 2018) and many populations face extirpation (Johnson et al. 2015). In the United States and Canada, woodland caribou (*R. t. caribou*) have been extirpated from the southern extent of their historical range and many populations are listed as special concern, threatened, or endangered (Committee on the Status of Endangered Wildlife in Canada 2014, United States Fish and Wildlife Service 2019). Landscape alteration, habitat loss, and altered predator-prey dynamics are implicated in declines of woodland caribou (Wittmer et al. 2005, Serrouya et al. 2017, Mumma et al. 2018). Although nutrition underpins virtually every life process in animals and is fundamentally important to population productivity through effects on survival and recruitment (Testa and Adams 1998, Cook et al. 2004, Monteith et al. 2014, Johnson et al. 2019), little is known about the nutritional environment available to woodland caribou during summer and its implications to caribou recovery.

Historically, studies of the nutritional ecology of northern ungulates largely focused on nutritional bottlenecks during winter (Klein 1968, Hobbs et al. 1982, Torbit et al. 1985, Adamczewski et al. 1987, Skogland 1990). Nutritional constraints during summer, however, are more widespread for northern ungulates than previously realized, including for some subspecies of caribou (Crête and Huot 1993, Post and Klein 1999, Cook et al. 2013, Hurley et al. 2014, Rolandsen et al. 2017). Acquisition of food and assimilation of nutrients during summer influence individual performance and fitness through a myriad of nutritional pathways (Gerhart et al. 1997, Russell et al. 1998, Testa and Adams 1998, Keech et al. 2000), including lactation, calf rearing, and growth or replenishment of body reserves (Rognmo et al. 1983, Oftedal 1985, Cook et al. 2004, Parker et al. 2009). Further, body reserves accumulated during summer are important for breeding in autumn, overwinter survival, and growth of offspring *in utero* and postpartum (Skogland 1990, Forchhammer et al. 2001, Cook et al. 2004, Barboza and Parker 2006), with effects that ultimately can scale up to influence population productivity (Crête and Huot 1993, Post and Klein 1999,

Cook et al. 2013). For woodland caribou, rigorous evaluation of nutritional status is rare, perhaps contributing to the perception that nutritional limitations are relatively unimportant (Wittmer et al. 2005, Festa-Bianchet et al. 2011, McLellan et al. 2012).

An animal's nutritional condition largely depends on its nutritional requirements and the nutrition it acquires; the latter is a function of the nutritional value of the environment in which the animal lives and feeds (Cook et al. 2004, 2016; Parker et al. 2009). Nutritional value of the environment is determined by the ability of foragers to satisfy their nutritional requirements, as influenced by forage selection and available forage quantity and quality. Forage selection is the base of the foraging hierarchy and ultimately constrains intake rates by determining which of available forages are accepted as food items (Cook et al. 2016, Denryter et al. 2020a). Quantity of accepted forages limits short-term intake rates as search times and travel rates increase between successive bites (Spalinger and Hobbs 1992, Cook et al. 2016, Denryter et al. 2020a), whereas forage quality limits intake through effects on digestion and rumination, which slow with declining quality (Shipley and Spalinger 1992, Holand 1994, Owen-Smith 2002, Tafaj et al. 2005, White et al. 2014). Forage quality and quantity vary as a function of biogeoclimatic effects on plant species composition, plant phenology and chemistry, and productivity (Johnstone et al. 2002, Cook et al. 2016). Thus, nutritional value of plant communities to woodland caribou is likely to vary substantially, particularly among disparate alpine, montane forest, upland boreal forest, and boreal wetland environments that are common across caribou ranges in western Canada.

Canada's Species at Risk Act and the United States Endangered Species Act mandate the identification of critical habitats needed for the survival and recovery of listed species. Critical habitats for caribou generally have been characterized as mature and old-growth forests (Rominger and Oldemeyer 1989, Seip 1998, Bergerud 2000, Mahoney and Virgl 2003, Ferguson and Elkie 2004) and boreal peatlands (including muskegs; Bradshaw et al. 1995, Stuart-Smith et al. 1997, Rettie and Messier 2000, McLoughlin et al. 2005). Alpine areas, subalpine parklands, subalpine forests, old subalpine forests, and mid-elevation forests also have been identified as providing critical habitats for mountain-dwelling caribou during spring, summer, and autumn (Environment Canada 2014). Alpine areas and older forests, including subalpine forests and boreal peatlands, allow caribou to spatially segregate from their predators and alternate prey species (Bergerud et al. 1984, Seip and Cichowski 1996, Gustine et al. 2006, Bowman et al. 2010, Nobert et al. 2016). Additionally, windswept alpine areas, older forests, and peatlands are considered nutritionally valuable to caribou because they provide arboreal or terrestrial lichens, which are the primary forage for caribou during winter (Bergerud 1972, Thomas et al. 1996, Johnson et al. 2000). The nutritional value of summer habitats of woodland caribou in western Canada, however, has not been quantified. Further, it is unclear whether older forests consistently provide better nutrition for caribou than younger forests, particularly during summer when deciduous shrubs and forbs, which generally are less abundant in older forests, compose large proportions of caribou diets (Bergerud 1972, Thompson and McCourt 1981, Thing 1984, Thomas et al. 1996, Denryter et al. 2017).

Our goal was to better understand the nutritional environment available to woodland caribou in northeastern British Columbia, Canada, where many populations are listed as threatened and special concern. To supplement recent findings on forage quantity (Denryter et al. 2017), we concentrated these efforts on quantifying dietary quality and intake by caribou. Using tame caribou as a habitat assessment tool (Cook et al. 2016, 2018; Shipley et al. 2020; Ulappa et al. 2020), we documented nutrient intake by tame caribou in the predominant plant communities in the mountains and boreal forests of northeastern British Columbia during summer. We focused on lactating females because they incur elevated nutritional demands for milk production on top of nutritional demands for replenishment of body reserves prior to winter. Our objectives were to quantify the nutritional value of habitats available to woodland caribou across seasonal, ecological, and successional gradients in northeastern British Columbia during summer–autumn, and test the hypotheses that older forests provide better nutrition for caribou than younger forests during summer and that plant communities available to caribou in northeastern British Columbia during summer–autumn afford caribou nutrient intakes needed to support nutritional requirements for lactation and replenishment of body fat and protein reserves (i.e., were nutritionally adequate). Finally, to better understand

potential implications of available nutritional resources to performance of lactating caribou across northeastern British Columbia, we simulated protein and energy intakes of free-ranging caribou foraging in 5 scenarios: random foraging among available plant communities; selective foraging in which caribou fed only in plant communities with abundant lichens (corresponding with many critical habitats); and selective foraging in plant communities that provided the top 40%, 20%, and 10% of daily intake of protein and energy.

STUDY AREA

Our study area encompassed 9 plant communities (i.e., potential natural vegetation communities; Table 1) spread across 65,354 km^2 in the Taiga Plains, Montane Cordillera, and Boreal Plains ecozones (Figure 1) in British Columbia. The climate was continental and characterized by cold winters (Nov–Mar) and moderately warm and short summers (Jun–Aug); spring was April–May and autumn was September–October (Wilken 1986). Mean daily temperatures in January were −20°C, −29°C, and −12.5°C in the Boreal Plains, Taiga Plains, and Montane Cordillera ecozones, respectively, and 15°C, 13°C, and 15.5°C in July. Precipitation averaged approximately 400 mm annually in the Boreal Plains and Taiga Plains ecozones and 800 mm annually in the Montane Cordillera Ecozone. Elevation ranged from approximately 300–2,600 m, with the Boreal Plains and Taiga Plains sites characterized by relatively flat topography and sites in the Montane Cordillera characterized by rolling topography, steep slopes, and high-elevation plateaus. Interannual variation in summer precipitation was substantial during our study in 2013–2015. From 15 June to 10 October, Fort St. John, British Columbia, near the center of our study area, received 282 mm of precipitation in 2013, compared with 104 mm in 2014 and 160 mm in 2015 (The Weather Network 2016); we observed signs of senescence (e.g., yellowing of leaves, leaf drop) earlier in the year during 2014 than in the other years of our study and we noted higher abundance of mushrooms in 2013 than in the other years of our study (Denryter 2017, Denryter et al. 2017). Based on long-term averages (1979–2010 at Fort St. John) of temperature and precipitation for the growing season (Apr–Sep), 2013 was slightly wetter (6%) and temperature was virtually identical to 30-year means; 2014 was substantially drier (59%) and was 0.5°C warmer than normal, and 2015 was slightly drier (89%) and was 0.8°C warmer than normal. Thus, our data encompass a substantial range in growing season weather, but in 2 of 3 years, weather generally matched that of long-term averages.

Dominant vegetation varied by plant communities and successional stage (Table 1) and common megafauna included Stone's sheep (*Ovis dalli stonei*), moose (*Alces alces*), wolves (*Canis lupus*), grizzly bears (*Ursus arctos horribilis*), and black bears (*Ursus americanus*). Primary land uses included forestry, oil and natural gas extraction, and mining. We sampled forests across early, mid, and late-successional stages, including forests resulting from re-generation after timber harvest and silvicultural activities and after forest fires. We categorized forested sites into young, mature, and old age categories following guidelines of the British Columbia Ministry of Forests and British Columbia Ministry of Environment (1995). The guidelines provided stand ages of early, mature, and old seral stages of forests by Biogeoclimatic Ecosystem Classification (BEC; Meidinger and Pojar 1991) zone (and variant), natural disturbance type, and, where applicable, whether a stand was dominated by coniferous or deciduous trees. We distinguished young, mature, and old forests by forest type (Table 2; British Columbia Ministry of Forests and British Columbia Ministry of Environment 1995).

Caribou populations across Canada were grouped as designatable units (DUs) that were spatially, ecologically, or genetically discrete (Committee on the Status of Endangered Wildlife in Canada 2011). Our sampling with tame caribou encompassed areas available to 3 populations of caribou in the Boreal Woodland DU (Chinchaga, Prophet, Snake-Sahtaneh), 2 populations in the Northern Mountain DU (Graham, Pink Mountain), and 5 populations in the Central Mountain DU (Kennedy Siding, Moberly, Burnt Pine, Quintette, Narraway; Figure 1). Accessibility by road and stock trailer on non-winter roads was greatest in the Boreal Woodland DU (~2,516 km of road length), followed by the Central Mountain DU (933 km), and Northern Mountain DU (437 km).

TABLE 1 Description of plant communities including corresponding Biogeoclimatic Ecosystem Classification (BEC) zone, dominant tree species, and common species of understory plants (adapted from Denryter et al. 2017)

Plant community[a]	BEC zone[b]	Dominant tree species	Common understory species
ADry	AT	None	No erect shrubs; crowberry (*Empetrum nigrum*), lingonberry (*Vaccinium vitis-idaea*), kinnickinnick (*Arctostaphylos uva-ursi*), net-veined willow (*Salix reticulata*), alkali grasses (*Festuca* spp.), boreal sagebrush (*Artemisia norvegica* ssp. *saxatilis*), Jacob's ladder (*Polemonium caeruleum*), and vetch (*Astragalus* spp.). Similar lichen species to AWillow and ABirch.
ABirch	SWB	None	Dwarf birch (*Betula glandulosa*), reindeer lichens (*Cladina* spp., *Cladonia* spp., *Cetraria* spp., *Flavocetraria* spp.), boreal sagebrush. Foam lichen (*Stereocaulon paschale*) dominated groundcover.
AWillow	SWB	None	Willows (*Salix* spp.), lichens (similar species as other alpine sites but much less foam lichen), locoweed (*Oxytropis* spp.), Jacob's ladder, boreal sagebrush, alpine meadow grasses (*Poa* spp., *Anthoxanthum monticola*).
HighSF	ESSF, SBS	Hybrid spruce (*Picea engelmannii* x *glauca*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*).	Dwarf birch (northern sites) or white-flowered rhododendron (*Rhododendron albiflorum*, southern sites). Crowberry, black huckleberry (*Vaccinium membranaceum*), bramble (*Rubus pedatus*), fireweed (*Epilobium angustifolium*), oak fern (*Gymnocarpium dryopteris*), mountain ash (*Sorbus scopulina*), and *Cladina* lichens.
MidSF	ESSF, SBS	Hybrid spruce, subalpine fir, black spruce (*Picea mariana*), lodgepole pine.	Arnica (*Arnica latifolia*), asters (Asteraceae), coltsfoot (*Petasites frigidus* var. *palmatus*), fireweed, horsetails (*Equisetum* spp.), Sitka valerian (*Valeriana sitchensis*), raspberry (*Rubus idaeus*), queen's cup (*Clintonia uniflora*), twinflower (*Linnaea borealis*), soapberry (*Shepherdia canadensis*), green alder (*Alnus viridis* ssp. *crispa*), willows, and blueberries (*Vaccinium* spp.).
BBS	BWBS	Black spruce.	Labrador tea (*Rhododendron groenlandicum*), lingonberry, cloudberry (*Rubus chamaemorus*), reindeer lichens. The ground layer supports sphagnum moss (*Sphagnum* spp.) with varying density of overstory trees, and this type also is referred to as peatland, muskeg, bog, or poor swamp; also includes nutrient-poor fens.

TABLE 1 (Continued)

Plant community[a]	BEC zone[b]	Dominant tree species	Common understory species
BTRF	BWBS	Tamarack (*Larix laricina*), black spruce.	Dwarf birch, willows.
BWS	BWBS	White spruce (*Picea glauca*) at late successional stages. Lodgepole pine or trembling aspen at mid-successional stages (dry and mesic sites, respectively). Also, balsam fir (*Abies balsamea*), cottonwood (*Populus balsamifera*), and paper birch (*Betula papyrifera*).	Asters, fireweed, Canada mayflower (*Maianthemum canadense*), pea (*Lathyrus* spp.), green alder, rose (*Rosa acicularis*), willow, paper birch, blueberries, high-bush cranberry (*Viburnum edule*), reindeer lichens, horsehair lichen (*Bryoria* spp.).
Wetland	Wf and Wm[c]	N/A	Sedges (*Carex* spp.) at montane wet meadows and boreal meadow marshes. Montane wet meadows also had an unidentified, unpalatable (to caribou) species of willow, and asters. Dwarf birch and sweet gale (*Myrica gale*) dominated the understory of one wetland site in the boreal forest.

[a]Plant communities are 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 fen (BTRF), boreal white spruce (BWS), and wetlands.

[b]Biogeoclimatic ecosystem classification zones are boreal white and black spruce (BWBS), Engelmann spruce-subalpine fir (ESSF), sub-boreal spruce (SBS), spruce-willow-birch (SWB), and alpine tundra (AT).

[c]Wf are fen wetlands, Wm are marsh wetlands, which are BEC classes or specific land cover types that occur within the ESSF and BWS BEC zones.

METHODS

Foraging studies

We collected foraging observations on tame caribou during the summers and early autumns (11 Jul–10 Oct) of 2013–2015. All caribou used in foraging trials were female and ranged in age from 1–6 years old during the study. Individuals in the initial cohort of hand-reared caribou (*R. t. granti*), which were captured from the wild at ≤3 days old from the Delta, Hodzana Hills, Macomb, Ray Mountains, and White Mountains populations in Alaska, USA (within the mountain caribou range that extends into northern BC), were raised at the Robert G. White Large Animal Research Station at the University of Alaska, Fairbanks (Parker and Barboza 2013) and later transported to a research facility operated by the National Council for Air and Stream Improvement near Fort St. John, where they were housed when not used for foraging trials. In captivity, animals were maintained on a pelleted ration developed for caribou (modified from Parker and Barboza 2013) and had access to pastures with several native plant species (Denryter et al. 2017, 2020*a*). For foraging studies, we intended to use lactating females only, but because of a shortage of tractable lactating adults in some years, we also collected data on tractable non-lactating adults and yearlings. Additional details regarding animal rearing, training, and care are provided in Denryter et al. (2017, 2020*a*).

We designed our sampling strategy to quantify the nutritional value of the predominant plant communities available to caribou in our study area, rather than just those considered to be providing critical habitat. Additionally,
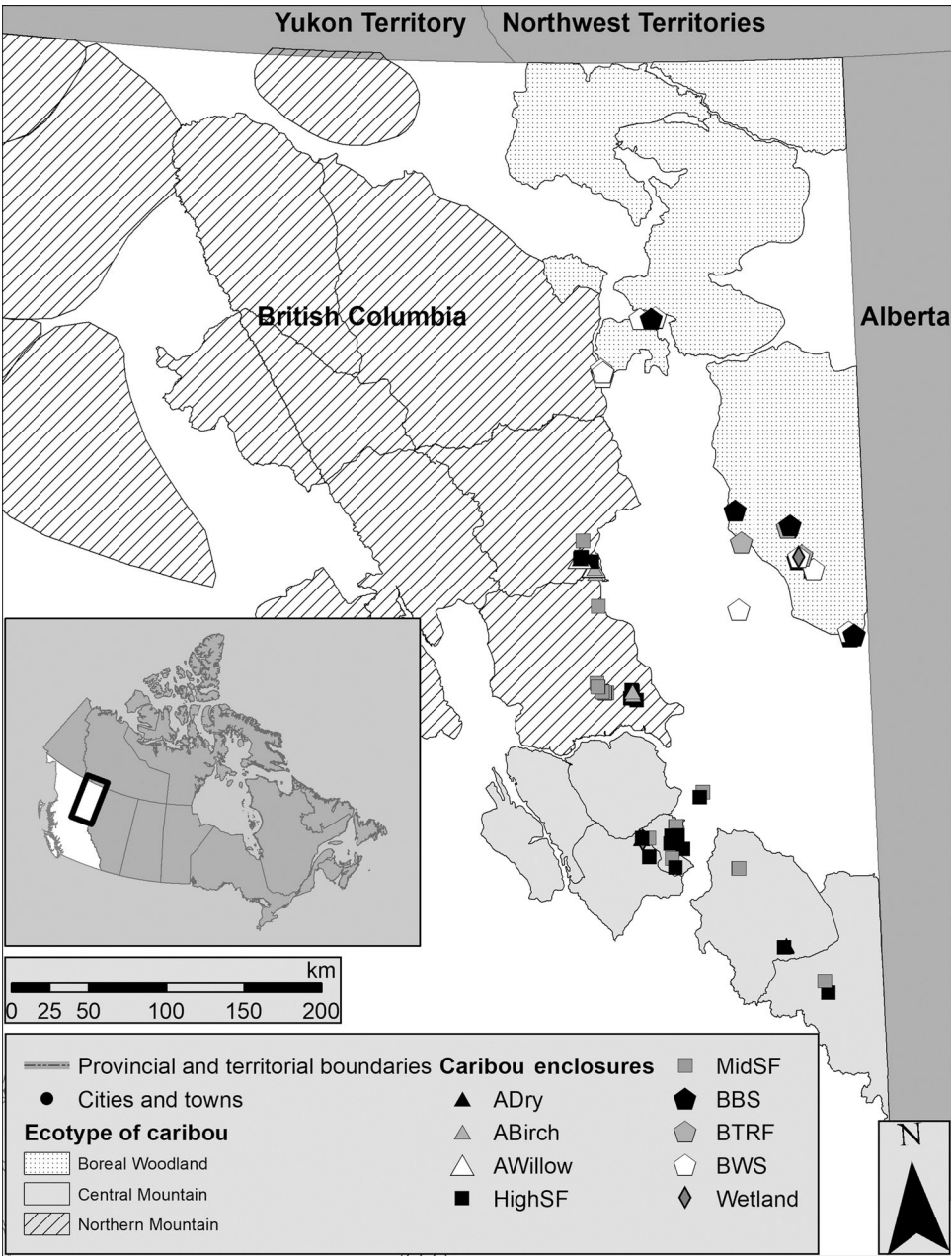
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FIGURE 1 Locations of sites where foraging observations and associated samples were collected on tame caribou during summer and early autumn of 2013–2015 in northeastern British Columbia, relative to ranges of wild caribou populations (shaded by designatable unit: Boreal Woodland, Northern Mountain, and Central Mountain). Sample sites were dry alpine (ADry), birch alpine (ABirch), willow alpine (AWillow), high-elevation spruce-fir (HighSF), mid-elevation spruce-fir (MidSF), boreal black spruce bog (BBS), boreal treed rich fen (BTRF), boreal white spruce (BWS), and wetland (Wetland)

TABLE 2 Classification of successional stages of plant communities available to caribou in northeastern British Columbia, Canada during summer and early autumn 2013–2015, using Biogeoclimatic Ecosystem Classification (BEC) zone, dominant (leading) tree species (from British Columbia Vegetation Resources Inventory [VRI]), landcover (from the Ducks Unlimited Enhanced Wetland Classification; EWC); numbers in young, mature, and old columns are ages (yr) of forest stands

System	BEC zone	Leading species (VRI)	Elevation (m)	EWC	Plant community	Young	Mature	Old
Boreal	Boreal white (Picea glauca) and black spruce (Picea mariana) (BWBS)	Lodgepole pine, black spruce	Any	Anything other than treed rich fen	Boreal black spruce (BBS)	<40	≥40–<140	≥140
		Tamarack	Any	Any	Boreal treed rich fen (BTRF)	<40	≥40–<140	≥140
		White spruce, hybrid spruce, Engelmann spruce, Sitka spruce, paper birch	Any	Anything other than treed rich fen	Boreal white spruce (BWS)	<20	≥20–<100	≥100
		Any	Any	Treed rich fen	Boreal treed rich fen (BTRF)	<40	≥40–<140	≥140
		No leading species	Any	Anything other than treed rich fen	Non-nutritive			
Montane	Engelmann spruce (Picea engelmannii)-subalpine fir (Abies lasiocarpa) (ESSF), sub-boreal spruce (SBS)	Any	Any	Treed rich fen	Boreal treed rich fen (BTRF)	<40	≥40–<140	≥140
		Any leading species	≥1,150	Anything other than treed rich fen	High-elevation spruce-fir (HighSF)	<40	≥40–<250	≥250
		Any leading species	<1,150	Anything other than treed rich fen	Mid-elevation spruce-fir (MidSF)	<40	≥40–<250	≥250
		No leading species	Any	Anything other than treed rich fen	Non-nutritive			

[a]Young, mature, and old categories based on descriptions in British Columbia Ministry of Forests and British Columbia Ministry of Environment (1995).

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using tame caribou allowed for comparisons of nutritional values of specific types of plant communities using standardized nutritional currencies (e.g., dietary digestible energy, daily intake of digestible energy), similar to study designs of Cook et al. (2016, 2018) and Ulappa et al. (2020). We emulated a stratified random sampling design, stratifying sample sites by plant community type, moisture gradient (for alpine sites), successional stage (for forested sites), and season (summer, late summer, autumn; Table 1; see detailed descriptions of our sampling strategy in online Supporting Information S1). Beginning in July each year, we constructed temporary enclosures with electrical fencing at sample sites (Denryter et al. 2017). Enclosures varied in size (i.e., 0.15–1.75 ha) inversely with available understory biomass. Enclosures built in low-biomass communities were larger than enclosures built in high-biomass communities to prevent confounding effects that depletion of biomass could have on foraging responses. We transported tame caribou and their calves in a trailer to these enclosures, where we held them for up to 48 hours (plus acclimation time of 0.5–6 hr). Caribou lived entirely on native vegetation in the enclosures and we provided *ad libitum* access to water.

Two trained observers collected all foraging data from 3 or 4 caribou per enclosure, usually at 2 adjacent sites. For each animal in an enclosure, we collected data during 2 foraging trials in the morning and 1 trial in the evening that were each 20 minutes in duration, and during 1 15-minute foraging trial in the afternoon for up to 5 hours of observations per site per day. We defined foraging to be continuous food intake (ingestion and searching) that ended when 3 minutes elapsed without intake. Observers recorded each bite caribou consumed by species and then collected replicate bite masses (Wallmo and Neff 1970, Cook et al. 2016, Anderson 2020, Ulappa et al. 2020). We dried bite mass samples in an oven at ≥70°C to a constant mass to determine the mean dry matter bite mass of each plant species at each site. We determined per-minute intake rates for each trial as the product of bite rate and bite mass in that trial and averaged those intake rates for each animal at each site to have one estimate of per-minute intake.

We also collected simulated diets based on bites consumed during foraging trials (Denryter et al. 2017, 2020a). Simulated diets consisted of 40–200 representative bites. Simulated diet samples required adequate plant material for laboratory assays and thus number of bites collected varied depending on bite mass of each species in the diet. The number of bites for each species in the simulated diet was proportional to the composition of each species relative to all bites consumed by each caribou during foraging trials at each site. For each species, we clipped plant parts for simulated diets as caribou consumed them (e.g., if caribou ate only berries of a specific plant, then we clipped only berries for the simulated diet). We buried diet samples in ice immediately after collection for up to 4 days before transferring to a freezer where they remained frozen until freeze-dried for analysis. The Washington State University Habitat Analysis Lab assayed simulated diets during 2014–2016 for gross energy (joules/g forage), total elemental nitrogen (multiplied by 6.25 to estimate crude protein %), fiber (sequential detergent analysis using filter bags, alpha amylase, and the ANKOM fiber analyzer200/200® [ANKOM, Fairport, NY, USA; Goering and Van Soest 1970]), and tannins (mg bovine serum albumin precipitated/mg forage; Goering and Van Soest 1970, Martin and Martin 1983), all on a dry-matter basis. For sequential detergent fiber analysis only, we analyzed diet samples in duplicate (using ~0.500 g/ replicate) unless differences between replicates were significant, in which case we ran a triplicate. We used powdered concentrate neutral detergent fiber (NDF) and acid detergent fiber (ADF) solution purchased from ANKOM and added 20 g of sodium sulfite to the ANKOM fiber analyzer at the NDF step for all diet samples. Beginning in 2012, sequential detergent fiber assays using the filter bag method and the ANKOM fiber analyzer200/200® began producing significantly lower NDF, ADF, acid detergent lignin (ADL), and acid insoluble ash (AIA) values (thus producing significantly higher estimates of digestible energy) when compared to the same sample assayed prior to 2012 (R. C. Cook, National Council for Air and Stream Improvement, unpublished data). Careful consideration of animal requirements and population performance of large ungulates strongly suggested pre-2012 results were more accurate leading R. C. Cook (unpublished data) to develop a series of correction equations using linear regression that we applied to our data (where $S_{y \cdot x}$ is the standard error of the estimate):

$$\text{Corrected NDF} = 1.03334 \times \text{NDF} + 4.8719; F_{1,99} = 498.59, P < 0.001, r^2 = 0.83; S_{y \cdot x} = 5.3 \tag{1}$$

$$\text{Corrected ADL} = 1.14617 \times \text{ADL} + 1.34973; F_{1,99} = 709.21, P < 0.001, r^2 = 0.88; S_{y \cdot x} = 2.05 \tag{2}$$

$$\text{Corrected AIA} = 2.8689 \times \text{AIA} - 0.35145; F_{1,99} = 140.66, P < 0.001, r^2 = 0.59; S_{y \cdot x} = 1.38 \tag{3}$$

We then calculated dietary digestible protein (DDP) and dietary digestible energy (DDE) content using equations from Robbins et al. (1987a, b) and Hanley et al. (1992).

Values of DDP and DDE multiplied by per-minute dry matter intake gave per-minute intake rates of digestible protein (DP) and digestible energy (DE). We calculated daily intake of DP and DE for each animal at each site by multiplying mean per-minute intake rates by daily foraging time derived from a combination of activity observations and automated activity recorders (Mini-Mitter® model AW64, Mini-Mitter, Bend, OR, USA) affixed to radio-collars (Wildlife Materials, Murphysboro, IL, USA). Calibration of activity recorders using direct observations indicated classification of foraging time was 93% accurate (Denryter 2017, Denryter et al. 2020a).

To quantify nutritional value of plant communities to lactating females, and to increase our sample size for these estimates, we needed to understand if and how foraging responses of lactating females differed from those of non-lactating or yearling females in our study. In previous work, Denryter et al. (2020a) evaluated diet selection, dietary quality (DDP and DDE content), per-minute intake, daily foraging time, and daily intake among tame caribou with different levels of nutritional requirements. The only difference detected was that lactating females had higher daily foraging times (and hence daily intake) than non-lactating females. The difference in daily intake, however, was eliminated when foraging times of non-lactating caribou were adjusted to foraging times of lactating caribou using the difference equation (Denryter et al. 2020b):

$$y = 0.202x + 1.4, \tag{4}$$

where y is difference in foraging time (in hours) between non-lactating and lactating caribou and x is per-minute intake of dry matter. We added the difference in foraging time from equation 4 to 108 estimates of daily foraging time of non-lactating caribou (non-lactating caribou accounted for ~26% of our samples) and multiplied this adjusted foraging time by the per-minute intake rates of DP and DE of each individual at each site to estimate daily intakes of DP and DE as if they were lactating caribou (Denryter et al. 2020a, b).

We compared dietary content (DDE, DDP) and intake rates of DE and DP to nutritional requirements of caribou as measures of nutritional value of different plant communities. For DDE and DDP, only one level of requirement is established for lactation: 12.1 kJ/g DDE and 8.6 g/100 g DDP (1 kJ = 0.239 kcal; National Research Council 2007, Denryter 2017). For daily intakes, we refer to the protein and energy required by lactating females without replenishment of lean mass and body fat as basic requirements, whereas optimal requirements include replenishment of body reserves. We assumed that daily DE requirements for a 110-kg female were 57 megajoule (MJ) of DE/day (1 MJ = 1,000 kJ) during lactation without replenishment of body fat and approximately 60 MJ of DE/day during lactation including replenishment of 9 kg of body fat (National Research Council 2007). Crude protein requirements for a 110-kg female caribou are 482 g/day during lactation without replenishment of body protein and 512 g/day during lactation including replenishment of 1 kg of body protein (National Research Council 2007: table 15-9). We assumed gain of fat and mass was 65% efficient (Boertje 1985) and occurred over 100 days. We determined DP requirements previously by regressing daily intake of DP against daily intake of crude protein (CP) as in equation 5 (Denryter 2017):

$$\text{g/day DP} = 0.651(\text{g/day CP}) - 43.5 \tag{5}$$

From equation 5, DP requirements for a 110-kg female were estimated to be 270 g/day during lactation without replenishment of body protein and 290 g/day during lactation with replenishment of 1 kg of body protein. The

values we used for nutritional requirements are the mean for the duration of lactation (though requirements are somewhat higher early in lactation and somewhat lower later in lactation [Parker et al. 1990, Gjøstein et al. 2004]) and are consistent with requirements estimated in other studies (Cook et al. 2004, Barboza 2014).

Statistical analyses

We conducted all statistical analyses in STATA 14 (StataCorp, College Station, TX, USA). We averaged dietary quality (DDP and DDE) and nutrient intake (after adjusting foraging times of non-lactating caribou to equivalent foraging times of lactating caribou) by caribou by enclosure, thereby treating enclosures as independent sampling units (Heffner et al. 1996).

To evaluate foraging responses (i.e., DDP, DDE, DP/min, DE/min, DP/day, DE/day) across all 9 plant communities sampled, we used analysis of covariance (ANCOVA) with main effects for ordinal day (to account for phenological changes over time that affect nutritional values of forages) and plant community type, and interactions between ordinal day and plant community type. We used Akaike's Information Criterion adjusted for small sample size (AIC_c) to rank competing models for each response variable (Burnham and Anderson 2002) and if ΔAIC_c between models was ≤2, we inspected models for uninformed parameters (Arnold 2010); we carried forward interaction terms only if they were in the highest-ranked model. After identifying top models (and associated significant interactions) from ANCOVA, we used linear regression to estimate main effects and any significant interactions for foraging responses of interest. We repeated the 2-stage analysis (ANCOVA and comparison of associated AIC_c, followed by linear regression) for analyses of successional stage in forested enclosures, including combinations of main effects (ordinal day, plant community type, successional stage) and interaction terms for plant community × ordinal day and successional stage × ordinal day or both. We evaluated all linear regression models for goodness of fit by visually inspecting plots of residuals versus fitted values. Lastly, we generated marginal (least square) means and 95% confidence intervals for response variables for each level of plant community or successional stage to determine where foraging responses differed.

Foraging simulations

To understand potential implications of the nutritional environment in northeastern British Columbia to lactating caribou during summer, we simulated intakes of DP and DE by caribou over 100 days (coinciding with our sampling season in Jul–Oct). We first generated a normal distribution of daily intakes of DP and DE by plant community type and successional stage (young, mature, old; Table 2), using the mean and standard deviation of these values determined with our tame caribou. Because of sample size limitations for late successional stages of boreal black spruce, boreal treed rich fen, and mid-elevation spruce-fir, and early successional stages of boreal treed rich fen, we used the mean and standard deviation of values across all successional stages within these plant communities, respectively. The distributions inherently reflected seasonal variation from July–October in protein and energy supplies in plant communities of northeastern British Columbia.

We mapped predominant plant communities available to caribou across northeastern British Columbia (Table 1; Figure 1) using information on BEC zones (Meidinger and Pojar 1991), leading (dominant) tree species from the British Columbia Vegetation Resources Inventory (VRI; Sandvoss et al. 2005), and landcover class from the Enhanced Wetland Classification produced by Ducks Unlimited (Ducks Unlimited Canada 2012). We acquired vegetation resources inventory data from the British Columbia Data Catalogue (https://catalogue.data.gov.bc.ca; accessed 31 Mar 2021) and CanFor Corporation, Fort St. John. Stand ages in VRI data were for the year they were inventoried. We adjusted stand ages to the year 2020 by adding the difference between 2020 and the year the age was reported to the reported stand age in VRI and differentiated young, mature, and old forests based on stand

attributes and age (Table 2). Although we sampled 3 types of alpine plant communities (dry alpine, birch (*Betula glandulosa*) alpine, willow (*Salix* spp.) alpine), resolution of spatial data was inadequate to differentiate birch and willow-alpine communities, so we combined these into a single category of shrub alpine for foraging simulations. We merged ranges of caribou populations that belonged to the same DU (i.e., Boreal Woodland, Northern Mountain, Central Mountain) into a single geographic area and then overlaid a 1 × 5-cell fishnet in ArcMap 10.4 (Esri, Redlands, CA, USA), which we used to divide the single area into 5 replicate landscapes for foraging simulations. We determined the proportionate availability of each plant community type and successional stage on each replicate landscape to generate foraging simulations.

Within each replicate landscape, we estimated 100-day intakes of DP and DE in foraging simulations related to 5 scenarios of habitat use: random foraging (using plant communities and successional stages in proportion to their availability on the landscape), foraging randomly but only in lichen-rich plant communities (i.e., dry alpine and old forests: high-elevation spruce (*Picea* spp.)-fir (*Abies lasiocarpa*), mid-elevation spruce-fir, boreal black spruce (*Picea mariana*) peatlands, and boreal white spruce (*Picea glauca*; Denryter et al. 2017), and foraging randomly but only in those plant communities offering the top 40%, top 20%, and top 10% of daily intake values. For the random foraging simulation, we simulated 1,000 (i.e., 10 per day) daily intake rates of DP and DE, drawn from normal distributions of daily DP and DE intakes we generated using mean and standard deviations for these values for each plant community, to capture the range of potential nutritional values of each plant community type and successional stage. For example, if boreal black spruce accounted for 90% of a simulated landscape and boreal white spruce accounted for the remaining 10% of the landscape, we drew 900 daily intake rates (drawn separately from the normal distributions of protein and energy) for boreal black spruce and 100 daily intake rates for boreal white spruce. We drew intake values only once, in the random foraging simulation, and carried these values through accordingly for lichen-rich and top 10–40% simulations. That is, lichen-rich and top 10–40% simulations were subsets of the random foraging simulation. For the top 10–40% simulations, we ranked each of the 1,000 draws in the random foraging simulation (i.e., what was available on the landscape) and carried through values from the top 400, 200, and 100 draws to the top daily intake simulations. We chose these values to illustrate a gradient of potential foraging strategies with varying levels of selectivity (i.e., moderately selective [top 40%] to extremely selective [top 10%]).

We chose daily intakes of DP and DE because they account for the intrinsic value of the plant community and digestive and other constraints on foraging time. We calculated 100-day intakes of DP and DE by averaging the values of daily intake of DP and DE in each simulation and multiplying that mean by 100. We calculated the proportionate difference in 100-day DP and DE intakes from 100-day protein and energy requirements (during lactation without replenishment of body reserves) as the difference between 100-day intake and 100-day requirements, divided by 100-day requirements (daily DP and DE requirements × 100).

RESULTS

We collected 942 hours of direct foraging observations on tame caribou, including bite counts, bite masses, and diet simulations, at 135 sites (Table 3; Table S2.1, available in Supporting Information S2). Additionally, we collected 1,682 hours of direct observations for calibration of automated activity recorders to estimate daily foraging time and hence, daily intake. Per-minute intake rates could not be estimated at 1 alpine birch site because of severe insect harassment that caused animals to cease foraging. We were unable to keep caribou in 11 enclosures for ≥24 hours because of concerns over animal or human safety or welfare and hence could not estimate daily intake in those enclosures (Table 3).

Quality of diets (as indicated by DDP and DDE) selected by caribou varied among plant communities (Figure 2) and decreased as ordinal day increased ($P < 0.001$; Figure 3), and the best models for DDP and DDE across plant communities did not include interaction terms (Table S2.2, available in Supporting Information S2). Across sites,

TABLE 3 Sample sizes for dietary quality (dietary digestible protein, dietary digestible energy), per-minute intake of digestible protein and digestible energy, and daily intake of digestible protein and digestible energy by tame caribou foraging in the predominant plant communities in northeastern British Columbia, Canada, July–October 2013–2015

Plant community	Dietary quality	Per-minute intake	Daily intake
Alpine birch (ABirch)	9	8	8
Alpine dry (ADry)	16	16	16
Alpine willow (AWillow)	4	4	4
High-elevation spruce-fir (HighSF)	33	33	27
Mid-elevation spruce-fir (MidSF)	28	28	26
Wetland (W)	4	4	4
Boreal black spruce (BBS)	14	14	12
Boreal treed rich fen (BTRF)	6	6	6
Boreal white spruce (BWS)	21	21	21
Total	135	134	124

DDP ranged from −0.4–11.2 g/100 g (Figure 3A) and was significantly (based on non-overlapping 95% CIs of marginal means) lower in boreal black spruce sites than all plant communities except dry alpine and willow alpine (Figure 2A); negative values of DDP occur when the protein content in the diet is less than the animal's endogenous losses—protein sloughed from the digestive tract during digestion—because of low nitrogen values or antinutritional factors binding protein and making it inaccessible to the animal (Robbins et al. 1987a, Robbins 1993, Lapierre and Lobley 2001, Spalinger et al. 2010). Dietary digestible energy ranged from 10.4–13.9 kJ/g (Figure 3B) and was significantly higher in wetland communities than all plant communities except boreal treed rich fen (Figure 2B). There were no other significant differences in DDP or DDE among plant communities, but some patterns were notable. In alpine communities, DDP tended to be higher in alpine birch and alpine willow than in dry alpine communities, but the pattern was reversed for DDE (Figure 2A, B). Similarly, in montane forests, DDP tended to be higher in mid-elevation spruce-fir forests than high-elevation spruce-fir forests, but the pattern was reversed for DDE (Figure 2A, B). In boreal forests, DDP and DDE were greatest in boreal treed rich fens and least in boreal black spruce (Figure 2A, B). On average, DDP was below requirements in all plant communities, and DDE averaged at or above requirements in dry alpine, high-elevation spruce-fir, wetlands, and boreal treed rich fen communities (Figure 2A, B).

Per-minute intake rates of DP and DE by caribou decreased as summer progressed ($P < 0.001$; Figure 3C, D) and the best models did not include interaction terms (Table S2.2). Per-minute intake rates of DP ranged from −0.01–0.94 g/minute (Figure 3C) and were greatest in willow alpine communities and least in boreal black spruce (Figure 2C). Per-minute intake rates of DE by caribou ranged from 16.0–123.1 kJ/minute (Figure 3D) and were greatest in willow alpine communities and least in dry alpine communities (Figure 2D).

Daily intake rates of DP and DE by caribou ranged from −9–739 g DP/day and 14–98 MJ DE/day across all sites sampled and the best models did not include interaction terms (Table S2.2). Daily intake of DP and DE decreased as summer progressed in all plant communities ($P < 0.001$; Figure 3E, F). On average, willow-dominated alpine communities afforded caribou the greatest daily intake of DP and DE and were the only plant community where mean daily DP and DE intake averaged at or above basic or optimal requirements (Figure 2E, F). Daily intake of DP was greatest in willow alpine communities and least in dry alpine and boreal black spruce communities (Figure 2E). Daily intake of DE was greatest in willow communities and least in dry alpine communities (Figure 2F).
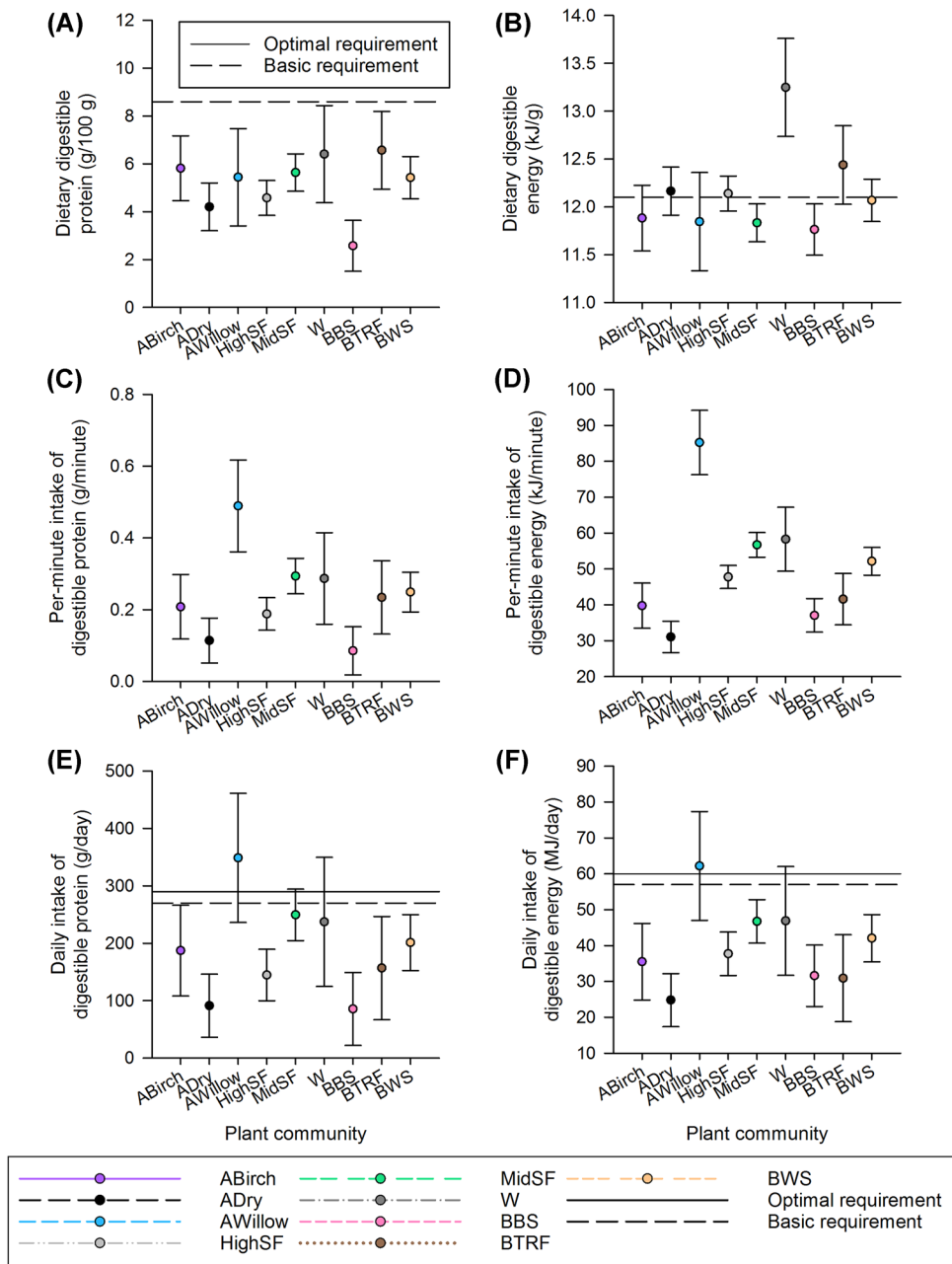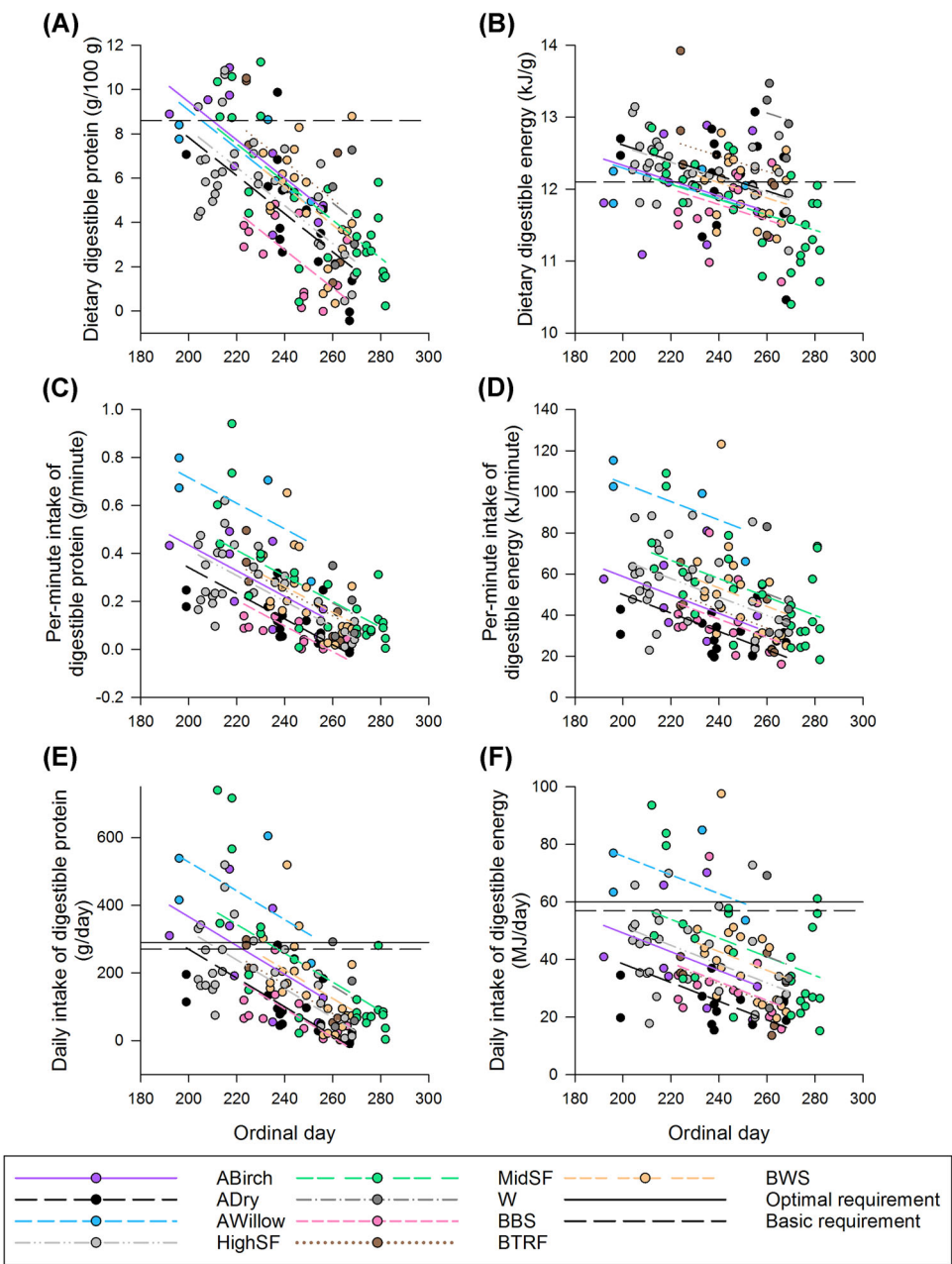
FIGURE 2 Marginal means (± CI) of dietary digestible protein (A), dietary digestible energy (B), per-minute intake of digestible protein (C), per-minute intake of digestible energy (D), daily intake of digestible protein (E), and daily intake of digestible energy (F) by tame caribou in plant communities sampled in northeastern British Columbia, Canada, during summer and early autumn, 2013–2015, relative to basic requirements for lactation and optimal requirements for lactation plus replenishment of body reserves. We estimated marginal means from modeled relationships between each response variable (A–F), ordinal day, and plant community. Plant communities are ABirch = alpine birch (n = 16, 16, 16; dietary quality, per-minute intake, daily intake), ADry = alpine dry (n = 9, 8, 8), AWillow = alpine willow (n = 4, 4, 4), HighSF = high-elevation spruce-fir (n = 33, 33, 27), MidSF = mid-elevation spruce-fir (n = 28, 28, 26), W = wetland (n = 4, 4, 4), BBS = boreal black spruce (n = 14, 14, 12), BTRF = boreal treed rich fen (n = 6, 6, 6), and BWS = boreal white spruce (n = 21, 21, 21)

FIGURE 3 Dietary digestible protein (A), dietary digestible energy (B), per-minute intake of digestible protein (C), per-minute intake of digestible energy (D), daily intake of digestible protein (E), and daily intake of digestible energy (F) by tame caribou in plant communities sampled in northeastern British Columbia, Canada, during summer and early autumn of 2013–2015, relative to basic requirements for lactation and optimal requirements for lactation plus replenishment of body reserves. Colored, diagonal lines depict fitted values estimated from modeled relationships for each response variable (A–F) as a function of ordinal day and type of plant community. Plant communities are ABirch = alpine birch (n = 16, 16, 16; dietary quality, per-minute intake, daily intake), ADry = alpine dry (n = 9, 8, 8), AWillow = alpine willow (n = 4, 4, 4), HighSF = high-elevation spruce-fir (n = 33, 33, 27), MidSF = mid-elevation spruce-fir (n = 28, 28, 26), W = wetland (n = 4, 4, 4), BBS = boreal black spruce (n = 14, 14, 12), BTRF = boreal treed rich fen (n = 6, 6, 6), and BWS = boreal white spruce (n = 21, 21, 21)

In alpine willow communities, daily intake of DP averaged >3 times that in dry alpine communities and nearly twice as much as alpine birch communities. Average daily intake of DE was more than twice as high in alpine willow than dry alpine communities (Figure 2E, F). In montane forests, daily intake of DP and DE, on average, was greater in mid-elevation spruce-fir forests than high-elevation spruce-fir forests (Figure 2E, F). In boreal forests, average daily intake of DP and DE was greatest in boreal white spruce communities and least in boreal black spruce communities (Figure 2E, F).

Across forest sites, we failed to detect effects of successional stage on DDP or DDE (95% CIs overlapped; Figures 4A, 5A). No interaction terms were present in the top model for DDP, but the top model for DDE included interaction terms and main effects for ordinal day × plant community and ordinal day × seral stage (Table S2.3, available in Supporting Information S2). Regardless of successional stage, DDP averaged below requirements (8.6 g/100 g) in every forested plant community sampled (Figure 4B). On average, DDE was below requirements (12.1 kJ/g) in mature and old forests but met basic requirements on average in young forests (Figure 5A). Specifically, DDE averaged at or above basic requirements in young and old boreal treed rich fens (young values were based on marginal means of models given that we did not sample any young boreal treed rich fens) and high-elevation spruce-fir forests, and young boreal white spruce forests (Figure 5B). The top models for per-minute and daily intakes of DP and DE did not include interaction terms (Table S2.3). Per-minute and daily intake of DP did not differ between young, mature, and old forests (Figure 4C–F; 95% CIs overlapped). Per-minute and daily intake of DE were significantly greater in young than in old forests, even when we accounted for effects of ordinal day and plant community (95% CIs did not overlap; Figure 5C–F), and the top models did not include interaction terms (Table S2.3). Among forested sites, daily intake of DP did not average above basic requirements in any plant communities but was greatest in young, mid-elevation spruce-fir forests and least in old boreal black spruce (Figure 4E, F). Daily intake of DE averaged below optimal and basic requirements for lactation in every forested plant community, regardless of successional stage but was greatest in young boreal white spruce and least in old boreal black spruce (Figure 5E, F).

Within plant community types, caribou satisfied dietary quality (DDP and DDE) requirements during lactation at 0–33% and 0–100% of sites sampled, respectively (Figure 6), but only 14% and 52% of 135 sites sampled overall satisfied DDP and DDE requirements. Caribou satisfied daily intake of DP and DE required during lactation at 0–75% of sites within each type of plant community sampled (Figure 7), and overall, only 23% and 14% of sites sampled provided caribou with adequate daily intake of DP and DE to satisfy requirements during lactation without replenishment of body reserves. In contrast, 19% and 12% of all sites sampled provided caribou with adequate nutrient intakes for lactation with replenishment of body fat and lean mass. Among alpine sites, caribou satisfied basic requirements for daily intake of DP at 75% of alpine willow, 50% of alpine birch, and 25% of dry alpine sites compared to DE requirements, which were satisfied at 75% of alpine willow, 25% of alpine birch, and 0% of dry alpine sites. In forests, caribou satisfied daily DP intake requirements at several young ($n = 9$) and mature ($n = 9$) forest sites; caribou satisfied DE intake requirements primarily at younger sites ($n = 10$), once at a mature forest site, and never at an old forest site (Figure 7). Caribou did not satisfy basic or optimal requirements for daily intake of DP at any boreal black spruce sites sampled or daily intake of DE at any boreal treed rich fen sites sampled (Figure 7).

Foraging simulations

Random foraging and foraging only in lichen-rich plant communities (dry alpine and older forests) resulted in negative protein and energy balances after 100 days—deficits that were most apparent in the simulation for the Boreal Woodland DU (Figure 8). On average, caribou in the Boreal Woodland DU simulation met or exceeded basic or optimal protein requirements when foraging exclusively in plant communities offering the top 10% of nutrition, but even so, they barely met basic energy requirements (Figure 8). Our simulations showed that caribou in the
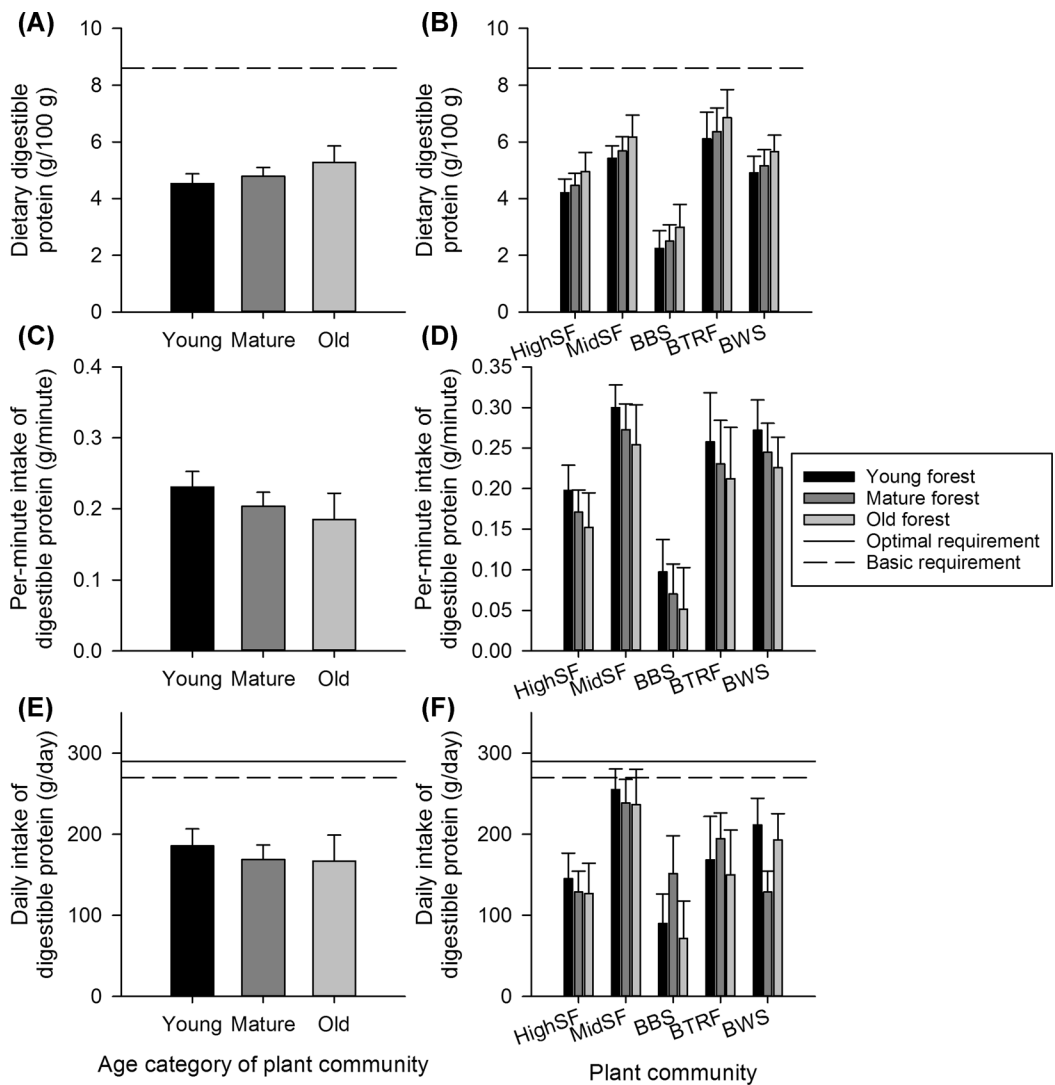
FIGURE 4 Marginal means (+ SE; by forest age category) of dietary digestible protein (A, B), per-minute intake of digestible protein (C, D), and daily intake of digestible protein (E, F) by tame caribou in young, mature, and old forests sampled in northeastern British Columbia, Canada, during summer and early autumn, 2013–2015, relative to basic requirements for lactation and optimal requirements for lactation plus replenishment of body reserves. We estimated marginal means from modeled relationships for each response variable (A–F) as a function of age category, ordinal day, and type of forested plant community. Plant communities are HighSF = high-elevation spruce-fir (n = 33, 33, 27), MidSF = mid-elevation spruce-fir (n = 28, 28, 26), W = wetland (n = 4, 4, 4), BBS = boreal black spruce (n = 14, 14, 12), BTRF = boreal treed rich fen (n = 6, 6, 6), and BWS = boreal white spruce (n = 21, 21, 21)

Northern Mountain simulations typically met or exceeded protein requirements when foraging in plant communities offering the top 40% (or better) of nutrition but generally met or exceeded energy requirements only when foraging in the top 20% or better. Simulations also showed that caribou in the Central Mountain DU would need to forage in plant communities offering the top 40% or better of nutrition to satisfy protein requirements and in the top 10% or better to satisfy energy requirements (Figure 8).

DISCUSSION

Our work using tame caribou to quantify the nutritional value of plant communities available to wild caribou in northeastern British Columbia during summer adds to a growing body of literature clarifying the role of nutrition as a limiting factor, particularly in the context of seasonality of nutritional limitations, for northern ungulates including caribou (Crête and Huot 1993, Dale et al. 2008, Hurley et al. 2014, Schaefer et al. 2016, Cook et al. 2021a). Less than 25% and 14% of sites sampled provided caribou with adequate daily intakes of DP and DE, respectively, to satisfy requirements during lactation without replenishment of body reserves and even fewer sites provided adequate daily intakes to support lactation plus replenishment of body reserves. The magnitude of nutritional inadequacies was stark: >33% of sites failed to provide caribou with 50% of DP and DE requirements and >60% of sites sampled failed to provide caribou with 80% of daily DP and DE requirements. The magnitude of deficiencies (i.e., typically 20–50% below requirements) also indicated that modest errors in our estimates of requirements would have little effect on our conclusions. Foraging simulations suggested the potential for widespread nutritional inadequacies across landscapes available to caribou in northeastern British Columbia during summer, especially in the boreal forest. Thus, our findings did not support the hypotheses that the nutritional environment available to caribou during summer in northeastern British Columbia fully supports lactating caribou or that nutritional resources typically are not limiting to caribou in Canada (Festa-Bianchet et al. 2011). Instead, our findings indicated that life for caribou in northeastern British Columbia is nutritionally more precarious than previously assumed.

Increasing evidence shows that late spring-early autumn is the season of nutritional limitation for caribou (Crête and Huot 1993, Post and Klein 1999, Dale et al. 2008, Schaefer et al. 2016, Cook et al. 2021a). Most caribou populations retain most body fat, or even increase body fat, over winter leading Couturier et al. (2009: 373) to call for increased focus on nutrition in summer in light of "the prominent influence of summer range on the body condition of caribou." Retaining body condition over winter was confirmed for boreal caribou in the southern Northwest Territories, Canada, and in northeastern British Columbia near and within our study area (Cook et al. 2021a). Further, annual cycles of body fat for 6 populations of caribou revealed that body fat of adult female caribou declined for most populations between March and early July, the annual minimum in body fat occurred in late spring–mid-summer, and the annual minimum was ≤4% body fat for most populations, with several as low as 1–2%—levels that may be life-threatening and indicate caribou experience bleak energetic environments during summer (Cook et al. 2021b). For the mountains of southern and central British Columbia, estimates of bone marrow fat indicated widespread occurrence of low body condition across all seasons (late winter = 74% mean marrow fat; spring = 69%; summer = 64%; early winter = 58%; McLellan et al. 2012). Of 61 female carcasses presented by McLellan et al. (2012), 30% had marrow fat ranging from 20–70%, corresponding to body fat between 1% and 6% (Cook et al. 2021b) and indicative of animals susceptible to predation, disease, or parasites (Mech and DelGiudice 1985, Bender et al. 2008, Sand et al. 2012). Another 15% had marrow fat <20% (indicative of starvation; Ratcliffe 1980, Peterson et al. 1984, Mech and DelGiudice 1985, Depperschmidt et al. 1987, Sand et al. 2012). Based on live-animal surveys of body condition (~900 adult females sampled from 2009–2019; J. G. Cook, National Council for Air and Stream Improvement, unpublished data) in British Columbia, the Northwest Territories, and Ontario, Canada, conducted in February and March (before fat levels evidently decline), adult female caribou in montane areas within our study area generally had body fat levels of 5–6%—among the lowest levels for caribou in the survey. Body fat of caribou in boreal populations of our study area was marginally higher (6–8% body fat), but body fat of both populations averaged well below that of caribou in boreal forests of southern Northwest Territories (9–10%).

The decline in body fat in late spring and early summer may be due to the combined effects of a variety of environmental influences including delayed initiation of vascular plant growth (well after parturition, particularly in far northern populations), such that caribou mothers may be forced to deplete endogenous reserves to produce milk during early lactation (late May, early Jun); severe harassment of biting insects late spring through early summer (Helle and Tarvainen 1984, Russell et al. 1993, Downes et al. 1996, Morschel and Klein 1997, Hagemoen
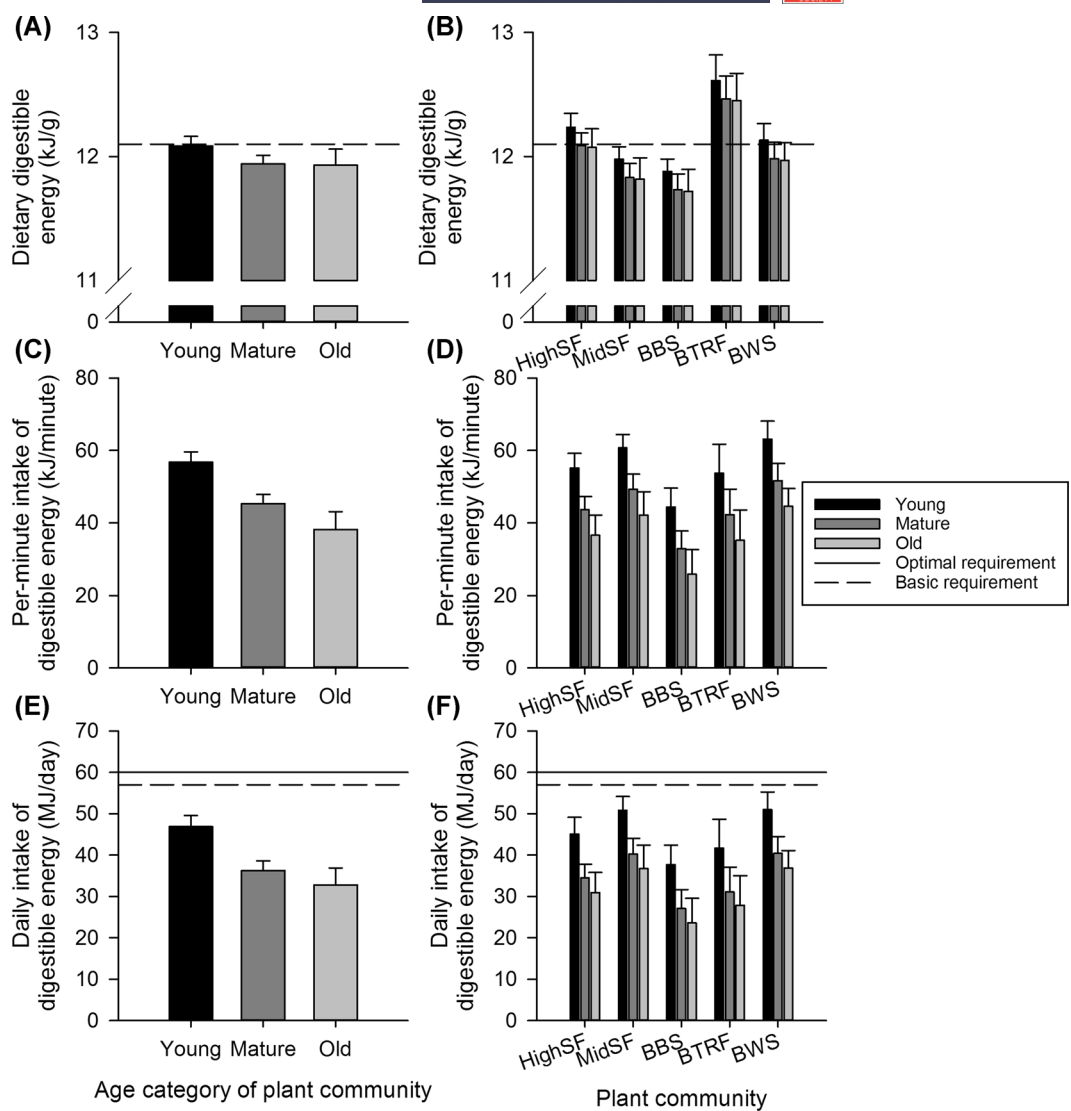
FIGURE 5 Marginal means (+ SE; by forest age category) of dietary digestible energy (A, B), per-minute intake of digestible energy (C, D), and daily intake of digestible energy (E, F) by tame caribou in young, mature, and old forests sampled in northeastern British Columbia, Canada, during summer and early autumn 2013–2015, relative to basic requirements for lactation and optimal requirements for lactation plus replenishment of body reserves. We estimated marginal means from modeled relationships for each response variable (A–F) as a function of age category, ordinal day, and type of forested plant community. Plant communities are HighSF = high-elevation spruce-fir (n = 33, 33, 27), MidSF = mid-elevation spruce-fir (n = 28, 28, 26), W = wetland (n = 4, 4, 4), BBS = boreal black spruce (n = 14, 14, 12), BTRF = boreal treed rich fen (n = 6, 6, 6), and BWS = boreal white spruce (n = 21, 21, 21)

and Reimers 2002); and sacrificed foraging time, foraging efficiency, and greater use of nutritionally inferior habitats to avoid predators (Eastland et al. 1989, Gustine et al. 2006, Viejou et al. 2018; though not all females may experience these costs in all environments, Barten et al. 2001). As biting insects wane and mothers increase mobility as their calves age, their ability to forage efficiently undoubtedly increases and thus mid-summer through early autumn may be a particularly crucial period for females to recover. Despite declining milk yields, nutritional
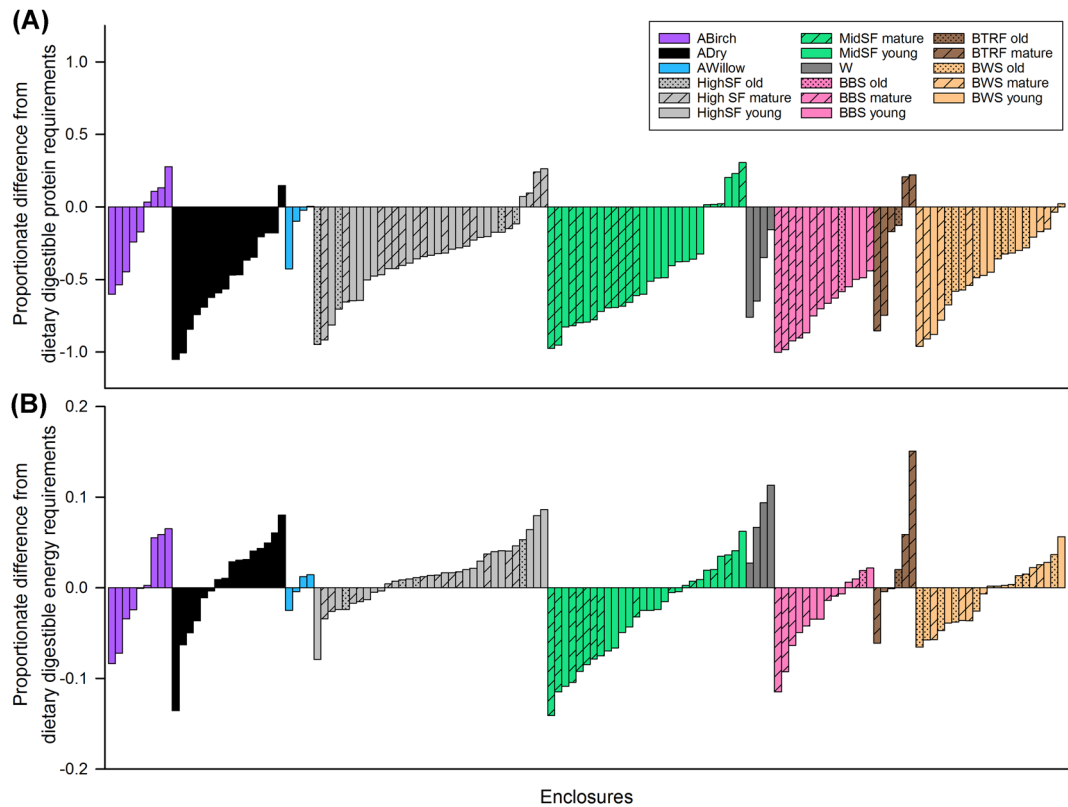
FIGURE 6 Dietary digestible protein (A) and dietary digestible energy (B) in each enclosure sampled with tame caribou in northeastern British Columbia, Canada, during summer and early autumn 2013–2015, as a proportionate change of basic requirements during lactation (without replenishment of body reserves). Plant communities are ABirch = alpine birch (n = 16), ADry = alpine dry (n = 9), AWillow = alpine willow (n = 4), HighSF = high-elevation spruce-fir (n = 33), MidSF = mid-elevation spruce-fir (n = 28), W = wetland (n = 4), BBS = boreal black spruce (n = 14), BTRF = boreal treed rich fen (n = 6), and BWS = boreal white spruce (n = 21)

requirements of mothers remain high to support lactation (Gjøstein et al. 2004) and simultaneously support re-covery of endogenous reserves catabolized in late spring and early summer (Cook et al. 2004). As summer wanes, forage quality (Figure 3) and quantity decrease and thus a nutritional bottleneck may occur (Klein 1968, Gates et al. 1986, Cook et al. 2004, Bender and Cook 2005), and our data suggest that lactating caribou and their calves in the mountains and boreal forest of northeastern British Columbia will be hard-pressed to acquire nutrients at rates that adequately support recovery of body fat and juvenile growth and development.

Summer nutrition also has important implications to demographic rates and productivity of populations. Re-searchers of the largest study of adult female caribou mortality (n = 169) in western Canada reported that most (~80%) females died between late March–April and July–early August; starvation accounted for 40% of mortalities during the post-calving period of 24 May–31 July; and poor body condition significantly elevated risk of mortality of adult females during late spring and early summer (Kelly 2020). Other researchers of caribou in western Canada also reported most caribou die in late spring and summer, not winter (Seip 1992, Wittmer et al. 2005, Whittington et al. 2011, McLoughlin et al. 2016). Further, improved nutrition during autumn (through supplemental feeding) in-crementally increased population growth across a range of wolf population densities (Heard and Zimmerman 2021). More generally, researchers of ungulate nutrition report that inadequate nutrition reduces milk yields, growth rates, and survival of juveniles; slows rate of sexual maturation; reduces pregnancy rate; and often delays timing of
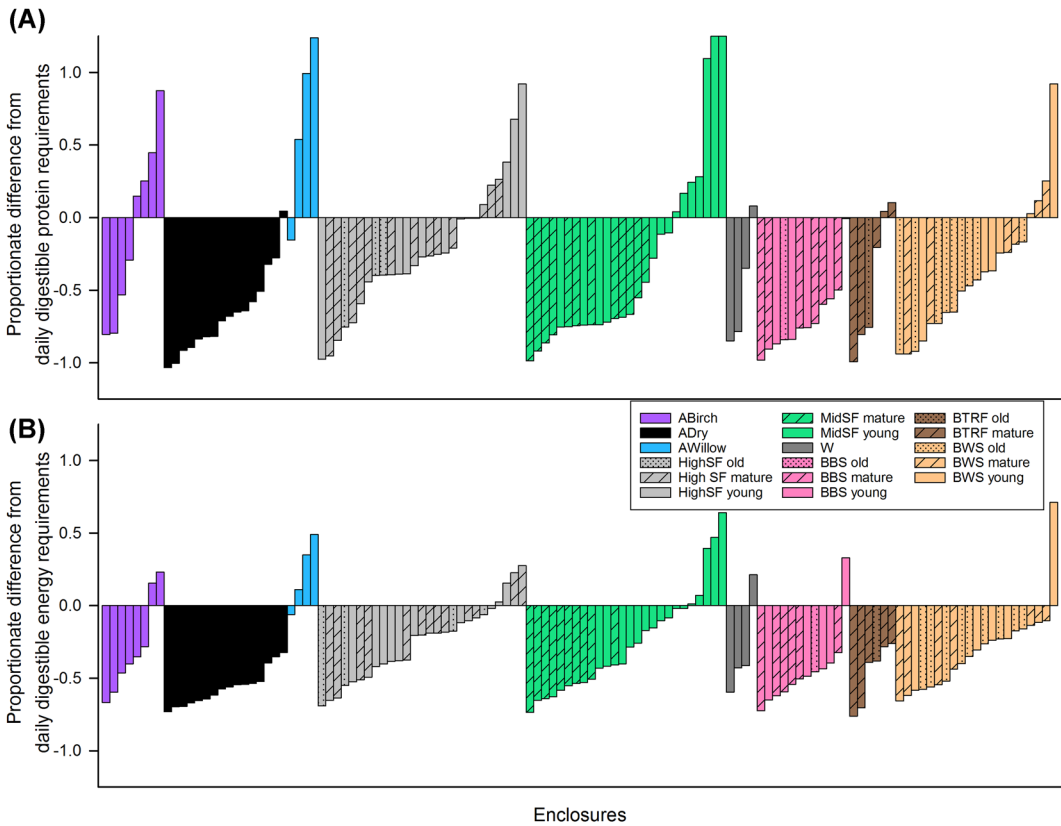
FIGURE 7 Daily intake of digestible protein (A) and digestible energy (B) by tame caribou in each enclosure sampled in northeastern British Columbia, Canada, during summer and early autumn 2013–2015, as a proportionate change of basic requirements during lactation (without replenishment of body reserves). Plant communities are ABirch = alpine birch (n = 16), ADry = alpine dry (n = 8), AWillow = alpine willow (n = 4), HighSF = high-elevation spruce-fir (n = 27), MidSF = mid-elevation spruce-fir (n = 26), W = wetland (n = 4), BBS = boreal black spruce (n = 12), BTRF = boreal treed rich fen (n = 6), and BWS = boreal white spruce (n = 21)

breeding, which together can affect population dynamics (Hjeljord and Histøl 1999, Cook et al. 2004, Hurley et al. 2014, Monteith et al. 2014, Rolandsen et al. 2017), including those of caribou (Cameron et al. 1993, Crête and Huot 1993, Adams and Dale 1998, Dale et al. 2008, Schaefer et al. 2016).

The nutritional value of plant communities depends on interactions among attributes of the plant community (e.g., species composition, quantity, quality of available foods), biogeoclimatic influences (e.g., site potential) on productivity and phenology of vegetation, and foraging responses of animals (e.g., bite mass, patterns of food selection; Shipley and Spalinger 1992, Spalinger and Hobbs 1992, Johnstone et al. 2002, Shipley 2007, Cook et al. 2016). How specific biogeoclimatic factors and interannual variability in precipitation, temperature, and other climatic effects interact with site characteristics to produce nutritional resources has yet to be quantified, but likely underpins the high variability in nutritional resources we documented within and across plant community types. In our study, productive and diverse understories with abundant, selected forages affording large bite masses and high intake rates (e.g., deciduous shrubs, mushrooms) characterized plant communities with the greatest nutritional value for caribou during summer (Denryter 2017, Denryter et al. 2017). In contrast, the nutritional deficiencies we documented likely were due to a combination of inadequate levels of DE and DP in diets selected by caribou, low abundance of selected forages, and a predominance of foods affording small bite masses (e.g., lichens, berries;
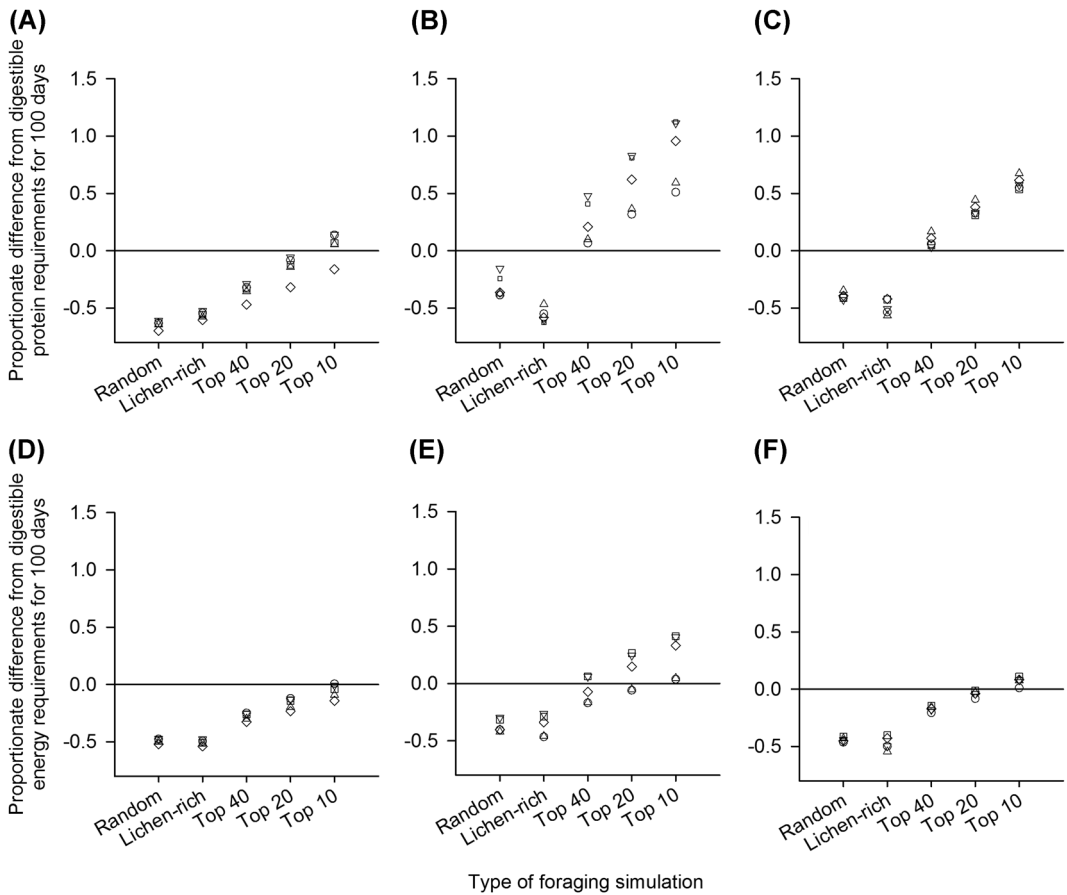
FIGURE 8 Proportionate differences from digestible protein (A–C) and digestible energy requirements (D–F) for 100 days estimated from foraging simulations across 5 simulated (replicate) landscapes for Boreal Woodland, Northern Mountain, and Central Mountain designatable units (DU) of caribou in northeastern British Columbia, Canada during summer and early autumn 2013–2015. Random foraging was the base simulation in which caribou were assumed to forage in plant communities proportionate to their availability on each replicate landscape; daily intake of protein and energy were simulated from a normal distribution (restricted to positive values) of daily intake, by tame caribou, of digestible protein and digestible energy by plant community and age category (young, mature, or old). The lichen-rich simulation assumed caribou foraged randomly in lichen-rich plant communities (i.e., dry alpine and old forests [boreal black spruce, boreal white spruce, high-elevation spruce-fir, mid-elevation spruce-fir]) available on the landscape used in the random foraging simulation. Top 10%, 20%, and 40% simulations assumed caribou foraged randomly in those plant communities offering the top 10%, 20%, and 40%, respectively, of nutrient intake available on the landscape used in the random foraging simulation. Each symbol represents a unique simulated landscape used across all types of foraging simulations within a DU

Trudell and White 1981, Spalinger and Hobbs 1992, Cook et al. 2016, Denryter 2017). For example, willow-dominated alpine communities provided the highest rates of DE and DP intake per day, whereas some of the lowest intakes occurred in alpine communities offering only mat-forming herbs and shrubs and scattered patches of alpine grasses and lichens. Dry alpine and boreal black spruce sites were almost wholly inadequate for daily DE and DP intake; however, on the rare occasion when mushrooms or selected deciduous shrubs were relatively abundant in these community types, caribou could achieve higher intake rates that approached or exceeded requirements (Denryter 2017, Denryter et al. 2017). Even small variation in nutritional value of forages or nutrient intake rates

can scale up to have disproportionately large multiplier effects (i.e., synergistic not additive) on individual performance (e.g., calf growth, fat gain, milk quality and production; White 1983, Cook et al. 2004, Cebrian et al. 2008) and population productivity (Post and Klein 1999, Kerby and Post 2013). For example, a 20% difference in dietary DE content through summer translated into a 5-fold difference in body fat in elk (*Cervus canadensis*), with further impacts on reproduction and survival (Cook et al. 2004).

Patterns of nutritional value among plant communities available to caribou in northeastern British Columbia during summer corresponded poorly with critical habitat designations. One of the most substantial discrepancies between nutritional value and critical habitat designations was for younger forests. Generally, younger forests have not been considered suitable for caribou because of low availability of lichens or high predation risk (McLoughlin et al. 2005, Latham et al. 2011, Dussault et al. 2012, Leblond et al. 2016), yet during summer and early autumn, younger forests often provide superior nutritional resources compared to older forests for many ungulates including caribou (Cook et al. 2016, Hull et al. 2020, Monzingo 2020, Ulappa et al. 2020, this study). In contrast, old-growth forests and boreal peatlands, often considered to provide critical habitats for caribou because they serve as refugia from predators and can have high abundance of lichens (an important winter food; Bradshaw et al. 1995, Stuart-Smith et al. 1997, Seip 1998, Rettie and Messier 2000, Latham et al. 2011), were among the most nutritionally inadequate plant communities available to caribou in northeastern British Columbia during summer and early autumn. Balancing predation risk with nutritional demands presumably requires caribou to use nutritionally valuable habitats in proximity to refugia (Hins et al. 2009, Dussault et al. 2012, Pinard et al. 2012, Wilson and Demars 2015, Leblond et al. 2016) or to make some other tradeoff.

Several habitat-use studies published for caribou in and near our study area (Culling et al. 2005, Gustine and Parker 2008, Mumma et al. 2018) grouped landcover and forest types differently than we did and did not account for successional stages of forests; thus, we cannot directly compare our results to infer how nutrition may have influenced habitat use or how habitat selection may have affected performance of wild caribou. Assessments of habitat use relative to nutritional resources on animal-centric foodscapes (Searle et al. 2007), which have yet to be rigorously defined for caribou in western Canada, would help to further elucidate how caribou try to balance nutritional demands with other factors (e.g., predation, insect harassment, disturbance) that influence their distribution. Our foraging simulations suggested caribou must be selective when choosing plant communities in which to forage or they may experience severe energy and protein deficits that could result in starvation, failure to rear a calf, or both (Moen et al. 1997). Although scenarios assuming random foraging and foraging exclusively in lichen-dominated plant communities during summer are unrealistic, results from these simulations highlight important variation in the nutritional adequacy of plant communities across northeastern British Columbia for caribou during summer. Further, these simulations illustrate that landscapes available to caribou in northeastern British Columbia were composed primarily of plant communities that do not provide lactating caribou with adequate nutrition during summer. In each of the 5 boreal landscapes used in our simulations, <1% of the landscape included early seral forests of high nutritional value and early seral forests composed only 3–6% of the landscape in the Central Mountain simulations. Early seral forests composed <1–2% of Northern Mountain landscapes in our simulations, but alpine shrub communities, which also provide high nutritional value, composed 0–51% of those landscapes. The extent to which animals may selectively forage and satisfy protein and energy requirements ultimately depends on the amount and spatial configuration of nutritional resources and how animals select resources across landscapes (Cook et al. 2018). Uncertainty about which plant communities free-ranging caribou select for foraging, particularly when the nutritional value of plant communities is so heterogeneous across northeastern British Columbia, makes it difficult to generalize about the influence of inadequate nutritional resources on caribou populations. Nonetheless, body fat data from the region (Cook et al. 2021a), in combination with our foraging simulations, suggest that selection for those plant communities that can satisfy nutritional requirements is unlikely to fully compensate for the nutritional environment in many areas of northeastern British Columbia or may not even be possible in some areas.

Nutritional deficiencies do not necessarily equate to a landscape that cannot support caribou. Rather, nutritional deficiencies imply that caribou must rely on strategies to compensate for inadequate nutrition to facilitate long-term persistence. When nutrition is inadequate, caribou may reduce investment in energetically demanding processes related to performance (e.g., reducing energy and protein allocation to milk production and quality; Loudon and Kay 1984, White and Luick 1984, Gerhart et al. 1997) that may significantly spare endogenous energy and protein reserves. Accretion rates of fat and protein, and growth rates of juveniles, dynamically adjust to the nutritional plane of the animal (Crête and Huot 1993, Cook et al. 2004). Modest reductions in performance attributes may be tolerated without significant reductions in reproduction, survival, and recruitment, but only to a point. Inadequate nutrition results in a predictable sequence of changes in vital rates of populations: reduced vigor and viability of neonates; lower growth rates and overwinter survival of juveniles; delays in age at first reproduction, breeding dates, and birthing dates; reproductive pauses; and finally, reduced adult survival (Eberhardt 2002, Monteith et al. 2014). The overall effect is a gradual reduction in population productivity that increases with increasing nutritional inadequacy, ultimately influencing population growth rates (Crête and Huot 1993, Monteith et al. 2014, Stephenson et al. 2020). The preponderance of information for our study area implicates nutrition as a potential limiting factor for caribou populations (Kelly 2020, Cook et al. 2021a, Heard and Zimmerman 2021), as it is elsewhere in North America (Crête and Huot 1993, Post and Klein 1999, Cameron et al. 2005, Dale et al. 2008, Schaefer et al. 2016). Although nutritional limitations on caribou generally are thought to be density-dependent (Crête and Huot 1993, Schaefer et al. 2016), our findings, coupled with low population densities of caribou in our study area, suggest nutrition may limit ungulates regardless of density (DeYoung et al. 2008, 2019; Cook et al. 2016), including in the boreal forests of Canada (Crête and Courtois 1997).

Although wild caribou performance data corroborate our findings, we acknowledge that applicability of our work depends on how well foraging dynamics of our tame caribou represent those of wild caribou for each plant community sampled. Many methods exist to estimate nutritional attributes (e.g., forage quantity and quality) of plant communities for ungulates, but most lack information on relationships between forage characteristics and nutritional outcomes of animals. Tame animals, however, allow for accurate measurements of bite mass, bite rate, species and parts of plants consumed, and provide for detailed, site-specific comparisons of use and availability by plant species in communities that wild animals select and avoid. Thus, we consider using tame caribou to quantify the nutritional value of the predominant plant communities of our study area to be superior to standard monitoring approaches that cannot directly infer nutritional value. Tame animals have a long history of successful application in studies of nutrition in wild settings (Baker and Hobbs 1982, Collins and Urness 1983, Wickstrom et al. 1984, Rominger et al. 1996, Ulappa et al. 2020), and various studies show that food selection, dietary composition, and foraging efficiency are indistinguishable between tame and wild animals (Bergerud and Nolan 1970, Wallmo and Neff 1970, Bergerud 1972, Olson-Rutz and Urness 1987, Spalinger et al. 1997). The main potential difference in foraging between tame and wild caribou is that wild caribou, foraging in the presence of predators and severe insect harassment (Toupin et al. 1996, Colman et al. 2003), are likely to achieve lower rates of intake than what our animals achieved in what we considered virtually optimal foraging conditions (i.e., foraging was not impeded by severe insect harassment or predators). Animal-defined metrics allow for rigorous evaluation of the nutritional value of plant communities, elucidation of why nutritional value varies among plant communities (Parker et al. 1999, Cook et al. 2016, Ulappa et al. 2020), and are useful for development of foodscapes (Searle et al. 2007) that reliably reflect animal nutrition (Cook et al. 2018).

The locations we sampled with tame caribou were limited by road access and animal welfare concerns and seasonally by snow conditions and insect abundance. Thus, food patches with higher nutritional value than we documented likely existed on the landscape, but so too did food patches with such low nutritional value that we could not hold animals for even 24 hours. Our objective was to sample the predominant plant communities available to wild caribou; extensive reconnaissance and vegetation sampling on these landscapes with and without caribou over 5 years (~450 sites sampled in addition to those where we deployed caribou; J. G. Cook, unpublished data) suggested we were successful. Additionally, in designing our study, we carefully considered the potential for forage

depletion by the caribou over time to affect estimates of intake rate and dietary quality, and enclosure size was adjusted accordingly (e.g., larger pens for plant communities with low biomass). The amount of biomass available to caribou within our enclosures ranged from hundreds to thousands of kilograms (Denryter et al. 2017), vastly exceeding the amount caribou could consume in the time they were in the enclosure (the highest intake we documented over 48 hours was ~80 kg for 4 lactating females). Thus, the foraging efficiencies that we documented for tame caribou are unlikely to be an artifact of enclosure size and biomass depletion. We also acknowledge that it is unlikely free-ranging caribou would forage in the same location for 24–48 hours during summer and that, theoretically, free-ranging caribou could achieve high intakes by moving among the best food patches on the landscape. If so, one could argue that short-term (per-minute) intakes of our caribou are more representative of how free-ranging caribou forage in these plant communities. Focusing on per-minute intakes, however, ignores important digestive constraints of ruminants that are better reflected by daily intake; in nutritionally depauperate environments, caribou may spend substantial time traveling between patches that provide high levels of nutrition, but increased travel may reduce intake rates (Denryter et al. 2020a). In addition, daily intakes, per-minute intakes, and accepted biomass all demonstrate deficient nutrition in most of the plant communities available to caribou in northeastern British Columbia (Denryter 2017, Denryter et al. 2017).

The recovery of woodland caribou is one of the greatest conservation challenges in Canada, owing to the complexity of factors affecting productivity and dynamics of caribou populations. In addition to habitat loss and disturbance, high rates of predation (Seip 1992, Seip and Cichowski 1996, Wittmer et al. 2005, Serrouya et al. 2017), and insect harassment (Russell et al. 1993, Toupin et al. 1996, Morschel and Klein 1997, Hagemoen and Reimers 2002, Colman et al. 2003), caribou in northeastern British Columbia face a bleak nutritional environment during summer. Numerous studies indicate that summer is a key season of nutritional limitations (based on a variety of caribou body condition studies; Couturier et al. 2009, Cook et al. 2021a); inadequate nutrition in summer is a biologically relevant contributor to mortality of adult female caribou (Kelly 2020); deficient summer nutrition is a widespread phenomenon for northern ungulates (Crête and Huot 1993, Cook et al. 2013, Hurley et al. 2014); and fine-scale nutritional resources are typically deficient across our study area (this study). These independent lines of evidence converge to suggest woodland caribou may be hard pressed to avoid levels of nutritional deprivation during summer that affect individual performance and that they must be selective in choosing where to forage if they are to satisfy nutritional requirements. Nutrition is the foundation of individual performance and population productivity and composes a primary mechanism of bottom-up influences on populations. Bottom-up and top-down forces undoubtedly act simultaneously on prey populations, and thus either-or perspectives regarding both forces are unduly limited and probably artificial (Hunter and Price 1992, Menge 1992, Gustine et al. 2006, Brown et al. 2007). We conclude that increasing evidence from various studies strongly corroborate our findings and indicate that the fine-scale nutritional deficiencies we documented probably scale up to affect productivity of caribou populations in our study area.

MANAGEMENT IMPLICATIONS

Management actions including habitat conservation, landscape restoration, maternal penning, captive rearing, and reductions in predators and alternate prey may be warranted as part of a comprehensive recovery plan for caribou. Nonetheless, our findings suggest conservation plans for caribou should consider and account for summer–autumn nutritional deficiencies to the extent possible. A first step is recognizing those vegetation community types that provide relatively good nutrition. For winter ranges, these include vegetation types that support abundant lichens. For summer ranges, our data indicate plant community types with relatively good nutrition include productive, willow-dominated alpine communities and montane and boreal communities that provide a diversity of deciduous shrubs, forbs, mushrooms, and lichens. Depending on site potential, early-seral communities can provide an abundance of diverse, palatable forage of high nutritional value to caribou during summer. Increasing these communities, however, may bolster populations of alternative prey (e.g., moose and

deer [*Odocoileus* spp.]) and their predators. Conservation plans should emphasize the value of landscape heterogeneity to provide diverse community types, including some early-seral communities for foraging, in appropriate balance with vegetation communities including older forests that provide caribou refuge from predators and relatively abundant winter forage.

CONFLICT OF INTERESTS

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

The University of Northern British Columbia Animal Care and Use Committee approved all study protocols (protocol number 2013-9).

DATA AVAILABILITY STATEMENT

Research data are not shared.

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