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Mineral constraints on arctic caribou (*Rangifer tarandus*): a spatial and phenological perspective

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Abstract. Arctic caribou (*Rangifer tarandus*) have the longest terrestrial migration of any ungulate but little is known about the spatial and seasonal variation of minerals in summer forages and the potential impacts of mineral nutrition on the foraging behavior and nutritional condition of arctic caribou. We investigated the phenology, availability, and mechanistic relationships of calcium, phosphorus, magnesium, sodium, potassium, iron, manganese, copper, and zinc in three species of woody browse, three species of graminoids, and one forb preferred by caribou over two transects bisecting the ranges of the Central Arctic (CAH) and Western Arctic (WAH) caribou herds in Alaska. Transects traversed three ecoregions (Coastal Plain, Arctic Foothills and Brooks Range) along known migration paths in the summer ranges of both herds. Concentrations of mineral in forages were compared to estimated dietary requirements of lactating female caribou. Spatial distribution of the abundance of minerals in caribou forage was associated with interactions of soil pH and mineral content, while temporal variation was related to plant maturity, and thus nitrogen and fiber content of forages. Concentrations of sodium were below caribou requirements in all forage species for most of the summer and adequate only on the Coastal Plain during the second half of summer. Phosphorus declined in plants from emergence to senescence and was below requirements in all forages by mid-summer, while concentrations of copper declined to marginal concentrations at plant senescence. Interactions of sodium with potassium, calcium with phosphorus, and copper with zinc in forages likely exacerbate the constraints of low concentrations sodium, phosphorus, and copper. Forages on the WAH contained significantly more phosphorus and copper than forages collected on the CAH transect. We suspect that migrations of caribou to the Arctic Coastal Plain may allow parturient females to replenish sodium stores depleted by foraging inland through the long arctic winters, while also extending the availability of adequate phosphorus, if animals are able to selectively track emerging waves of forage.

Key words: forage; migration; phosphorus; sodium; soil; tundra.

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Introduction

The spatial and temporal distribution of mineral nutrients on the landscape can influence the movement and productivity of ungulate populations (Frank et al. 1998), yet much of the literature on ungulate forage conditions has focused on energy and nitrogen (N) availability. Nitrogen, digestible energy, and minerals vary over time among species of the three plant functional groups used by ungulates (graminoids, browse, and forbs) and with plant maturity, temperature, and precipitation (Fynn 2012). These forage nutrients also vary over space and time, with

differences primarily driven by plant maturity and plant community composition, which is regulated by variation in precipitation, temperature, and soil fertility (Skarpe and Hester 2008). The transfer of soil minerals to plants and then to ungulates is affected by soil pH and by interactions among minerals and organic matter (Deng and Dixon 2002). For example, apparent copper (Cu) deficiencies in moose (*Alces alces*) have been associated with increased availability of sulfur (S) and molybdenum (Mo) in regions affected by acid rain due to interactions of Cu, Mo, and S forming insoluble thiomolybdates in the gut (Suttle 1991, Frank et al. 1994).

Over the growing season, nitrogen (N) concentrations decline from a peak at or shortly after emergence as the proportion of fiber and other structural components increase to senescence (VanSomeren 2014). N contained within proteins is mainly associated with photosynthetic components at the surface of leaves and stems that are diluted by fiber as plants mature. At senescence, photosynthetic components are withdrawn into woody or belowground tissues as stores for growth in the next season. Minerals in plants follow similar trends to N or fiber depending on their function in the structure and metabolism in plants: Phosphorus (P), potassium (K), and Cu are associated with photosynthetic parts and decline to senescence, while calcium (Ca), iron (Fe), zinc (Zn), and other trace mineral may be tied to structural components (i.e., fiber matrices) and will generally increase in concentration to senescence (Suttle and Underwood 2010).

Ungulate feeding strategies range from almost exclusive use of woody browse (i.e., browser) to that of graminoid plants (i.e., grazers) with mixed strategies that combine browse and grass with forbs and available fruits and tubers (Duncan and Poppi 2008). Broad-leafed forbs and browse typically contain the highest N concentrations but browse species are often defended with higher concentrations of plant secondary metabolites (PSM). Graminoids contain higher concentrations of fiber than leaves of browse but are relatively free of PSM. Mixed feeders such as arctic caribou begin to shift from winter diets during their spring migration to a diet primarily composed of graminoid sedges followed by an abrupt shift to browse after parturition (Thompson and McCourt 1981) which likely reflect phenological windows of nitrogen availability over the summer (Barboza et al. 2018). Phenological differences in mineral availability between forbs, browse, and graminoids are poorly defined for most plants. For this reason, it is unclear what challenges herbivores face with feeding strategies in terms of mineral nutrition, especially those that migrate long distances through their annual cycle.

Annual patterns of movement vary among ungulate species depending on forage biomass, landscape physiognomy, weather conditions, predation risk, and specific nutrient requirements of age classes or sexes (Mysterud et al. 2001, Monteith et al. 2011, Middleton et al. 2013). Migratory ungulates can extend the window of available nutrients by synchronizing movements with patterns of plant emergence (green wave hypothesis) across gradients of precipitation, elevation, or latitude (Albon and Langvatn 1992, Lendrum et al. 2014, Merkle et al. 2016, Aikens et al. 2017). For example, spatial variation in rainfall and forage P has been related to the aggregation and migration of wildebeest (*Connochaetes taurinus)* and the selection of foraging areas by elephants (*Loxodonta africana*) in Africa (McNaughton 1988, Hopcraft et al. 2010, Pretorius et al. 2011). Similarly, sodium (Na) distributions on the landscape have been associated with ungulate movements in North America and Europe (Jones and Hanson 1985, Staaland and White 2001, Ayotte et al. 2006, Slabach et al. 2015).

Caribou (*Rangifer tarandus*) in Alaska's Arctic undergo the longest land migration of any ungulate (Fancy et al. 1989, Nicholson et al. 2016, Fullman et al. 2017). Female caribou in Alaska migrate 3000 km annually between the wintering grounds in the Brooks Range and the calving grounds on the Coastal Plain. Migrations begin on the wintering grounds south of the Brooks Range in April and continue through May when they arrive on the Arctic Coastal Plain to give birth. Caribou continue to move after parturition, balancing nutritional needs with insect relief on the windswept Arctic coast or onto remaining patches of snow in the Arctic Foothills. Beginning in September, groups of caribou begin to congregate into larger groups in preparation for the fall migration back to their wintering grounds, arriving south of the Brooks Range by the end of October (Fancy et al. 1989, Fig. 1).

Winter diets are primarily composed of lichens with smaller proportions of senescent vegetation and bryophytes (Joly et al. 2007*b*, Gustine et al. 2012) Overall, the winter diet of arctic caribou in Alaska is low in concentrations of N and most minerals (Staaland et al. 1986). Consequently, caribou rely on acquiring and conserving body stores of minerals and protein gained over the summer to survive the long arctic winters (White et al. 1984, Barboza et al. 2018).

The objective of this study was to investigate regional and temporal differences in mineral nutrients on Alaska's Arctic tundra in order to assess how mineral constraints on arctic caribou may influence patterns of movement and the life history of reproductive females. We examined seven known caribou forages from the ranges of Central Arctic Herd (CAH) and Western Arctic Herd (WAH) caribou for a combined total of five transect years to describe the abundance, phenology, and spatial distribution of nine mineral nutrients on the landscape. Next, we assessed mineral constraints by comparing the availability of mineral nutrients over space and time with estimates of mineral requirements for caribou.

Methods

We estimated forage biomass and characteristics of forage and soil on transects on the summer ranges of two migratory caribou herds, spanning the three northernmost arctic ecoregions of Alaska (Gustine et al. 2017*a*, Barboza et al. 2018). Sample sites on the CAH transect were spaced evenly over a 200 km latitudinal gradient, while sites on the WAH were spaced over a similarly

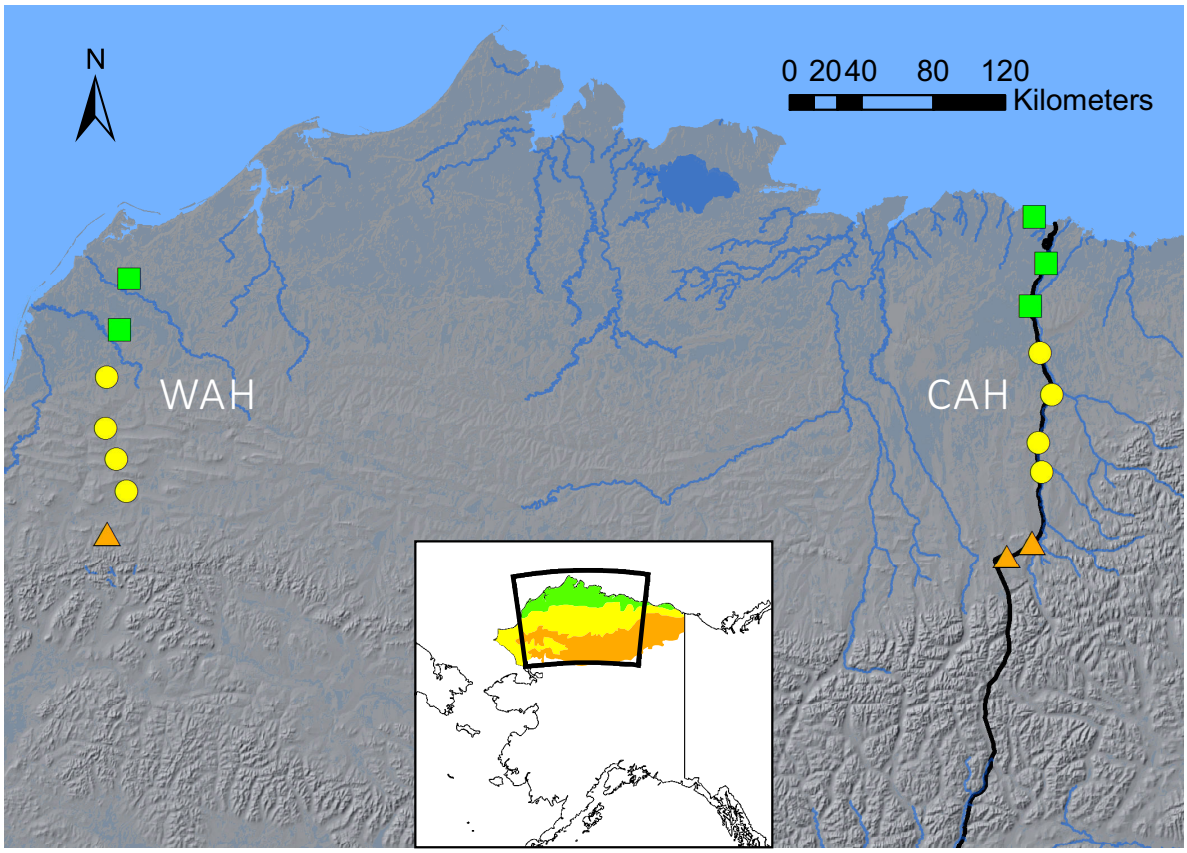

Fig. 1. Transects and sites for sampling forages used by two herds of arctic caribou in Alaska: Western Arctic Herd (WAH) and Central Arctic Herd (CAH). Solid shadings on inset map indicate ecoregions from the Brooks Range (orange) through the Arctic Foothills (yellow) to the Coastal Plain (green). Site marker colors correspond to the ecoregion each site lies in. Solid black line through the CAH transect represents the James W. Dalton Highway.

orientated 150-km transect (Fig. 1). CAH caribou typically winter in the southern foothills of the Brooks Range and migrate to calve on the Coastal Plain in early summer. Western Arctic Herd caribou follow a similar pattern, wintering south of the Brooks Range and onto the Seward Peninsula. Since the start of regular monitoring in 1975, the CAH increased from 5000 animals to 70,000 in 2010, but has since declined to 22,000 individuals (Lenart 2016). The WAH declined in the 1970s to a population near 70,000 animals, followed by an increase to become the largest caribou herd in Alaska at 490,000 animals in 2003. Since 2003, the herd has declined to approximately 200,000 animals (Dau 2015).

The primary species of caribou forage we collected and measured were three species of woody browse (*Betula nana, Salix richardsonii, Salix pulchra*), three species of graminoids (*Carex bigalowii, Carex aquatilis, Eriophorum vaginatum*), and forbs of the genus *Pedicularis*. We estimated biomass by completely sampling all study species in five randomly selected " m by " m quadrats at each sampling site through the summer. Samples of forage biomass collected at each quadrat were placed into pre-weighed dry paper bags by species, oven dried at 55°C, and weighed. Samples for mineral assays were collected adjacent to the biomass plots for later determination of mineral content and availability. In 2011–2014, forage samples were collected from each transect every two weeks from late May through September (ordinal days [ODs] 149–273), weather permitting. Sample species were selected to match prior studies (Whitten and Cameron 1980, Jorgenson et al. 2002) and to include known summer forages from direct observation and micro-histological analysis of fecal pellets (White and Trudell 1980, Ihl and Klein 2001). Soil samples were collected once per year in five locations at each sampling site.

Dried forage samples were homogenized through a 1-mm mesh in a centrifugal mill (Retsch ZM 200; Verder Scientific, Haan, Germany) for analyses of ash, carbon (C), and N (Gustine et al. 2017*a*). Samples for each study site and forage species were separated into three subsets for analysis: samples with the maximum concentration of nitrogen for the year; samples collected at peak biomass; and the final collection at senescence (Gustine et al. 2017*a*). Subsets were weighed in duplicate to 0.25–0.30 g and digested in 8 mL HNO_3 with a microwave system (MARS 6; CEM, Mathews, North Carolina, USA) at 200°C for 10 min. Each set of 40 digestions included duplicates of a reference material with known concentration (NIST; National Institute Standards and Technology; US Department of Commerce, Gaithersburg, Maryland, USA) and two method blanks (no sample). Sample digests and method blanks were diluted with 60 mL of deionized water (−18 MΩ/cm; Thermo-Scientific Gen-CAD, Waltham, Massachusetts, USA) to produce a mineral solution in 10% v/v HNO_3. Diluted sample digests were aspirated into a microwave plasma and analyzed by atomic emission spectra (MP-AES 4200; Agilent Technologies, Tokyo, Japan). Typical ranges of concentration in the diluted standards were estimated to prepare a series of 5–7 analytical standards in 10% w/v HNO_3 for a linear relationship between emission intensity and digest concentration for each of nine elements.

Calibration standards were prepared from single element standards for atomic absorption spectroscopy (1000 μg/mL; Specpure, Alfa Aesar, Ward Hill, Massachusetts, USA). We validated the digestion/assay method by using single element standards to detect contamination of our elements of interest in each stock solution. Standards were prepared in the following groups to minimize interference: magnesium (Mg)-Ca, Fe-P, manganese (Mn)-Zn, K, Na, and Cu. Concentration of each element was expressed on the basis of dry mass. We applied a correction for bias to each sample by using the NIST standards to regress observed concentration against expected concentration. Mineral availability was assessed via in vitro digestion of forage samples in a 1 N solution of HCl followed by assaying minerals in in vitro residues. Mineral availability was calculated as the difference of total minerals and residual minerals divided by total minerals. Available minerals in soils were assessed via Mehlich III extraction for Ca, P, Mg, Na, and K while Fe, Mn, Cu, and Zn were assessed via diethylenetriaminepentaacetic acid (DTPA) extractable minerals. Extracted soil mineral solutions were then measured by inductively coupled plasma mass spectrometry. All soil laboratory analyses were conducted at the Texas A&M Soil, Water and Forage Testing laboratory in College Station, Texas 77845, USA. Total N was estimated using an elemental analyzer (CNS2000; LECO, St. Joseph,

Michigan, USA). Assays of PSM were completed using a reaction of extracted phenolics with Folin–Ciocalteu reagent expressed as gallic acid equivalents, while acid detergent fiber (ADF) of forages was assessed using a solution of sulfuric acid and cetyl trimethyl ammonium bromide digested in a fiber analyzer (Ankom 200 Fiber Analyzer; Ankom, Macedon, New York, USA; Thompson and Barboza 2014).

We used mixed effects regression to model the phenology and spatial distribution of minerals in forages (STATA 14.0; StataCorp, College Station, Texas, USA). The full spatiotemporal model for each forage mineral (Y) included the fixed effects of ecoregion (ECO), transect (TRAN), species (SPEC), OD, and OD^2 where $Y = ECO + TRAN + SPEC + OD + OD^2 + SPEC \times OD + SPEC \times OD^2 + \varepsilon$. We also used mixed effects models to examine drivers of minerals in forages concentration (Y) with fixed effects for SPEC, soil minerals (SOIL), soil pH (pH), and forage components of total nitrogen content (N) and ADF where $Y = SPEC + SOIL + ADF + N + pH + \varepsilon$. Soil mineral concentrations and pH (Y) were examined with a mixed model including transect and ecoregion: $Y = TRAN + ECO + \varepsilon$. The availability of each mineral in forages (Y) was examined with a mixed model with species and season (emergence or senescence) as fixed effects: $Y = SPEC + Season + \varepsilon$. In all mixed effect models, we added sample site as a random effect to account for repeated measures at each site within each transect. We used a stepwise selection procedure in the phenology models to retain only those coefficients that differed significantly from zero ($P \leq 0.05$). Post hoc tests of fixed effects included pairwise comparisons of predicted margins ($\bar{X} \pm$ standard error) with Bonferroni's adjustments for multiple comparisons (Rabe-Hesketh and Skrondal 2010, Mitchell 2012). Model predictions of mineral concentrations in forages were compared with estimated dietary requirements (g/kg dietary intake) of caribou at early and late lactation calculated to represent a minimum dietary concentration required in the diet to maintain zero balance (Oster 2017).

Data disposition

Data are available from the U.S. Geological Survey: https://doi.org/10.5066/f7jq106w (Gustine et al. 2017*b*).

Results

We collected 1296 samples of caribou forages over transects bisecting the summer ranges of the CAH and WAH northern Alaska (Fig. 1); of those, 585 samples were included in phenologically representative subsets. Variation in forage minerals among ecoregions and transects was primarily driven by soil pH and secondarily by soil mineral concentrations, while variation over time and among species was influenced by phenological changes in concentrations of N and fiber. Ranges of Ca in soil were greater in the CAH transect than on the WAH transect (Table 1), which corresponded with greater soil pH on the CAH transect (5.8 ± 0.4 vs. 4.7 ± 0.2; $z = -1.99$ $P = 0.046$).

Concentrations of Ca and P differed among species of forage over the season and between transects. Concentrations of Ca increased with OD in all species and were greater in browse than graminoids with especially high concentrations in *Salix richardsonii* and *Pedicularis* spp. (Fig. 2). In contrast, concentrations of P declined over the growing season and were lower in graminoids than browse and the forb (Fig. 2). Soil pH was positively related to forage Ca (Table 2), which corresponded to greater Ca concentrations on the CAH transect (7060 ± 500 vs. 4740 ± 280 mg/kg; $z = -4.65$ $P = 0.000$). Concentrations of P in forages increased with forage N (Table 2) but only 10% of the forage samples contained sufficient P to meet the estimated requirement of caribou (Table 3). Increased soil pH and soil Ca (Table 2) were associated with decreases in forage P between the CAH and the WAH transects (1690 ± 80 vs. 1990 ± 50 mg/kg, $z = 3.33$ $P = 0.001$). The lowest concentrations of P coincided with the highest concentrations of Ca (Fig. 2); in other words, the ratios of Ca:P increased through the growing season. The range of ratios for Ca to P was greater among browse species (1–213 g Ca/g P) than either graminoids or the forb (1–42 g Ca/g P). Forage Ca:P ratios were greater on the CAH transect than the WAH transect (8.3 ± 0.8 vs. 4.2 ± 0.4; $z = -6.26$ $P < 0.001$) even after removing Ca-rich species (*Salix richarsonii* and *Pedicularis* forbs) that were less represented on the WAH transect (5.3 ± 0.4 vs. 2.0 ± 0.1; $z = -8.04$ $P < 0.001$). Ratios of Ca:P in graminoids were low and accompanied by more available P than browse ($56\% \pm 1\%$ vs. $43\% \pm 4\%$; $z = 2.86$ $P = 0.004$; Table 4) even though

Table 1. Observed concentrations (mg/kg dry mass) of available minerals and pH in soils by ecoregion and transect ($\bar{X}$ ± standard deviation).

Parameter	Ecoregion	N	WAH	N	CAH
pH	Brooks Range	6	4.1 ± 0.3^{a}	20	4.7 ± 0.7^{ab}
	Arctic Foothills	20	4.5 ± 0.6^{ab}	40	5.5 ± 1.4^{ab}
	Coastal Plain	0	–	30	7.0 ± 1.0^{b}
Ca	Brooks Range	6	430 ± 260^{a}	20	1140 ± 900^{a}
	Arctic Foothills	20	950 ± 460^{a}	40	3530 ± 4820^{a}
	Coastal Plain	0	–	30	8870 ± 6840^{a}
P	Brooks Range	6	6.7 ± 4.4^{bc}	20	14.9 ± 9.2^{d}
	Arctic Foothills	20	5.1 ± 1.8^{a}	40	9.5 ± 5.2^{c}
	Coastal Plain	0	–	30	5.5 ± 3.5^{ab}
Mg	Brooks Range	6	116 ± 36^{bc}	20	81.0 ± 37.8^{a}
	Arctic Foothills	20	201 ± 85^{c}	40	98.3 ± 43.2^{ab}
	Coastal Plain	0	–	30	85.2 ± 18.2^{a}
Na	Brooks Range	6	8.7 ± 3.1^{bc}	20	5.8 ± 1.4^{a}
	Arctic Foothills	20	8.9 ± 2.5^{c}	40	4.8 ± 7.2^{ab}
	Coastal Plain	0	–	30	16.9 ± 21.3^{abc}
K	Brooks Range	6	22.0 ± 8.4^{a}	20	37.5 ± 13.0^{a}
	Arctic Foothills	20	48.8 ± 22.4^{a}	40	26.5 ± 13.0^{a}
	Coastal Plain	0	–	30	22.3 ± 11.6^{a}
Fe	Brooks Range	6	409 ± 113^{a}	20	206 ± 105^{a}
	Arctic Foothills	20	313 ± 122^{a}	40	251 ± 148^{a}
	Coastal Plain	0	–	30	119 ± 110^{a}
Mn	Brooks Range	6	9.6 ± 5.3^{a}	20	50.2 ± 44.9^{a}
	Arctic Foothills	20	41.2 ± 43.3^{a}	40	25.4 ± 25.7^{a}
	Coastal Plain	0	–	30	15.7 ± 11.5^{a}
Cu	Brooks Range	6	1.9 ± 0.6^{a}	20	1.5 ± 0.7^{a}
	Arctic Foothills	20	2.2 ± 1.0^{a}	40	1.1 ± 0.8^{a}
	Coastal Plain	0	–	30	1.3 ± 0.6^{a}
Zn	Brooks Range	6	1.0 ± 1.0^{abc}	20	2.8 ± 3.2^{a}
	Arctic Foothills	20	0.8 ± 0.5^{a}	40	2.9 ± 3.0^{bc}
	Coastal Plain	0	–	30	2.1 ± 1.6^{c}

Notes: Different letters indicate significant pairwise differences between groups within each mineral ($P < 0.05$). WAH, Western Arctic Herd, CAH, Central Arctic Herd; -, no soil samples were collected from WAH coastal plain.

availabilities of Ca were similar among plant groups (80% ± 2%). Availabilities of Ca and P varied widely among species with the lowest availabilities for *Betula nana* (Table 4). Availability of Ca declined between early and late season for *B. nana* but increased over the season for three other species. (Table 4).

Availability of Mg in forages was much more consistent than those of Ca and P. Forage Mg was 88–98% available in concentrations that were above estimated dietary requirements of caribou for 94% of the samples (Table 3; Appendix S1: Fig. S1). Forage concentrations of Mg were greater on the WAH transect than the CAH (2100 ± 60 vs. 1730 ± 100 mg/kg; $z = 3.45$ $P < 0.001$). Soil concentrations of Mg were likewise higher on the WAH than on the CAH transect (Table 1). However, the concentration of Mg in forages was not related to the concentration of Mg in soil but was significantly reduced by increases in soil pH and by increases in forage fiber (Table 2).

Concentrations of forage Na were much lower than those for K throughout the growing season (Fig. 3). The ranges of concentrations for Na in forage and soil were greatest on the Coastal Plain (Tables 1, 3). Forage Na was positively associated with soil Na (Table 2) and only exceeded the estimated requirement of caribou on the Coastal Plain (Table 3) in 1% of all samples. Conversely, K concentrations exceeded the estimated requirement of caribou in 94% of samples (Table 3) even though K concentration declined through the season (Fig. 3) with the concentration of N and with decreases in soil pH (Table 2).

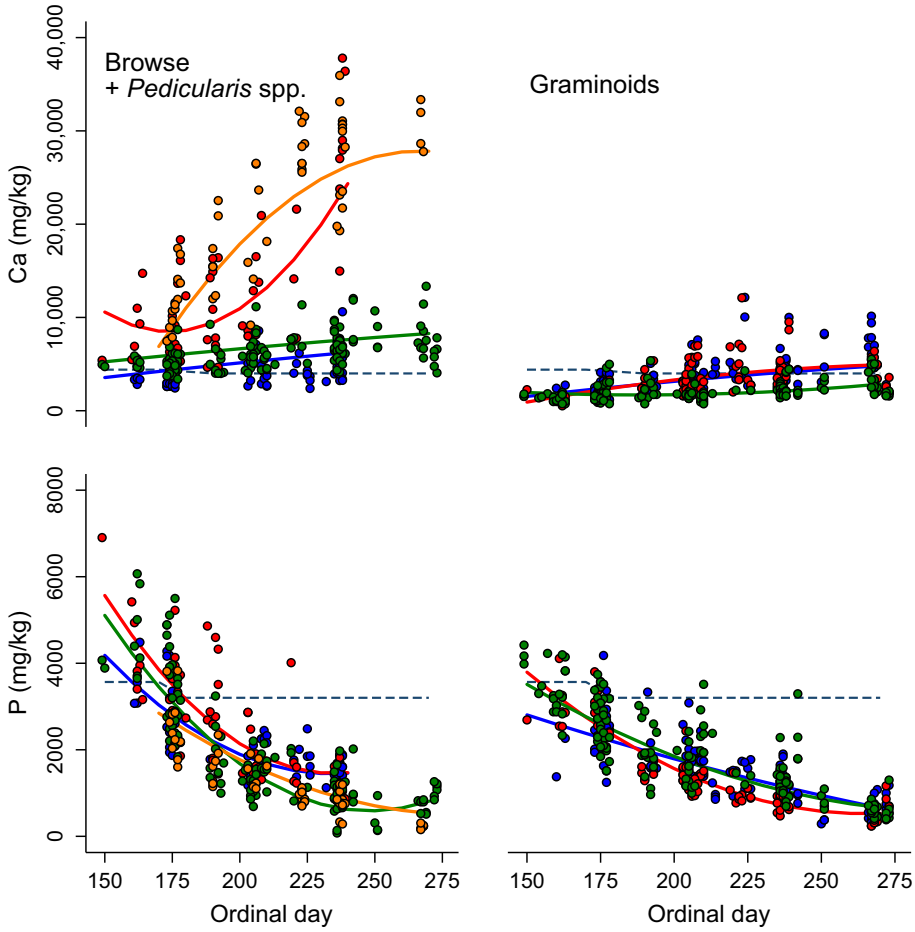

Fig. 2. Concentrations (mg/kg dry matter) of Ca (top panels) and P (bottom panels) in forages used by arctic caribou in Alaska. Dashed lines represent estimated dietary requirements of lactating caribou. Browse (left panels): *Betula nana* (blue), *Salix pulchra* (green), *Salix richardsonii* (orange), and forb *Pedicularis* spp. (red). Graminoids (right panels): *Carex aquatilis* (blue), *Carex bigelowii* (red), and *Eriophorum vaginatum* (green).

Concentrations of Cu in forages declined through the season in both browse and graminoid species (Fig. 4). Forage Cu was positively associated with N and fiber (Table 2), and with concentrations of Cu in soil. Forage concentrations of Cu were greater on the WAH transect than the CAH transect (5.14 ± 0.2 vs. 4.51 ± 0.2 mg/kg; $z = 2.19$ $P = 0.029$). Concentrations of Cu in forages were adequate early in the season but were marginal at the end of the season (Fig. 4). Forage Zn was highly available in both early and late season (Table 4) and present in much greater concentrations than those for Cu especially among browse species (Fig. 4). Although forage Zn was negatively associated with fiber (Table 2), Zn concentrations were greater than the estimated requirement for caribou (Table 3).

Forage concentrations of Fe increased with soil pH and were greater on the CAH than the WAH transect (170.9 ± 27.8 vs. 108.1 ± 10.2 mg/kg; $z = -2.63$ $P = 0.009$; Table 2). Availabilities of Fe in forages were lower than those of all other minerals and <21% for Fe in *B. nana* (Table 4). In contrast, the availability of Mn in forages was high and ranged from 68% to 97%. Forage concentrations of Mn were negatively associated with soil pH, forage N, and fiber and were also positively associated with phenolic activity (Table 2). Concentrations of Mn in forage were highest in the

Table 2. Linear effects of composition of forage and the respective soil minerals on minerals in forages used by arctic caribou in Alaska.

	Independent variables			
Element	N	Acid detergent fiber	Soil	pH
Ca	−	−		+
P	+			−
Mg		−		−
Na			+	+
K	+			+
Fe				+
Mn	−	−		−
Cu	+	+	+	
Zn	−	−	+	

Notes: Effects are based on a mixed model regression with sample site as a random effect. Plus and minus signs indicate the direction of significant effects ($P < 0.05$). Model coefficients of mechanistic relationships are found in Appendix S1: Table S1.

Brooks Range and lowest on the Coastal Plain (Table 3). Concentrations of Fe and Mn in forages were well above the dietary requirements estimated for lactating caribou (Table 3).

Discussion

This is the first study of the spatial distribution of mineral nutrients in relation to the requirements of an arctic herbivore. Our result supports that spatial and temporal distribution of Na, P, and Cu and respective interactions with K, Ca, and Zn are likely to influence patterns of movement and life histories of caribou in Alaska's arctic. Migrations of caribou to the Arctic Coastal Plain of Alaska may allow animals to replenish Na stores after foraging on mineral poor diets through the long arctic winters and offset the

Table 3. Observed concentrations (mg/kg dry mass) of minerals in forages used by caribou in arctic ecoregions of Alaska.

Mineral	Ecoregion	N	Range (mg/kg)	Requirement (mg/kg)	Adequate (%)	Adequate (days)
Ca	Brooks Range	125	530–21,609		40	149–269
	Arctic Foothills	320	752–37,798	4406	45	162–273
	Coastal Plain	225	740–36,400		54	173–272
P	Brooks Range	125	78–6904		9	149–175
	Arctic Foothills	320	135–6068	3567	7	149–176
	Coastal Plain	225	150–5498		9	157–219
Mg	Brooks Range	125	511–3930		96	149–273
	Arctic Foothills	320	310–7335	719	94	149–273
	Coastal Plain	225	332–4279		92	154–272
Na	Brooks Range	125	0–151		0	None
	Arctic Foothills	320	0–558	691	0	None
	Coastal Plain	225	3–1981		4	203–272
K	Brooks Range	125	2291–22,491		94	149–273
	Arctic Foothills	320	1133–20,470	3775	92	149–273
	Coastal Plain	225	2010–21,293		92	154–272
Fe	Brooks Range	125	39–365		100	149–273
	Arctic Foothills	320	14–1044	12.43	100	149–273
	Coastal Plain	225	36–2681		100	154–272
Mn	Brooks Range	125	104–3164		100	149–273
	Arctic Foothills	320	35–2775	5.56	100	149–273
	Coastal Plain	225	46–1821		100	154–272
Cu	Brooks Range	125	0–14		78	149–273
	Arctic Foothills	320	1–14	3.04	71	149–273
	Coastal Plain	225	1–12		85	154–272
Zn	Brooks Range	125	15–503		100	149–273
	Arctic Foothills	320	23–778	11.22	100	149–273
	Coastal Plain	225	30–945		100	154–272

Note: Dietary requirements for each mineral (Oster 2017) are listed with the proportion of samples above requirement (adequate) and the range of days where at least one sample exceeded the respective requirement. None indicates no days over the summer contained adequate Na concentrations.

Table 4. Availability ($\bar{X}$ ± standard deviation) of minerals in forages used by arctic caribou in Alaska at early and late season.

Mineral	Species	N	Early	N	Late	Comparison	
Ca	*Betula nana*	5	68 ± 10.4	5	35 ± 13.7	c	(−)
	Salix pulchra	6	86 ± 1.8	6	92 ± 1.1	b	(+)
	Salix. richardsonii	2	95 ± 1.6	4	94 ± 1.4	d	
	Pedicularis spp.	2	94 ± 3.1	0	–		
	Carex aquatilis	5	74 ± 7.7	7	83 ± 4.7	a	
	Carex bigalowii	4	65 ± 8.5	5	90 ± 2	a	(+)
	Eriophorum vaginatum	7	81 ± 6.1	8	87 ± 5.5	ab	(+)
P	*B. nana*	5	29 ± 9	5	29 ± 9.2	c	
	S. pulchra	6	41 ± 7.4	6	47 ± 4.5	d	
	S. richardsonii	2	60 ± 5.2	4	68 ± 2.1	b	
	Pedicularis spp.	2	64 ± 5.7	0	–		
	C. aquatilis	5	64 ± 8.5	7	55 ± 8.6	ab	
	C. bigalowii	4	62 ± 2.5	5	53 ± 3.5	ab	
	E. vaginatum	7	58 ± 9	8	50 ± 3.1	a	
Fe	*B. nana*	5	12 ± 8.9	5	7 ± 5.8	c	
	S. pulchra	6	44 ± 10.7	6	56 ± 9.4	b	
	S. richardsonii	2	45 ± 16.2	4	38 ± 8.1	ab	
	Pedicularis spp.	2	46 ± 4.7	0	–		
	C. aquatilis	5	39 ± 12.8	7	57 ± 10.8	ab	
	C. bigalowii	4	41 ± 10	5	54 ± 16.4	ab	
	E. vaginatum	7	41 ± 15.7	8	39 ± 5.4	a	
Zn	*B. nana*	5	90 ± 7.0	5	85 ± 6.2	a	
	S. pulchra	6	96 ± 1.3	6	96 ± 1.0	b	
	S. richardsonii	2	97 ± 0.3	4	95 ± 0.9	b	
	Pedicularis spp.	2	96 ± 1.5	0	–		
	C. aquatilis	5	86 ± 11.9	7	89 ± 4.4	a	
	C. bigalowii	4	86 ± 6.9	5	99 ± 1.1	ab	(+)
	E. vaginatum	7	98 ± 1.0	8	100 ± 0.5	c	

Notes: Letters represent significant pairwise differences between species within each mineral. Plus and minus signs indicate the direction of a significant difference between early and late season within species ($P < 0.05$). –, missing value for *Pedicularis* spp. due to inadequate samples.

high concentrations of K in emergent vegetation. Migrations of arctic caribou to the Coastal Plain also extend availability of adequate concentrations of P for 30–40 d over that which was available in the Brooks Range and Arctic Foothills (Table 3). Slow decomposition of organic matter in arctic soils releases humic acids that reduce soil pH (Deng and Dixon 2002). However, calcareous loess titrates acidity and raises soil pH over much of the Coastal Plain and through the Arctic Foothills across the CAH transect (Walker et al. 2001). Windblown loess maintains alkaline conditions in moist non-acidic tundra that has cascading effects on land cover composition, forage mineral composition and soil processes (e.g., thaw depth, cryoturbation; Gough et al. 2000, Hobbie and Gough 2002). Ice movement in soils (i.e., cryoturbation) brings minerals from lower soil horizons to the surface especially in moist non-acidic tundra but increased pH and Ca content of soils tends to reduce availability of P, Mg, Mn and Zn in soils (Bockheim et al. 1998). The strong role of soil pH and Ca was indicated by greater concentrations of Ca and Fe in forages, but lower concentrations of P and Mg on the CAH transect than the WAH transect (Tables 1, 2). Soil pH may also affect concentrations of Mn in forages, which declined from the Brooks Range to the Coastal Plain without an apparent relationship with soil Mn (Table 1; Doner and Grossl 2002). Conversely, soil Na and aerosolized Na from seawater probably influenced regional concentrations of Na in forage, which were only available in concentrations that were adequate for caribou on the Coastal Plain (Tables 1, 2).

Minerals phenologies that decline in plants as they mature are typically associated with plant proteins in photosynthetic parts while those that

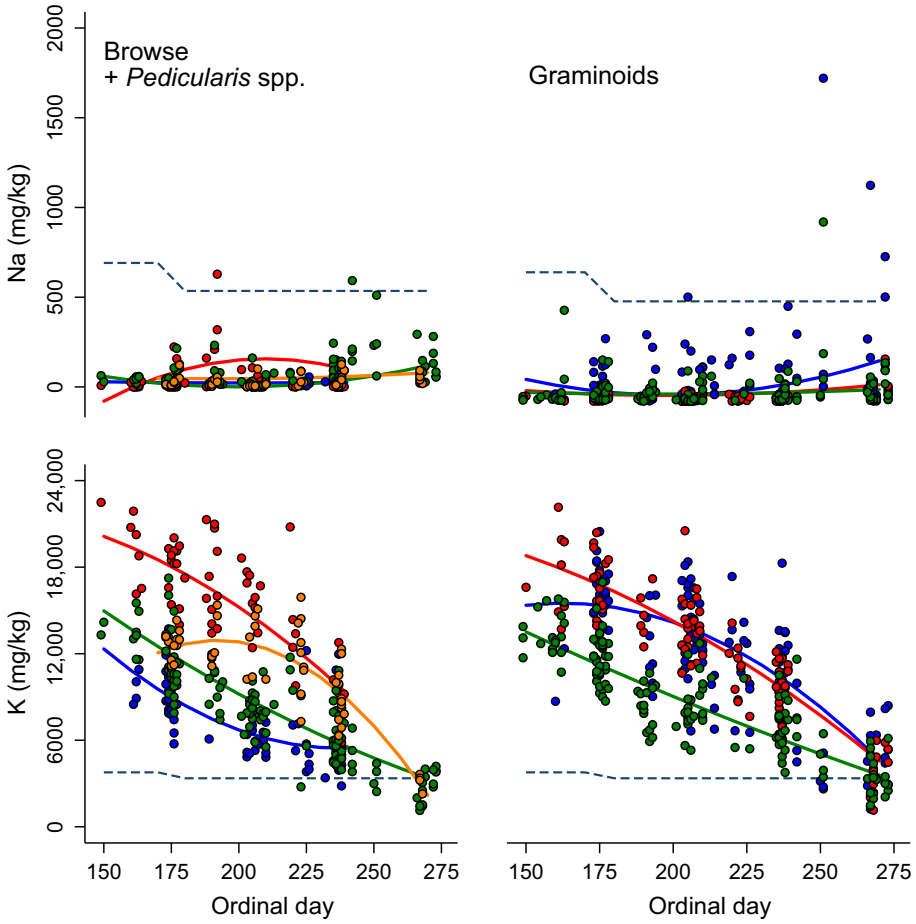

Fig. 3. Concentrations (mg/kg dry matter) of Na (top panels) and K (bottom panels) in forages used by arctic caribou in Alaska. Dashed lines represent estimated dietary requirements of lactating caribou. Browse (left panels): *Betula nana* (blue), *Salix pulchra* (green), *Salix richardsonii* (orange) and forb *Pedicularis* spp. (red). Graminoids (right panels): *Carex aquatilis* (blue), *Carex bigelowii* (red), and *Eriophorum vaginatum* (green).

increase with maturity are likely associated with fiber matrices. Concentrations of P, K, and Cu were positively associated with forage N (Table 2) and all declined from plant emergence to senescence (Figs. 2–4). However, the concentration of Ca, Mn, and Zn in forages increased over the season (Figs. 2, 4; Appendix S1: Fig. S1) but decreased with increasing concentrations of N and also fiber in plants (Table 2). This pattern implies that Ca, Mn, and Zn were not associated with either the fiber matrix of plant cell walls or the photosynthetic structures within cells but were probably incorporated in cuticular structures of the leaf (e.g., pubescence) or as a component of PSM (Garten 1978, De Silva et al. 1996, Millaleo et al. 2010) which is consistent with seasonal changes in cuticular waxes (Carnahan 2011) and plant toxins of arctic forages (Dormann 2003).

Contrasting phenologies of mineral availability indicated large imbalances in Ca, P, Zn, and Cu supplies. Browse and forb species provided the highest concentrations of P early in the season but declines in P concentration were accompanied by increasing concentrations of Ca as plants matured. Caribou are likely to tolerate Ca:P ratios as high at 7:1 as long as P is available in adequate concentrations but as P concentrations decline below marginal levels, increasing concentrations of Ca bind P to form insoluble complexes in the gut (Barboza et al. 2009, Suttle and Underwood 2010). Interactions of Ca and P have the potential

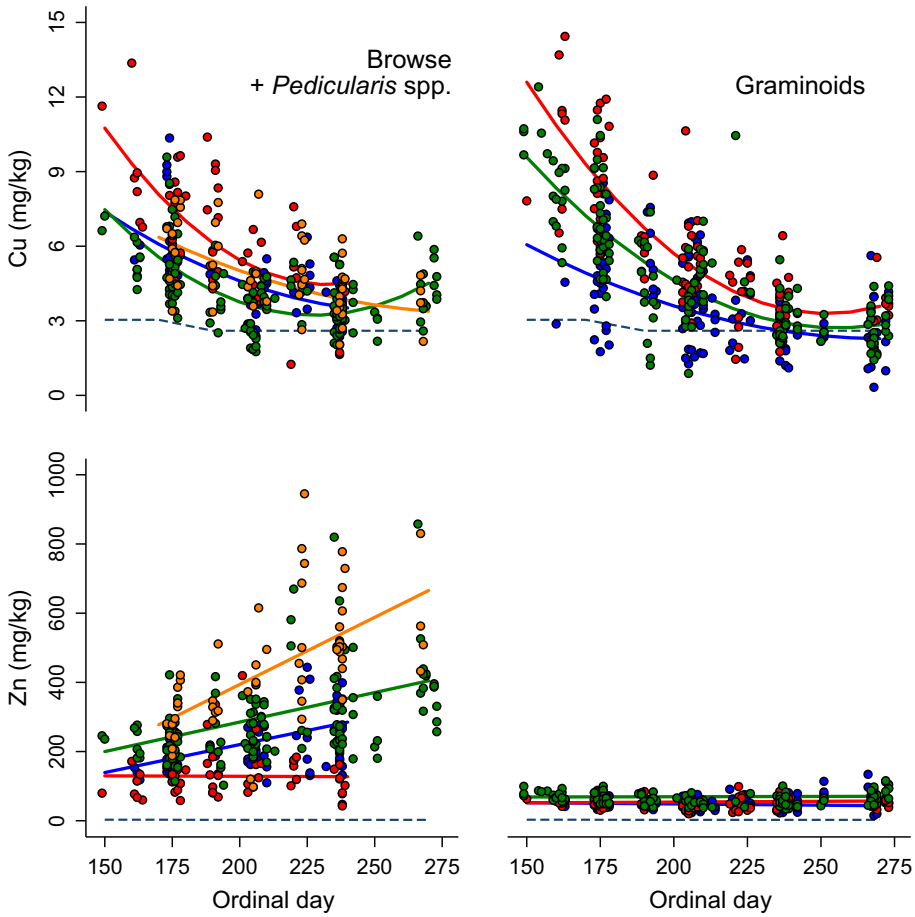

Fig. 4. Concentrations (mg/kg dry matter) of Cu (top panels) and Zn (bottom panels) in forages used by arctic caribou in Alaska. Dashed lines represent estimated dietary requirements of lactating caribou. Browse (left panels): *Betula nana* (blue), *Salix pulchra* (green), *Salix richardsonii* (orange), and forb *Pedicularis* spp. (red). Graminoids (right panels): *Carex aquatilis* (blue), *Carex bigelowii* (red), and *Eriophorum vaginatum* (green).

to influence mass gain and movement of lactating caribou and their calves because P concentrations declined below requirements in all forage species after emergence (Fig. 2; Suttle and Underwood 2010). Lower concentrations of P also coincided with higher Ca content and hence higher Ca:P ratios of forages on the CAH transect, which may affect reproductive success. In domesticated ruminants, P supplementation for animals on natural forages can have marked effects on food intake, feed efficiency, body condition, calving success, and calf survival (McDowell 2003). Barriers to movement of migratory ungulates in Africa may have resulted in limitations of forage P for wildebeest and have coincided with marked declines of wildebeest populations (Voeten et al. 2010). Therefore, unrestricted migration is likely integral to maintaining large population sizes of arctic caribou herds.

The tolerance of ungulates to high Zn concentrations late in the growing season is dependent on interactions of Zn with Cu, Mo, and S in forages. High concentrations of Zn in late season browse will compete with Cu for active sites on transport proteins (e.g., metallothionein). Therefore, browse may allow for mineral loading of Ca, P, Cu, and Zn early in the season but high concentrations of Ca and Zn in browse late in the season may limit absorption of low concentrations of Cu and P in senescing plants (Thompson and McCourt 1981). Caribou do not appear to be limited by spatial or temporal trends in forage

concentrations of Mg, Fe, or Mn in the WAH or CAH transects.

Development of geologic and oil resources in the arctic may impact the seasonal movements and nutritional qualities of forages near developments (Cameron et al. 2005, Johnson and St-Laurent 2011). Caribou of the CAH caribou herd show minimal disturbance from the Dalton Highway, which is geographically aligned (north–south) with their annual migration (Bergerud et al. 1984, Nicholson et al. 2016). Roads perpendicular to migration routes on the range of WAH caribou may have a greater effect on migration routes, thereby limiting foraging time on autumn ranges (Wilson et al. 2016). Road dust blown from trucks carrying mining ore have also been shown to contaminate vegetation concentrating potentially toxic levels of lead and zinc in downwind forages (Brumbaugh et al. 2011). However, windblown dust only has been detected on forages within 1.5 km from roads in Alaska's arctic, which is a small portion of the summer range (Walker and Everett 1987).

Concentrations of P on the Brooks Range and Arctic Foothills ecoregions were only adequate for 30–40 d from parturition, but the adequate period was extended on the Coastal Plain for 70 d from parturition. High concentrations of P and low concentrations of Ca early in the growing season could support bone deposition, which may be impaired late in the summer without supplemental P from geophagy or from consumption of cast antlers. Bone is probably mobilized to offset low concentrations of P from late season forages when antlers are mineralized at the start of rut (Baksi and Newbrey 1989, Baxter et al. 1999). Previous studies of P in white tailed deer (*Odocoileus virginianus*) and elk (*Cervus elaphus*) have hypothesized that large male ungulates, especially caribou, would be most susceptible to P limitation due to allometry of skeletal growth and because caribou have the largest antlers per body mass of any cervid (Grasman and Hellgren 1993). Female caribou must deposit P in both milk and antlers and are also likely to be susceptible to P limitations over non-antlered female cervids (Luick et al. 1974, Moen and Pastor 1998). However, up to 35% of calves are lost during summer after parturition (Cameron et al. 1993, Arthur and Del Vecchio 2009). Females that lose a calf early in the summer may be better able to replenish body stores and reproduce the following year while those that suckle a calf all summer may have reduced stores of protein and minerals such as Ca and P that could have carry-over effects (Cameron et al. 1993, Cameron 1994).

Arctic caribou probably emerge from winter with limited stores of Na that are further depleted by high concentrations of K in emergent vegetation (White et al. 1984; Fig. 3). Previous studies have reported similar limitations of Na for caribou in interior Alaska and Eurasia with adequate concentrations only found near the coast (Staaland and White 2001). Our data in Alaska support the same conclusions with one caveat: Adequate concentrations of Na are not available in any forage or ecoregion when the need for Na is greatest in late spring/early summer (Table 3). Even though high concentrations of Na are present in soil on the Coastal Plain (Table 1), forage concentrations are not adequate for caribou until mid-summer because plants appear to accumulate Na through the growing season (Fig. 3, Table 3). If forage concentrations of Na are inadequate when needs are greatest, caribou may need to utilize spring brine pools caused by freeze thaw cycles of permafrost or brackish water to meet Na requirements (Osterkamp and Romanovsky 1997). WAH caribou typically do not migrate as far into the Coastal Plain for calving and it is thus unclear what sources of Na are utilized for this herd. We were unable to collect sufficient soil samples from the Coastal Plain on WAH due to weather limitations, though WAH caribou may benefit from their association with the western coast of Alaska throughout their range. Mineral licks are used by migratory caribou but their use may be limited to only small portions of the migratory range (Calef and Lortie 1975). Calcareous and clay rich lick soils may have a role in binding plant secondary compounds in browse, especially as browse increases in the arctic with projected climate change (Euskirchen et al. 2009, Worker et al. 2015). Soils at lick sites also often contain high concentrations of Na (Calef and Lortie 1975, Ayotte et al. 2006). However, while resident populations of ungulates are often constrained by the availability of mineral licks, lick use by migratory ungulates is opportunistic and often only available to a small subset of those populations (Jones and Hanson 1985).

Cu may not limit lactating caribou in Arctic Alaska but could limit the survival of their calves late in the summer, when Zn concentrations are high in browse. Furthermore, caribou calves are born with stores of liver copper that are depleted through the lactation period because concentrations of Cu in milk are low (Luick et al. 1974, Knott et al. 2005). As the summer progresses, caribou calves gradually increase intakes of forages at a time when forage Cu concentrations are rapidly declining (Fig. 4). Limitations on late summer feeding due to early snow fall may limit uptake of Cu for calves and increase their vulnerability to winter (Hendrichsen and Tyler 2014).

Fire is implicated in movement of caribou during winter because lichens recover slowly from burning (Gustine et al. 2014). However, vascular plants that recover more quickly from fire can increase N content and biomass for grazers (Sensenig et al. 2010, Allred et al. 2011). Fires in tropical, subtropical and temperate regions are known to increase forage quality and thus influence movement of ungulates (Ralph 1982, McNaughton et al. 1988) but the effect of fire on quality of tundra forages and in turn arctic ungulates is not established. One of our sampling sites on the WAH transect burned early in the summer of 2013. Forages were sampled at an adjacent unburned site as well as from within the burned site for two summers. Concentrations of N, P, K, and Cu in forages were significantly greater on the burned site than the adjacent unburned site, which is consistent with the effect of fires on ungulate forages at lower latitudes (Carlson et al. 1993, Hanselka 2016). Although fires on the arctic tundra are rare, the frequency of burning is projected to increase with warming (Bret-Harte et al. 2013). The long-term effects of fire on the mineral and nutrient availability in arctic tundra have yet to be clearly established but fires likely benefit caribou foraging during summer even though they adversely affect their winter supplies of lichen (Joly et al. 2007*a*).

Climate change projections for Alaska predict continued expansion of shrubs into the Arctic which may reduce supplies of N for caribou (Tape et al. 2006, Thompson and Barboza 2014, Barboza et al. 2018). Increased temperatures and subsequent changes to permafrost, soil active layers, snow cover, hydrology, and soil mineralization rates all have the potential to alter the distribution and availability of minerals in arctic plants (Schmidt et al. 2002, Welker et al. 2005, Deslippe et al. 2012). Samples collected on the same CAH transect in 1977 were significantly greater in concentrations of Ca, P, Mg, Na, and K for *Carex aquatilis*, *Eriophorum vaginatum*, *Salix pulchra,* and *Pedicularis* spp. than those we collected (Whitten and Cameron 1980). However, the N concentrations of these forages were not significantly different between 1977 and 2011–2013 (Gustine et al. 2017*a*). The uniform positive bias observed for minerals indicates this comparison may be confounded by differences in analytical methods. Simulated changes to warming and precipitation increase the prevalence of the shrub *Betula nana,* which may also affect mineral availability for caribou because this species had the lowest availability of Ca, P, and Fe among the forages (Table 4; Euskirchen et al. 2009).

Migrations over latitudinal and elevational gradients can significantly extend windows of high nutrient quality for caribou that track phenological "green waves" (Merkle et al. 2016, Aikens et al. 2017). Further, micro-topography within the arctic (i.e., tundra polygons, pingos, anticlinals) produces gradients of snowmelt through the early summer by the variable accumulation and surface removal of windblown snow throughout the winter (Cooper et al. 2011). Areas that accumulate deeper snow thaw later and result in phenological micro-gradients which may further extend the availability of high-quality emergent vegetation for arctic caribou in summer (Nellemann and Thomsen 1994). However, nutrient phenologies are not synchronized in space and time. Caribou must therefore balance dietary supplies with body stores of minerals acquired through migratory movements.

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Literature Cited

Aikens, E. O., M. J. Kauffman, J. A. Merkle, S. P. Dwinnell, G. L. Fralick, and K. L. Monteith. 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. Ecology Letters 20:741–750.

Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65:502–513.

Allred, B. W., S. D. Fuhlendorf, D. M. Engle, and R. D. Elmore. 2011. Ungulate preference for burned patches reveals strength of fire-grazing interaction. Ecology and Evolution 1:132–144.

Arthur, S. M., and P. A. Del Vecchio. 2009. Effects of oil field development on calf production and survival in the Central Arctic herd. Alaska Department of Fish and Game. Federal Aid in WIldlife Restoration. Final Research Technical Report. Grants W-27-5 and W-33-1 through W-33-4. Project 3.46. Juneau, Alaska.

Ayotte, J. B., K. L. Parker, J. M. Arocena, and M. P. Gillingham. 2006. Chemical composition of lick soils: functions of soil ingestion by four ungulate species. Journal of Mammalogy 87:878–888.

Baksi, S. N., and J. W. Newbrey. 1989. Bone metabolism during antler growth in female reindeer. Calcified Tissue International 45:314–317.

Barboza, P. S., K. L. Parker, and I. D. Hume. 2009. Integrative wildlife nutrition. Springer - Verlag, Heidelberg, Germany.

Barboza, P. S., L. L. Van Someren, D. D. Gustine, and M. S. Bret-Harte. 2018. The nitrogen window for arctic herbivores: plant phenology and protein gain of migratory caribou (*Rangifer tarandus*). Ecosphere 9:e02073.

Baxter, B. J., R. N. Andrews, and G. K. Barrell. 1999. Bone turnover associated with antler growth in red deer (*Cervus elaphus*). Anatomical Record 256:14–19.

Bergerud, A. T., R. D. Jakimchuk, and D. R. Carruthers. 1984. The buffalo of the north: caribou (*Rangifer tarandus*) and human developments. Arctic 37: 7–22.

Bockheim, J. G., D. A. Walker, L. R. Everett, F. E. Nelson, and N. I. Shiklomanov. 1998. Soils and cryoturbation in moist nonacidic and acidic tundra in the Kuparuk River Basin, Arctic Alaska, USA. Arctic and Alpine Research 30:166–174.

Bret-Harte, M. S., M. C. Mack, G. R. Shaver, D. C. Huebner, M. Johnston, C. A. Mojica, C. Pizano, and J. A. Reiskind. 2013. The response of Arctic vegetation and soils following an unusually severe tundra fire. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 368:20120490.

Brumbaugh, W. G., S. A. Morman, and T. W. May. 2011. Concentrations and bioaccessibility of metals in vegetation and dust near a mining haul road, Cape Krusenstern National Monument, Alaska. Environmental Monitoring and Assessment 182: 325–340.

Calef, G. W., and G. M. Lortie. 1975. A mineral lick of the barren-ground caribou. Journal of Mammalogy 56:240–242.

Cameron, R. D. 1994. Reproductive pauses by female caribou. Journal of Mammalogy 75:10–13.

Cameron, R. D., W. T. Smith, S. G. Fancy, K. L. Gerhart, and R. G. White. 1993. Calving success of female caribou in relation to body weight. Canadian Journal of Zoology 71:480–486.

Cameron, R. D., W. T. Smith, R. G. White, and B. Griffith. 2005. Central arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. Arctic 58:1–9.

Carlson, P. C., G. W. Tanner, J. M. Wood, and S. R. Humphrey. 1993. Fire in key deer habitat improves browse, prevents succession, and preserves endemic herbs. Journal of Wildlife Management 57:914–928.

Carnahan, A. M. 2011. Determining the diets of moose (*Alces alces*) in Alaska using plant wax compounds. Thesis. University of Alaska Anchorage, Anchorage, Alaska, USA.

Cooper, E. J., S. Dullinger, and P. Semenchuk. 2011. Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. Plant Science 180:157–167.

Dau, J. R. 2015. Units 21D, 22A, 22B, 22C, 22D, 22E, 23, 24 and 26A. *In* P. Harper and L. A. McCarthy, editors. Caribou management report of survey and inventory activities 1 July 2012–30 June 2014. Alaska Department of Fish and Game, Juneau, Alaska, USA.

De Silva, D. L. R., A. M. Hetherington, and T. A. Mansfield. 1996. Where does all the calcium go? Evidence of an important regulatory role for trichomes in two calcicoles. Plant, Cell & Environment 19:880–886.

Deng, Y., and J. B. Dixon. 2002. Soil organic matter and organic-mineral interactions. *In* J. B. Dixon and D. G. Schulze, editors. Soil mineralogy with environmental applications. Soil Science Society of America, Madison, Wisconsin USA.

Deslippe, J. R., M. Hartmann, S. W. Simard, and W. W. Mohn. 2012. Long-term warming alters the composition of Arctic soil microbial communities. FEMS Microbiology Ecology 82:303–315.

Doner, H. E., and P. R. Grossl. 2002. Carbonates and evaporates. Pages 199–228 *in* J. B. Dixon and D. G. Schulze, editors. Soil mineralogy with environmental applications. Soil Science Society of America, Madison, Wisconsin, USA.

Dormann, C. F. 2003. Consequences of manipulations in carbon and nitrogen supply for concentration of anti-herbivore defence compounds in *Salix polaris*. Ecoscience 10:312–318.

Duncan, A. J., and D. P. Poppi. 2008. Nutritional ecology of grazing and browsing ruminants. Pages 89–116 *in* I. J. Gordon and H. H. T. Prins, editors. The ecology of browsing and grazing. Springer-Verlag, Heidelberg, Germany.

Euskirchen, E. S., A. D. McGuire, F. S. Chapin, S. Yi, and C. C. Thompson. 2009. Changes in vegetation in northern Alaska under scenarios of climate change, 2003–2100: implications for climate feedbacks. Ecological Applications 19:1022–1043.

Fancy, S. G., L. F. Pank, K. R. Whitten, and W. L. Regelin. 1989. Seasonal movements of caribou in arctic Alaska as determined by satellite. Canadian Journal of Zoology 67:644–650.

Frank, A., V. Galgan, and L. R. Petersson. 1994. Secondary copper deficiency, chromium deficiency and trace element imbalance in the moose (*Alces alces* L.): effect of anthropogenic activity. Ambio 23:315–317.

Frank, D. A., S. J. McNaughton, and B. F. Tracy. 1998. The ecology of the earth's grazing ecosystems. BioScience 48:513–521.

Fullman, T. J., K. Joly, and A. Ackerman. 2017. Effects of environmental features and sport hunting on caribou migration in northwestern Alaska. Movement Ecology 5:4.

Fynn, R. W. S. 2012. Functional resource heterogeneity increases livestock and rangeland productivity. Rangeland Ecology & Management 65:319–329.

Garten, C. T. 1978. Multivariate perspectives on the ecology of plant mineral element composition. American Naturalist 112:533–544.

Gough, L., G. R. Shaver, J. Carroll, D. L. Royer, and J. A. Laundre. 2000. Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. Journal of Ecology 88:54–66.

Grasman, B. T., and E. C. Hellgren. 1993. Phosphorus nutrition in white-tailed deer: nutrient balance, physiological responses, and antler growth. Ecology 74:2279–2296.

Gustine, D., P. Barboza, L. Adams, B. Griffith, R. Cameron, and K. Whitten. 2017*a*. Advancing the match-mismatch framework for large herbivores in the Arctic: evaluating the evidence for a trophic mismatch in caribou. PLoS ONE 12:e0171807.

Gustine, D. D., P. S. Barboza, R. D. Shively, L. L. V. Someren, and K. W. Oster. 2017*b*. Caribou forage data, Central and Western Arctic, 2011-2014. U.S. Geological Survey data release: https://doi.org/10.5066/f7jq106w. U.S. Department of Interior, Alaska Science Center U.S. Geological Survey, Anchorage, Alaska, USA.

Gustine, D. D., P. S. Barboza, J. P. Lawler, L. G. Adams, K. L. Parker, S. M. Arthur, and B. S. Shults. 2012. Diversity of nitrogen isotopes and protein status in caribou: implications for monitoring northern ungulates. Journal of Mammalogy 93:778–790.

Gustine, D. D., T. Brinkman, M. Lindgren, J. L. Schmidt, T. S. Rupp, and L. G. Adams. 2014. Climate-driven effects of fire on winter habitat for caribou in the Alaskan-Yukon Arctic. PLoS ONE 9:e100588.

Hanselka, C. W. 2016. Forage quality of common buffelgrass as influenced by prescribed fire. Texas Journal of Agriculture and Natural Resources 3: 15–18.

Hendrichsen, D. K., and N. J. C. Tyler. 2014. How the timing of weather events influences early development in a large mammal. Ecology 95:1737–1745.

Hobbie, S. E., and L. Gough. 2002. Foliar and soil nutrients in tundra on glacial landscapes of contrasting ages in northern Alaska. Oecologia 131: 453–462.

Hopcraft, J. G., H. Olff, and A. R. Sinclair. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends in Ecology & Evolution 25:119–128.

Ihl, C., and D. R. Klein. 2001. Habitat and diet selection by muskoxen and reindeer in western Alaska. Journal of Wildlife Management 65:964–972.

Johnson, C. J., and M.-H. St-Laurent. 2011. Unifying framework for understanding impacts of human developments on wildlife. Pages 27–54 *in* D. E. Naugle, editor. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C., USA.

Joly, K., P. Bente, and J. Dau. 2007*a*. Response of overwintering caribou to burned habitat in northwest Alaska. Arctic 60:401–410.

Joly, K., M. J. Cole, and R. R. Jandt. 2007*b*. Diets of overwintering caribou, *Rangifer tarandus*, track

decadal changes in Arctic tundra vegetation. Canadian Field-Naturalist 121:379–383.

Jones, R. L., and H. C. Hanson. 1985. Mineral licks, geophagy, and biogeochemistry of North American ungulates. Iowa State University Press, Iowa City, Iowa, USA.

Jorgenson, J. C., M. S. Udevitz, and N. A. Felix. 2002. Forage quantity and quality. Pages 46–50 *in* D. C. Douglas, P. E. Reynolds, and E. B. Rhode, editors. Arctic refuge coastal plain terrestrial wildlife research summaries. Biological Resources Division, U.S. Geological Survey, Reston, Virginia, USA.

Knott, K. K., P. S. Barboza, and R. T. Bowyer. 2005. Growth in arctic ungulates: postnatal development and organ maturation in *Rangifer tarandus* and *Ovibos moschatus*. Journal of Mammalogy 86:121–130.

Lenart, B. 2016. Central arctic caribou decline may result in stricter hunting regulations. Page 1 *in* S. Cotten, editor. Alaska Department of Fish and Game, Juneau, Alaska, USA.

Lendrum, P. E., C. R. Anderson, K. L. Monteith, J. A. Jenks, and R. T. Bowyer. 2014. Relating the movement of a rapidly migrating ungulate to spatiotemporal patterns of forage quality. Mammalian Biology – Zeitschrift für Säugetierkunde 79:369–375.

Luick, J. R., R. G. White, A. M. Gau, and R. Jenness. 1974. Compositional changes in the milk secreted by grazing reindeer I. Gross composition and ash. Journal of Dairy Science 57:1325–1333.

McDowell, L. R. 2003. Minerals in animal and human nutrition. Second edition. Elsevier, Philadelphia, Pennsylvania, USA.

McNaughton, S. J. 1988. Mineral nutrition and spatial concentrations of African ungulates. Nature 334: 343–345.

McNaughton, S. J., R. W. Ruess, and S. W. Seagle. 1988. Large mammals and process dynamics in African ecosystems. BioScience 38:794–800.

Merkle, J. A., K. L. Monteith, E. O. Aikens, M. M. Hayes, K. R. Hersey, A. D. Middleton, B. A. Oates, H. Sawyer, B. M. Scurlock, and M. J. Kauffman. 2016. Large herbivores surf waves of green-up during spring. Proceedings of the Royal Society of London. Series B: Biological Sciences 283:20160456.

Middleton, A. D., M. J. Kauffman, D. E. McWhirter, J. G. Cook, R. C. Cook, A. A. Nelson, M. D. Jimenez, and R. W. Klaver. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology 94: 1245–1256.

Millaleo, R., M. Reyes-Díaz, A. Ivanov, M. Mora, and M. Alberdi. 2010. Manganese as essential and toxic element for plants: transport, accumulation and resistance mechanisms. Journal of Soil Science and Plant Nutrition 10:470–481.

Mitchell, M. N. 2012. Interpreting and visualizing regression models using Stata. First edition. Stata Press, College Station, Texas, USA.

Moen, R., and J. Pastor. 1998. Simulating antler growth and energy, nitrogen, calcium and phosphorus metabolism in caribou. Rangifer 18:85–97.

Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2:1–34.

Mysterud, A., R. Langvatn, N. G. Yoccoz, and N. Chr. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. Journal of Animal Ecology 70:915–923.

Nellemann, C., and M. G. Thomsen. 1994. Terrain ruggedness and caribou forage availability during snowmelt on the Arctic Coastal Plain, Alaska. Arctic 47:361–367.

Nicholson, K. L., S. M. Arthur, J. S. Horne, E. O. Garton, and P. A. Del Vecchio. 2016. Modeling caribou movements: seasonal ranges and migration routes of the Central Arctic Herd. PLoS ONE 11:e0150333.

Oster, K. W. 2017. A spatial and phenological perspective of forage minerals for arctic caribou. Thesis. Texas A&M, College Station, Texas, USA.

Osterkamp, T., and V. Romanovsky. 1997. Freezing of the active layer on the coastal plain of the Alaskan Arctic. Permafrost and Periglacial Processes 8:23–44.

Pretorius, Y., et al. 2011. Soil nutrient status determines how elephant utilize trees and shape environments. Journal of Animal Ecology 80:875–883.

Rabe-Hesketh, S., and A. Skrondal. 2010. Multilevel and longitudinal modeling using Stata. Third edition. Stata Press Publication, College Station, Texas, USA.

Ralph, E. J. B. 1982. Fire and nutrient cycling in temperate ecosystems. BioScience 32:187–192.

Schmidt, I. K., S. Jonasson, G. Shaver, A. Michelsen, and A. Nordin. 2002. Mineralization and distribution of nutrients in plants and microbes in four arctic ecosystems: responses to warming. Plant and Soil 242:93–106.

Sensenig, R. L., M. W. Demment, and E. A. Laca. 2010. Allometric scaling predicts preferences for burned patches in a guild of East African grazers. Ecology 91:2898–2907.

Skarpe, C., and A. J. Hester. 2008. Plant traits, browsing and grazing herbivores, and vegetation dynamics. Pages 217–261 *in* I. J. Gordon and H. H. Prins, editors. The ecology of browsing and grazing. Springer, Heidelberg, Germany.

Slabach, B. L., T. B. Corey, J. R. Aprille, P. T. Starks, and B. Dane. 2015. Geophagic behavior in the mountain

goat (Oreamnosamericanus): support for meeting metabolic demands. Canadian Journal of Zoology 93:599–604.

Staaland, H., K. Hove, and R. G. White. 1986. Mineral absorption in relation to nutritional ecology of reindeer. Rangifer 6:279–287.

Staaland, H., and R. G. White. 2001. Regional variation in mineral contents of plants and its significance for migration by arctic reindeer and caribou. Alces 37:497–509.

Suttle, N. F. 1991. The interactions between copper, molybdenum, and sulphur in ruminant nutrition. Annual Review of Nutrition 11:121–140.

Suttle, N. F., and E. J. Underwood. 2010. Mineral nutrition of livestock. Fourth edition. CABI, Wallingford, Oxfordshire, UK.

Tape, K. E. N., M. Sturm, and C. Racine. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Global Change Biology 12:686–702.

Thompson, D. P., and P. S. Barboza. 2014. Nutritional implications of increased shrub cover for caribou (*Rangifer tarandus*) in the Arctic. Canadian Journal of Zoology 92:339–351.

Thompson, D. C., and K. H. McCourt. 1981. Seasonal diets of the Porcupine Caribou herd. American Midland Naturalist 105:70–76.

VanSomeren, L. L. 2014. Monitoring energy and nitrogen availability for Arctic caribou (*Rangifer tarandus*). Thesis. University of Alaska Fairbanks, Fairbanks, Alaska, USA.

Voeten, M. M., C. A. Van De Vijver, H. Olff, and F. Van Langevelde. 2010. Possible causes of decreasing migratory ungulate populations in an East African savannah after restrictions in their seasonal movements. African Journal of Ecology 48:169–179.

Walker, D., J. Bockheim, F. Chapin Iii, W. Eugster, F. Nelson, and C. Ping. 2001. Calcium-rich tundra, wildlife, and the "Mammoth Steppe". Quaternary Science Reviews 20:149–163.

Walker, D. A., and K. R. Everett. 1987. Road dust and its environmental impact on Alaskan taiga and tundra. Arctic and Alpine Research 19:479–489.

Welker, J., J. Fahnestock, P. Sullivan, and R. Chimner. 2005. Leaf mineral nutrition of Arctic plants in response to warming and deeper snow in northern Alaska. Oikos 109:167–177.

White, R., E. Jacobsen, and H. Staaland. 1984. Secretion and absorption of nutrients in the alimentary tract of reindeer fed lichens or concentrates during the winter. Canadian Journal of Zoology 62: 2364–2376.

White, R. G., and J. Trudell. 1980. Habitat preference and forage consumption by reindeer and caribou near Atkasook, Alaska. Arctic and Alpine Research 12:511–529.

Whitten, K. R., and R. D. Cameron. 1980. Nutrient dynamics of caribou forage on Alaska's arctic slope. Pages 159–166 *in* E. Reimers, E. Gaare, and S. Skjenneberg, editors. Proceedings of the Second International Reindeer/Caribou Symposium, 17–21 Sept 1979. Direktoratet for vilt og ferskvannsfisk, Trondheim, Norway.

Wilson, R. R., L. S. Parrett, K. Joly, and J. R. Dau. 2016. Effects of roads on individual caribou movements during migration. Biological Conservation 195:2–8.

Worker, S. B., K. Kielland, and P. S. Barboza. 2015. Effects of geophagy on food intake, body mass, and nutrient dynamics of snowshoe hares (*Lepus americanus*). Canadian Journal of Zoology 93: 323–329.

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