A SPATIAL AND PHENOLOGICAL PERSPECTIVE OF FORAGE MINERALS FOR

ARCTIC CARIBOU

A Thesis

by

KEITH WESTLEY OSTER

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Chair of Committee,	Perry S. Barboza
Committee Members,	David D. Gustine
	Fred E. Smeins
	Jason B. West
Head of Department,	Michael P. Masser

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ABSTRACT

The central question of this thesis is to assess whether concentrations of mineral nutrients in Alaskan tundra vegetation have the potential to influence patterns of movement and productivity of arctic caribou (*Rangifer tarandus*). Chapter II proposes a method for the estimation of mineral requirements of wild ungulates using caribou as an example. This method incorporates observed rates of food intake, mass change, antlergenesis, lactation and milk mineral composition of *Rangifer* over the summer season, which were then applied to relationships for maintenance and growth requirements of domestic animals. For each mineral, we averaged the requirements from domestic species projections to arrive at a consensus of caribou mineral requirements. Chapter III describes the spatial and phenological trends of 9 mineral nutrients in known caribou forages with interpretations of those trends in relation to the requirements derived in Chapter II.

Requirements of Ca, P, Mg, Na and K declined from parturition as dietary intake increased over the summer. Conversely, requirements of Fe, Mn, Cu, and Zn increased over the summer season due to their greater association to lean mass gain. From Chapter III, Caribou are unlikely to be affected by spatial to temporal trends of Mg, Fe or Mn. Na was the most limiting nutrient on the landscape for caribou which was exacerbated by high concentrations of K in emergent vegetation. Soil pH was heavily influenced by concentrations of Ca in soils in the range of the Central Arctic caribou herd, which in turn limited availability of P in caribou forages and resulted in higher Ca:P ratios on that transect. Copper alone was not limiting to arctic caribou in our study. However, increasing concentrations of Zn in forages over the summer are likely to limit the availability of marginal Cu concentrations as the summer progresses. Overall, this work shows that arctic caribou are extremely limited in the availability

of Na on the landscape, and have short windows of opportunity to gain adequate concentrations of P and Cu to survive the long arctic winter. These limitations have the potential to influence movement patterns and productivity of arctic caribou in Alaska.

DEDICATION

To my parents, Eric and Dana, my siblings Rachel and Eric, and to my loyal mutt

Tucker for his constant encouragement to get up from my desk.

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Contributors

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The data analyzed for Chapter II was provided by Professor Perry S. Barboza. The laboratory analyses which supported Chapter III were conducted in part by Rachel S. Shively of the Department of Wildlife and Fisheries Sciences. Kyle Joly from the National Park Service played an instrumental role designing and securing funding work which was conducted in the western arctic of Alaska. Data on nitrogen and fiber concentrations of forages used in Chapter III was compiled and analyzed by Lindsay VanSomeren as part of her masters thesis.

All other work conducted for the thesis was completed by the student independently.

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CHAPTER I

INTRODUCTION

Arctic populations of caribou fluctuate widely in both numbers and distribution for reasons that have yet to be fully elucidated. For example, the western arctic caribou herd in Alaska has increased from roughly 5000 individuals in the early 1970's to become the largest herd in Alaska at an estimated 490,000 individuals by 2003. Since 2003 the herd has subsequently declined to 220,000 individuals (Harper 2015). Large caribou herds tend to overwhelm the ability of predators to significantly impact population levels in positive growth phases but can have an significant effect during negative phases and at low population densities (Haskell and Ballard 2007). Population trends of arctic caribou in Alaska have been correlated with multi-decadal time scale weather patterns (e.g. Pacific Decadal Oscillation, Arctic Oscillation) (Joly et al. 2011). Ocean oscillations likely affect caribou habitat in Alaska's arctic by limiting access to winter forages through increased snowfall or icing events, or on summer habitat by impacting the productivity and community composition of summer forages, which indicates a bottom up regulation of caribou populations.

Diets of caribou in Alaska change drastically over the course of the year such that winter diets of caribou are comprised primarily of lichens and senescent vegetation while summer diets are comprised of growing vegetation (Thompson and McCourt 1981, Klein 1990). Winter diets typically persist from September to May and are generally high in digestible energy but contain marginal concentrations of protein and most mineral nutrients. Conversely, in the short summer caribou utilize a broad swath of high quality vegetation including graminoids, woody browse, and forbs over the summer (White and Trudell 1980, Trudell and White 1981).

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Winter limitations of nutrients are mitigated by changing activity and metabolism to conserve stores of energy and nutrients that were deposited over the summer (Staaland et al. 1986a). Minerals are stored throughout the body in bones, tissues and recyclable body pools (e.g. P in salivary pools, Na in ruminal pools) (Suttle and Underwood 2010). Animals with inadequate stores of protein, energy and minerals at the start of winter risk reproductive failure or ultimately death (Adams and Dale 1998).

Movements and distributions of wildebeest in Africa have been correlated with patterns of rainfall and phosphorus (P) while sodium (Na) influences the aggregation and number of North American ungulates (Jones and Hanson 1985, McNaughton et al. 1988, McNaughton 1990). Further, wildebeest in Africa have experienced P limitation and reduced population sizes due to human caused barriers of traditional migration routes (Voeten et al. 2010, Morrison et al. 2016). Previous studies on the distributions of minerals available to Eurasian caribou have implicated Na as a potential driver of migration but relationships of caribou populations to the availability of minerals on the landscape have yet to be fully investigated in Alaska (Staaland and White 2001). Caribou in Alaska have the longest migrations of any land mammal and may be similarly influenced by distribution of mineral nutrients in forages as are Eurasian caribou and tropical ungulates (Fancy et al. 1989a).

Although mineral availabilities have been correlated with movement and with productivity of ungulates, these relationships assume requirements that have not been quantified for most wild species (Jones and Hanson 1985, Robbins 1993). However the mineral requirements of domestic ungulates have been clearly defined, especially in North America (NRC 2000, 2007a, b, 2016). The estimation of mineral requirements of ungulates typically requires intensive measures of diet quality in a captive setting that may not be feasible for wild

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species. For this reason it is currently impossible to assess the impact of changing availabilities of minerals on the ecology and management of wild ungulates such as caribou.

In Chapter 2 we propose a method of estimating the mineral requirements of 9 minerals for lactating caribou over the summer. We apply observed intakes, mass gain, lactation rates and milk mineral content of Alaskan caribou to factorial relationships of domestic species to reach a consensus of mineral requirements of caribou. The resulting 5 projections of mineral requirements were averaged over early and late lactation periods over the summer. In chapter 3 we describe the phenology of the same 9 minerals over the summer growing season on transects bisecting the Western Arctic and Central Arctic Caribou herds. Each transect traverses a north-south gradient along known migration corridors. Spatial and temporal distributions of minerals are then interpreted in relation to mineral requirements estimated in Chapter 2 in order to assess how minerals may affect the productivity and movements of arctic caribou in Alaska.

CHAPTER II

MINERAL REQUIREMENTS OF ARCTIC CARIBOU

Introduction

All animals require up to 29 mineral nutrients to support proper physiological function of the body (McDowell 2003). Ungulates that depend on fermentation to aid in digestion must also maintain concentrations of dietary minerals to support function of microbial communities for the optimal incorporation of food nutrients into bodily tissues (Suttle and Underwood 2010). The availability of mineral nutrients to ungulates on rangelands can vary widely with changes in temperature, hydrology, soil type, plant community, and with phenological changes of plants within seasons (Spears 1994). Patterns of movement and production in wild ungulates may be effected by variation in the availability of mineral nutrients in forages. Variation in rainfall amounts and plant phosphorus are correlated with migrations of wildebeest (*Connochaetes taurinus*) in Africa (McNaughton 1988a), while variation in sodium may drive regional movements of Eurasian reindeer (*Rangifer tarandus*) and North American ungulates (Jones and Hanson 1985, Staaland and White 2001). Changes in precipitation may alter the chemical form of mineral nutrients thereby making minerals unavailable for uptake by forage plants and herbivores (Mincher et al. 2007). Furthermore, changing climatic patterns can alter the productivity and community composition of forage plants which may affect the availability of mineral nutrients on the landscape for wild ungulates (Jeffries et al. 1992).

Many wild ungulates are able to compensate for shortages in available minerals or periods of high mineral nutrient demand through migration (McNaughton 1990), mobilization of stored minerals in body tissues (Baksi and Newbrey 1989) and by physiological adaptations for retaining minerals in the body (Hellgren and Pitts 1997). Female caribou in North America

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migrate over 5000 km each year to complete an annual cycle that begins with the spring migration to calving grounds on the arctic coastal plain following phenological trends of emergent vegetation (Fancy et al. 1989a, Gustine et al. 2017). Caribou rely upon the highly productive arctic growing season to replenish nutrient stores lost during the preceding winter and to support the high costs of lactation and body mass gain over the summer (Gerhart et al. 1996). Females that fail to store adequate nutrients during the summer are not likely to breed in the following year and may be vulnerable to winter mortality (Adams and Dale 1998). The mineral status of caribou at the end of the summer is dependent on the timing of mineral availability on the landscape, timing of nutrient requirements over the summer and the ability of caribou to store mineral nutrients.

Although mineral availabilities have been correlated with movement and with productivity of ungulates, these relationships assume requirements that have not been quantified for most wild species (Jones and Hanson 1985, Robbins 1993). Consequently, we are unable to assess the effects of changing mineral availabilities on rangelands for wild ungulates. The estimation of mineral requirements requires extensive measures of changing body stores with corresponding measures of food supply that are rarely feasible for wildlife (Barboza et al. 2009). Requirements for most mineral nutrients have been established for domestic ungulates to sustain productivity across a wide range of environments and food supplies, especially those in North American rangelands.

We used a factorial approach to derive mineral requirements of lactating female caribou from measures of intake and body mass change of captive caribou and published requirements for domestic ungulates (Fig. 2.1). Factorial estimates combine requirements for maintenance (i.e. survival) and production (i.e. body mass gain and reproduction). Models of nutrient requirements in wild ungulates traditionally focus on requirements of protein and energy by using a census of

literature on specific guilds of ruminants (Dryden 2011), functional relationships between net primary production, body size and population size (Coughenour 1993), or by incorporating data on wild ungulates with factorial requirements of domestic ruminants (Hackmann 2011). Our model is the first to estimate minerals requirements by incorporating seasonal patterns of food intake and body mass gain of a wild ungulate with factorial estimates of mineral requirements in domestic species. This framework can assist range managers in assessing the effects of changing forage resources and environmental demands on movement and production of wild ungulates on rangelands.

Methods

Daily dry matter intake (DMI) and body mass (BM) were predicted as a function of average daily air temperature and the number of days from calving (Barboza 2015) for wild caught, captive caribou in Fairbanks, Alaska (65°N 146°W). This model was derived from individual measures of food intake and body mass of 10 parturient caribou consuming rations formulated to mimic the low energy density of sedges (digestible energy content 10.8 kJ $\cdot$ g^{-1} of dry mass). We simulated food intake and body mass of female caribou in Alaska from parturition in spring to the start of the mating season in early fall (120 d). Air temperature (T) was simulated from day of parturition (B) as:

$$T = (0.1680286 \cdot B) + (-0.0005179 \cdot B^2) + (-8.24 \cdot 10^{-6} \cdot B^3) + (10.16155). \qquad (1)$$

Mass specific intakes of dry food (DMI g $\cdot$ kg$^{-0.75}$ $\cdot$ d^{-1}) were calculated as follows:

$$DMI = (5.576509 \cdot B) + (-0.0726042 \cdot B2) + (0.0002894 \cdot B3)$$
$$+ (-2.692504 \cdot T) + (124.7071). \qquad (2)$$

Body mass (BM kg) was calculated from day of parturition as:

$$BM = (-0.1181081 \cdot B) + (0.0019413 \cdot B2) + 92.07143. \qquad (3)$$

Food intake was calculated from DMI and BM on a daily time step. Mass change was calculated at a daily time step from the simulated body mass. Milk yield (MY) was derived from the curve of Parker et al. (1990) to achieve a peak yield of 1.9 kg/d at 30 days from birth by the following expression in SigmaPlot (version 12.0; Systat Software Inc., San Jose CA):

$$MY = 1.1081 + 27.2543 \bullet \frac{e^{-0.5 \bullet \left(\frac{\ln\left(\frac{B}{37.7865} \right)}{0.4872} \right)}}{B} \qquad (4)$$

We used a factorial approach to calculate total intake of minerals required to meet demands for maintenance as well as body mass change, lactation and antler deposition (Fig. 2.1). Mineral requirements of caribou were simulated with relationships that were derived for goats (*Capra aegagrus hircus*), sheep (*Ovis aries*), dairy cattle (*Bos taurus*), beef cattle (*Bos taurus*) and horses (*Equus ferus caballus*) at maintenance and in production for Ca, P, Mg, Na, K, Mn, Fe, Cu and Zn (Tables 2.1 and 2.2) (NRC 2000, 2007b, a, 2016). Factorial requirements for the amount of mineral needed as a function of body mass were not available for all minerals and for all domestic species. We only used factorial data for estimating the requirements of caribou because the fixed estimates of dietary concentration are set to include safe and adequate levels for maintenance, all stages of production and were well above the factorial estimates of total daily mineral requirements (NRC 2007b).

Published requirements of minerals for maintenance were based on food intake (dry matter basis), and body mass (Tables 2.1 and 2.2). Model caribou were 92 kg at parturition and 106 kg at the end of lactation (Fig. 2.2). Model caribou increased food intakes over the first 50 d from parturition. High air temperatures coincide with a plateau of intake in mid lactation, which is followed by another increase in food intake from 90 to 120 days from parturition (Fig. 2.2). Daily mass change of model caribou increased in a linear fashion from -116 to +346 g $\bullet$ d^{-1} through the summer. Factorial requirements of minerals for body mass change were based on

daily body mass and change in mass (i.e. live weight gain) in relation to a target mass (i.e. mature mass) (Tables 2.1 and 2.2). We assumed that estimates of mineral requirements for growth were applicable to both body mass loss and body mass gain of adult female caribou. Minerals released from mobilization of body mass were therefore completely used for mineral demands that in turn reduced the mineral demand from the diet. We used mineral concentration of reindeer milk to estimate requirements for lactation in all model projections as a product of the caribou milk yield curve (Fig. 2.2) (Luick et al. 1974).

We calculated the deposition of dry antler at a linear rate from day of calving to a final antler mass of 375 g, which was 0.34% of the maximum body mass (110 kg) attained in December (Thomas and Barry 2005). Dry antler composition was calculated as containing 70% ash when combusted at 500 °C for 4 hours (P.S. Barboza, unpublished data). Antler ash was then assumed to be composed of pure hydroxyapatite with hydrogen and oxygen components volatilized during combustion (68% Ca, 32% P) (Windholz et al. 1976). Requirements for maintenance, growth, lactation and antler growth were summed and divided by an absorption coefficient (AC) for each projection to determine the daily requirement of dietary minerals. Daily requirements were divided by the daily food intake to project the minimum concentration of minerals in the diet (mg • kg^{-1} dry mass) required to achieve zero balance (Fig. 2.1). Early lactation requirements in caribou were calculated as the mean of all projections from 1−28 d of lactation while late lactation requirements were calculated from 29−120 d of lactation. We used ordinary least squares regression of minimum dietary mineral concentration (Y) against time from birth (X) to describe the dietary requirement of each mineral for caribou as a cubic polynomial function (STATA version 14.1; Stata Corp., College Station TX).

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Results

Calcium, Phosphorus and Magnesium

Projections of daily requirements of dietary Ca at maintenance increased over the summer and ranged from 4.2–10.8 g Ca • d^{-1}. Lactation demands for dietary Ca added 7.1–20.4 g • d^{-1} to daily mineral demands. Mobilization of Ca from body tissue in early lactation reduced dietary demand by 1.9 g • d^{-1} whereas 11.5 g • d^{-1} was needed from the diet to deposit Ca in tissue at the end of summer. Daily requirements of Ca for antlergenesis were constant over time and ranged from 2.98–3.5 g Ca • d^{-1} among domestic species projections. Total daily requirements for dietary Ca increased throughout the summer and were lowest for projections from the sheep model (12.7–24.5 g Ca • d^{-1}) and highest for projections from the dairy cattle model (16.1–32.4 g Ca • d^{-1}). Our estimate of minimum dietary Ca concentration decreased from days 1–80 (4694 to 3917 mg Ca • kg^{-1}) as intakes increased (Table 2.3). Increases in the minimum concentration of dietary Ca during late lactation were associated with demands for mass gain (Fig. 2.3). Consequently, estimates of minimum dietary concentration of Ca were not significantly different between early and late lactation windows (Table 2.4).

Projections of daily dietary requirements of P for maintenance increased over the summer and ranged from 4.2 to 13.4 g P • d^{-1}. Projected dietary requirements of P for lactation in addition to maintenance ranged from 4.4–14.8 g P • d^{-1}. Mobilization of P from body tissue reduced dietary demand by 0.9 g P • d^{-1} during early lactation while 7.9 g • d^{-1} of dietary P was required to support tissue gain at the end of summer. Daily P requirements for antlergenesis ranged from 1.1–2.0 g P • d^{-1} among domestic species models. Total daily requirements of dietary P increased through the summer and were lowest in projections of the goat model (9.3–19.0 g P • d^{-1}) and greatest in projections of the horse model (17.0–27.0 g P • d^{-1}). Estimates of minimum dietary concentration required to achieve zero balance in caribou decreased from days

1 - 95 (3721–3119 mg P • kg $^{-1}$) as intakes increased (Table 2.3). Increases in dietary concentration after day 95 were associated with demands of mass gain (Fig. 2.3). As a result, required dietary concentrations of P were not significantly different between early and late lactation (Table 2.4).

Daily requirements of dietary Mg for maintenance increased over the summer and ranged from 1.6 g–3.2 g Mg • d^{-1}. Minimum and maximum projections for lactation in addition to maintenance ranged from 0.4–2.3 g Mg • d^{-1}. Tissue mobilization at the start of lactation reduced dietary demands of Mg by 0.3 g • d^{-1} while mass gain at the end of the summer increased requirements by 1.0 g Mg • d^{-1}. Absolute daily dietary requirements of Mg increased throughout the summer and were lowest in projections of the beef cattle model (2.4–3.4 g Mg • d^{-1}) and highest in projection of the horse model (3.0–4.5 g Mg • d^{-1}). Our estimates of minimum dietary concentration of Mg decreased from days 1 - 60 (819–537 mg Mg • kg $^{-1}$) and remained at 537 to 554 mg Mg • kg $^{-1}$ (Fig. 2.3, Table 2.3). Consequently, required dietary concentrations of Mg were significantly greater in early lactation than in late lactation (Table 2.4).

Sodium and Potassium

Daily requirements of Na for maintenance increased over the summer from 0.7 to 4.5 g Na • d^{-1}. Lactation increased demands for dietary Na by 0.7–1.4 g • d^{-1}. Mass loss reduced the dietary demand of Na by 0.2 g • d^{-1} at the start of lactation whereas mass gain at the end of summer increased Na demands by 0.7 g • d^{-1}. Daily requirements for total dietary sodium increased throughout the summer and were lowest in projections of the sheep model (1.7–2.4 g Na• d^{-1}) and greatest in projections of the dairy cattle model (4.5–5.8 g Na • d^{-1}). Minimum dietary concentrations of required Na decreased from days 1 - 60 (827 to 512 mg Na • kg $^{-1}$) and remained at 520-540 mg Na • kg $^{-1}$ until the end of summer (Fig. 2.4, Table 2.3) but dietary minima for Na were not significantly different between early and late lactation (Table 2.4).

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Projected requirements of K for maintenance differed significantly between model ruminants and horses: projections for the horse were only 5.8–6.8 g K • d^{-1} whereas projections for maintenance of sheep, goats, and dairy cattle were 12.3–27.3 g K • d^{-1}. Lactation increased demands of dietary K from 1.9–4.0 g K • d^{-1} among species projections. Tissue mobilization in early lactation reduced dietary demands by 0.3 g K • d^{-1} while deposition of body tissue at the end of summer increased dietary demand by 0.9 g K • d^{-1}. Daily requirements of dietary K increased through the summer and were lowest in projections of the horse model (8.0–9.8 g K • d^{-1}) but were comparable in projections of sheep, goat and dairy cattle models (14.4–28.4 g K • d^{-1}). Minimum dietary concentration of K concentration decreased from days 1–80 (4081–3278 mg K • kg^{-1}) and remained at 3279–3336 mg K • kg^{-1} through late lactation (Fig. 2.4, Table 2.3).

Iron, Manganese, Copper and Zinc

Projections of daily maintenance requirements of Fe were only based on the models for sheep and dairy cattle because requirements for beef cattle, goats and horses are unavailable from the National Research Council. Maintenance requirements were 12.6–14.8 mg Fe • d^{-1} with an additional 0.8–0.13 mg Fe • d^{-1} for lactation. Tissue mobilization in early lactation reduced dietary demands for Fe by 6.4 mg Fe• d^{-1} while tissue accretion at the end of summer increased dietary demand by 190 mg Fe required • d^{-1}. Total daily requirements increased over the lactation period in sheep (6.6–205.1 mg Fe • d^{-1}) and dairy cattle (0–117.7 mg Fe • d^{-1}) model projections. Minimum dietary concentration of Fe required in the diet were only 0.6–1.5 mg Fe • kg^{-1} from days 1 - 20 but increased through lactation to 21.7 mg Fe • kg^{-1} (Fig. 2.5, Table 2.3).

Daily maintenance requirements for Mn increased over the summer (18.1–28.8 mg Mn • d^{-1}) with an additional 0.09–0.20 mg Mn • d^{-1} required for lactation. Tissue mobilization at early lactation reduced dietary demands by 0.08 mg Mn • d^{-1} while deposition of tissue at the end of

summer increased dietary demands by 32.3 mg Mn • d^{-1}. Total daily requirements of Mn increased through the summer and were lowest in projections of the dairy cattle model (3.2–6.2 mg Mn • d^{-1}) and highest in projections of the goat model (4.2–8.2 mg Mn • d^{-1}). Minimum dietary concentrations of Mn declined from 6.8–4.0 mg Mn • kg^{-1} until day 40 but increased to 7.0 mg Mn • kg^{-1} by day 110 of lactation (Fig. 2.5, Table 2.3).

Daily maintenance requirements for Cu increased over summer (6.0–20.9 mg Cu • d^{-1}) with only 0.003–0.04 mg Cu • d^{-1} required for lactation. Tissue mobilization reduced dietary demands in early lactation by 0.13 mg Cu • d^{-1} while tissue deposition at the end of summer only increased dietary demands of Cu by up to 10 mg Cu • d^{-1}. Daily demands for copper increased through the summer and were lowest in projections of the sheep model (6.0–13.2 mg Cu • d^{-1}) and highest in projections of the horse model (16.0–28.8 mg Cu • d^{-1}). Minimum dietary concentrations of Cu required in the diet declined from 4.0 to 2.2 mg Cu • kg^{-1} to day 50 and increased to 3.0 mg Cu • kg^{-1} through late lactation (Fig. 2.5, Table 2.3).

Maintenance requirements of Zn increased over the summer (27.1–53.6 mg Zn • d^{-1} among models) with an additional 8.3–14.4 mg Zn • d^{-1} required for lactation. Tissue mobilization at early lactation reduced dietary demand by 2.9 mg Zn • d^{-1} while tissue accretion at the end of summer increased dietary demand by 57.6 mg Zn • d^{-1}. Daily demands for Zn increased through the summer and were lowest in projections of the dairy cattle model (33.1–95.5 mg Zn • d^{-1}) and highest in projection of the sheep model (52.2–117.4 mg Zn • d^{-1}). Minimum dietary concentrations of Zn decreased from 11.9–8.4 mg Zn • kg^{-1} over days 1-40 and rose to 14.0 mg Zn • kg^{-1} through late lactation (Fig. 2.5, Table 2.3).

Discussion

We used a consensus approach to estimate the mineral requirements of caribou by applying production curves of captive caribou to factorial requirements of domestic ungulates that were compiled from the literature by the National Research Council. Our results show that total requirements of minerals $(g \cdot d^{-1})$ are greater in late lactation than in early lactation even though digestible contents of energy and protein are greatest in early lactation (VanSomeren et al. 2017). Maintenance costs of minerals $(g \cdot d^{-1})$ increased throughout the summer due to increased fecal and urinary excretion as both intake and body mass increased. Daily mineral demands for lactation $(g \cdot d^{-1})$ were highest at peak lactation but similar at the start and end of the lactation period. Mass loss in early lactation reduced mineral demand from the diet $(g \cdot d^{-1})$ but restoration of body mass at the end of summer greatly increased mineral demand because those elements were absorbed at an efficiency of <100% before they became available for deposition into body mass. The costs of maintenance and/or mass gain outweighed the demands for lactation such that daily mineral demands for all minerals in our study were highest at the end of summer.

Our projection of daily food intake had a large influence the estimate of minimum required dietary concentration $(mg \cdot kg^{-1})$, that is high demands at low intakes in early lactation elevated minima whereas high intakes in late lactation offset high demands to depress the estimate of minimum concentration. For example, dietary minima $(mg \cdot kg^{-1})$ of macrominerals (Ca, P, Mg, Na and K) were high in early lactation due to low intakes early in the summer but declined through peak lactation as intakes increased (Figs. 2.2 – 2.4). Conversely, dietary minima for trace minerals such as Fe, Mn, Cu and Zn $(mg \cdot kg^{-1})$ increased in late lactation with increasing demands for tissue gain even though food intakes also increased during this period (Fig. 2.5).

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Our estimates of mineral demands include those for growing domestic animals that are probably higher than those required for seasonal regain of fat and lean mass in adult animals such as reproductive caribou (Table 2.1). Allometric effects on our estimates were probably small because we used body mass relationships to predict the demands of a species at ~100kg, which is within the distribution of body masses of sheep, goats, cattle and horses in the source data. Estimated requirements of Ca, P and Mg (g • d^{-1}) for mass gain of caribou may be overestimated because the factor is partly based on young domestic animals that are building bones with high concentrations of these minerals. Trace minerals that are incorporated into the lean mass of soft tissues may be less influenced by our bias towards young animals. However, development of mineral stores may differ among species. For example, Cu is deposited in the liver of young caribou and muskoxen during late lactation as they progress towards weaning (Rombach et al. 2002, Swor 2002).

Absorption efficiency has a strong effect on the estimate of mineral requirements when animals are gaining mass (Table 2.1 and 2.2). Absorption efficiencies vary depending on the mineral in question, the physiological state of the animal and interactions among minerals in the diet (McDowell 2003). Bioavailable inorganic mineral additives used in formulated rations tend to be better absorbed than minerals in natural forages (Suttle and Underwood 2010). Mineral absorption from natural forages also changes with plant phenology as minerals become less digestible as forages approach senescence (Spears 1994). True absorption coefficients have been traditionally determined by feeding captive animals formulated diets with mineral concentrations below minimum requirements in order to fully activate physiological absorption mechanisms (NRC 2016). While absorption coefficients for natural forages were used when available, most domestic species models of mineral requirements used coefficients from animals on formulated

rations in marginal mineral balance. As a result our model projections likely overestimate true absorption efficiency in caribou on a natural forage diet.

Our estimates of minimum dietary concentrations of Ca, P, Mg, Na and K for lactating caribou (Table 2.4) are within the range of concentrations reported for forages used by caribou in Alaska during summer (Whitten and Cameron 1980). Furthermore, our estimates of minimal concentration of Ca and P required for caribou are similar to those derived for cervids by the National Research Council (2007b). We applied the National Research Council's recommended requirements of Ca and P for cervids to our model of caribou production and found that the cervid projections for Ca were higher than the models projected for other domestic species (Table 2.4) and declined from 7476 to 4956 mg Ca $\cdot$ kg^{-1}. Alternatively, the cervid projection for P was lower than those projected from the other models (Table 2.4) and declined from 3960 to 2248 mg P $\cdot$ kg^{-1}. Staaland and White (2001) estimated dietary concentrations of Ca, P, Mg, Na, K, Mn and Cu required in the diet of caribou at peak lactation based on data for lactating sheep (2 L $\cdot$ d^{-1} milk yield). Our estimates in Table 2.4 are 27–75% greater than those reported by Staaland and White for macro-minerals (2685 mg Ca $\cdot$ kg^{-1}; 2694 mg P $\cdot$ kg^{-1}, 505 mg Na $\cdot$ kg^{-1}, and 3206 mg Na $\cdot$ kg^{-1}) but only 30–80% of the reported concentrations for Mg, Mn and Cu (1507 mg Mg $\cdot$ kg^{-1}, 22 mg Mn $\cdot$ kg^{-1}, and 5 mg Cu $\cdot$ kg^{-1}). Our estimates include those for Ca, P and Mg for antlergenesis and mass gain that may have been omitted by Staaland and White (2001). In addition, we used concentrations of Ca, P, Na and K for reindeer milk that are higher than those for sheep. Conversely, concentrations of Mg, Mn and Cu in sheep milk (NRC 2007b) are higher than those reported for reindeer milk and may explain lower estimates of dietary minima derived in our models.

The method described in this paper provides a framework to determine mineral requirements for wild ungulates to assess the effects of changes in quality and quantity of

forages on rangelands. The importance of phenological changes have been emphasized for conservation of terrestrial herbivores (Morellato et al. 2016). Arctic and temperate zone forages peak in digestible concentrations of energy and N soon after emergence but decline in digestibility as structural components dilute the digestible energy and N contents progressively as temperatures increase in mid-summer. Minerals in forages also exhibit phenological trends in concentration with plant growth stage that can affect the nutritional ecology of ungulates (McNaughton 1990, Staaland and White 2001). Forage phenology has been linked to ungulate reproductive patterns across a wide variety of latitudes and climates (Stoner et al. 2016) but the relationships between mineral availability and production of wild ungulates are poorly studied. Latitudes nearest the poles are most sensitive to changes in plant phenology due to the greater effect of increased temperature on forage phenology in cold regions (Prevéy et al. 2017). Advances in thaw date and increases in growing season length have been observed in the North American Arctic though no significant changes have been observed in the energy and protein content of arctic forages (Gustine et al. 2017). The effects of changing forage phenology on mineral nutrients in forages have yet to be fully investigated. Further study of mineral nutrient phenology in forages in concert with mineral demands are required to better define the constraints of migratory ungulates on rangelands.
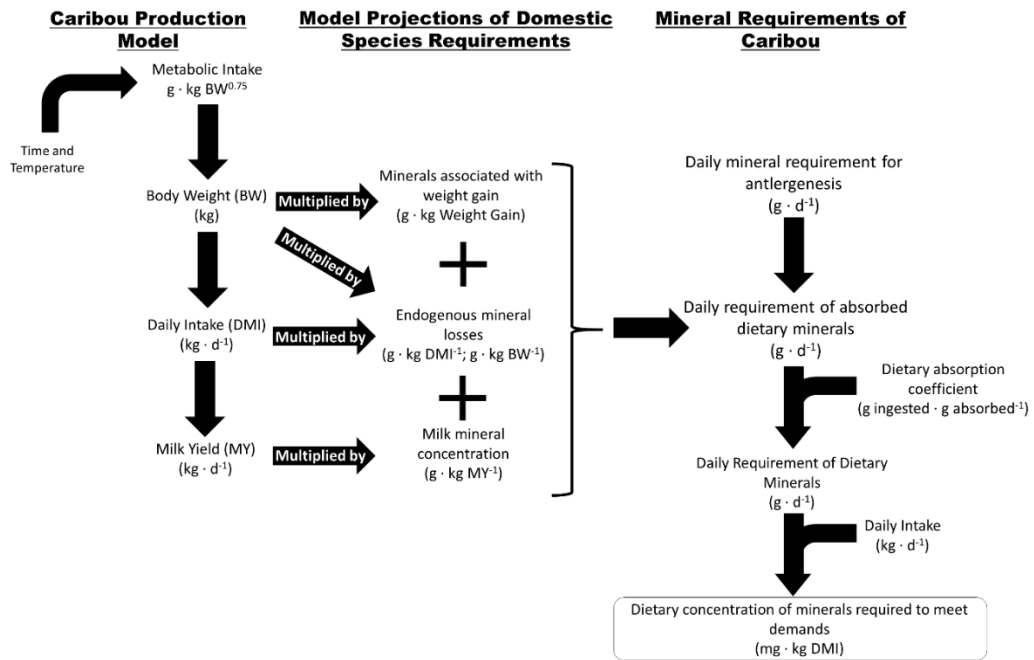
Figure 2.1. Conceptual diagram for estimating the mineral requirements and the minimum dietary concentration for lactating female caribou.
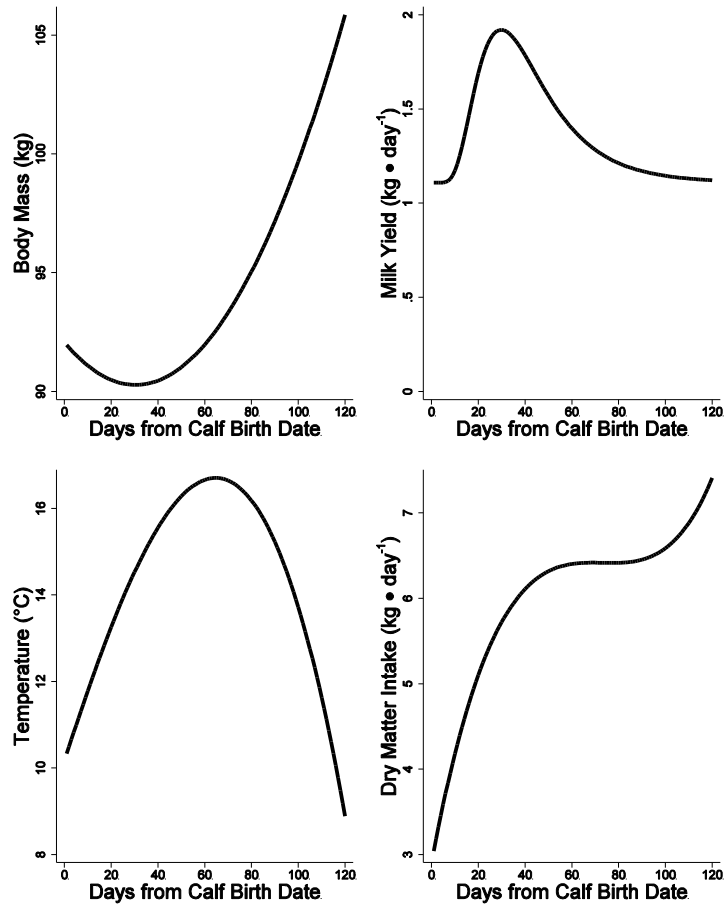
Figure 2.2. Model inputs for estimating requirements of female caribou from parturition through 120 days of lactation. Body mass (kg), milk yields (kg • d^{-1}), temperature (°C) and dry matter intake (kg • d^{-1}) were derived from measures of captive caribou in interior Alaska. Body mass, dry matter intake and temperature curves were estimated by Barboza (2015). The milk yield curve was estimated from caribou calf milk intake presented in Parker et al. (1990).

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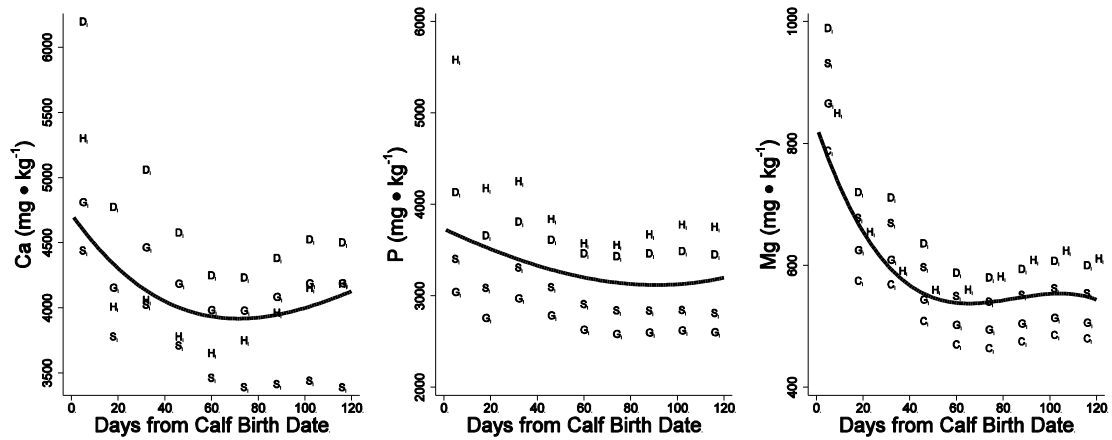
Figure 2.3. Minimum dietary concentration (dry matter basis) of Ca, P and Mg calculated for lactating caribou with factorial relationships for domestic ungulates. S = sheep model projection, G = goat model projection, D = dairy cattle model projection, C = beef cattle model projection, and H = horse model projection. Solid lines represent the regression of all species projections used for each element.
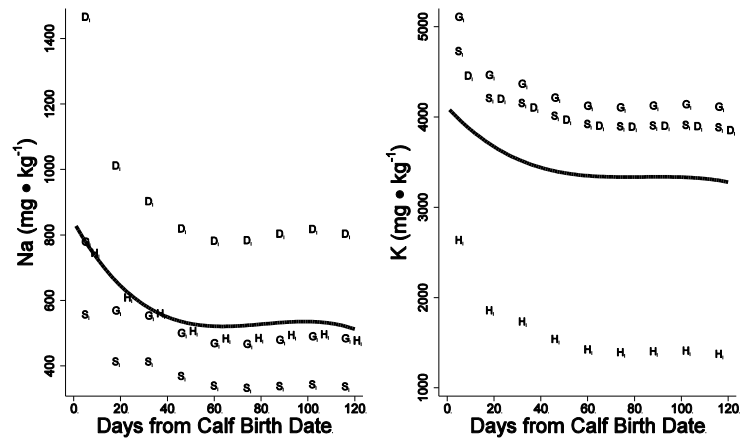
Figure 2.4. Minimum dietary concentration (dry matter basis) of Na and K calculated for lactating caribou with factorial relationships for domestic ungulates. S = sheep model projection, G = goat model projection, D = dairy cattle model projection, and H = horse model projection, Solid line represents the regression of species projections used for each element.

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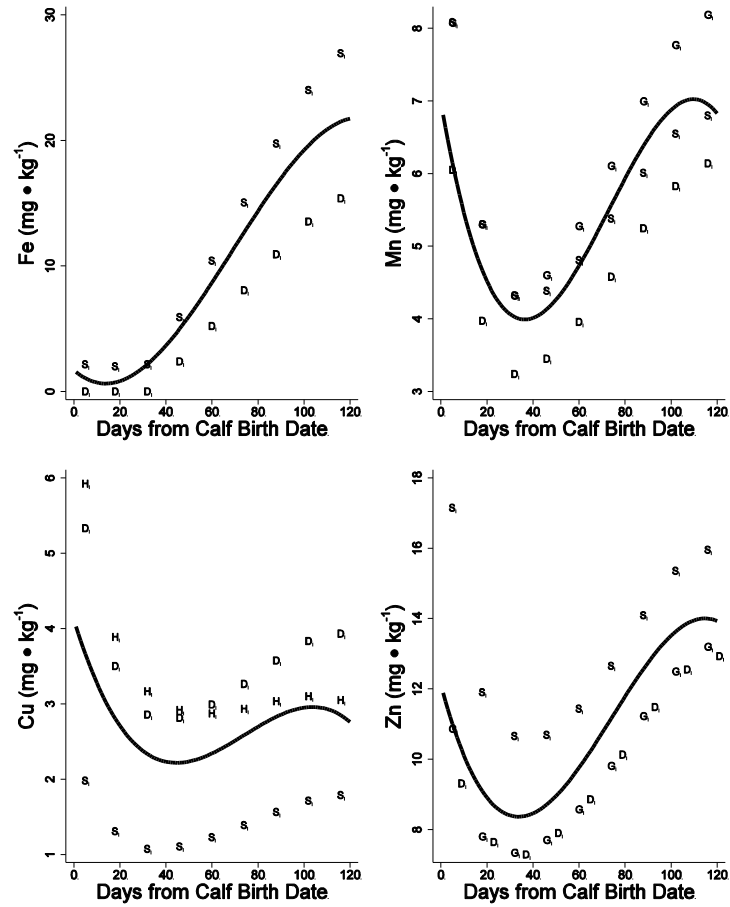
Figure 2.5. Minimum dietary concentration (dry matter basis) of Fe, Mn, Cu and Zn calculated for lactating caribou with factorial relationships for domestic ungulates. S = sheep model projection, G = goat model projection, D = dairy cattle model projection, and H = horse model projection, Solid line represents the regression of species projections used for each element.

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Table 2.1. Factorial relationships for requirements of Ca, P, Mg, Na, and K in sheep, goats, beef cattle, dairy cattle, and horses. BW = Body Weight (kg), MW = Mature Weight (kg), DMI = Dry matter Intake (kg), LWG = Live Weight Gain (kg), LMG = Lean Mass Gain (kg), MY = Milk Yield (kg), and AC = Absorption Coefficient.

Element	Factorial Requirement	AC $(g \cdot g^{-1})$	Maintenance $(g \cdot d^{-1})$	Body mass change $(g \cdot d^{-1})$	Lactation $(g \cdot d^{-1})$
Ca	Sheep	0.5	$(0.623 \cdot DMI^{-1}) + 0.228$	$LWG \cdot 6.25 \cdot MW^{0.28} \cdot BW^{-0.28}$	$3.2 \cdot MY^{-1}$
	Goat	0.45	$(0.623 \cdot DMI^{-1}) + 0.228$	$11 \cdot LWG^{-1}$	$3.2 \cdot MY^{-1}$
	Beef Cattle	0.5	$0.0154 \cdot BW^{-1}$	$71 \cdot LMG^{-1}$	$3.2 \cdot MY^{-1}$
	Dairy Cattle	0.3	$0.0154 \cdot BW^{-1}$	$9.83 \cdot (MW^{0.22}) \cdot (BW^{-0.22})) \cdot LWG$	$3.2 \cdot MY^{-1}$
	Horse	0.5	$0.043 \cdot BW^{-1}$	$16 \cdot LWG^{-1}$	$3.2 \cdot MY^{-1}$
P	Sheep	0.6	$1.6 \cdot (0.603 \cdot DMI - 0.06)$	$LWG \cdot (1.2+3.188 \cdot MW^{0.28} \cdot BW^{-0.28})$	$2.7 \cdot MY^{-1}$
	Goat	0.65	$0.081 + (0.88 \cdot DMI^{-1})$	$5.8 \cdot LWG^{-1}$	$2.7 \cdot MY^{-1}$
	Beef Cattle	0.64	$0.016 \cdot BW^{-1}$	[a] $39 \cdot LMG^{-1}$	$2.7 \cdot MY^{-1}$
	Dairy Cattle	0.68	$(1.2 \cdot DMI^{-1}) + (0.002 \cdot BW^{-1})$	$1.2 + (4.635 \cdot MW^{0.22}) \cdot (BW^{-0.22}) \cdot LWG$	$2.7 \cdot MY^{-1}$
	Horse	0.35	$0.028 \cdot BW^{-1}$	$8.0 \cdot LWG^{-1}$	$2.7 \cdot MY^{-1}$
Mg	Sheep	0.17	$0.003 \cdot BW^{-1}$	$0.41 \cdot LWG^{-1}$	$0.193 \cdot MY^{-1}$
	Goat	0.2	$0.0035 \cdot BW^{-1}$	$0.4 \cdot LWG^{-1}$	$0.193 \cdot MY^{-1}$
	Beef Cattle	0.2	$0.003 \cdot BW^{-1}$	$0.45 \cdot LWG^{-1}$	$0.193 \cdot MY^{-1}$
	Dairy Cattle	0.16	$0.003 \cdot BW^{-1}$	$0.45 \cdot LWG^{-1}$	$0.193 \cdot MY^{-1}$
	Horse	0.5	$0.0015 \cdot BW^{-1}$	$1.25 \cdot LWG^{-1}$	$0.193 \cdot MY^{-1}$
Na	Sheep	0.91	$0.0108 \cdot BW^{-1}$	$1.1 \cdot LWG^{-1}$	$0.6 \cdot MY^{-1}$
	Goat	0.8	$0.015 \cdot BW^{-1}$	$1.6 \cdot LWG^{-1}$	$0.6 \cdot MY^{-1}$
	Dairy Cattle	0.9	$0.038 \cdot BW^{-1}$	$1.4 \cdot LWG^{-1}$	$0.6 \cdot MY^{-1}$
	Horse	0.9	$0.02 \cdot BW^{-1}$	$1.0 \cdot LWG^{-1}$	$0.6 \cdot MY^{-1}$
K	Sheep	0.9	$(2.6\ g \cdot DMI^{-1}) + (0.038\ g \cdot BW^{-1})$	$1.8 \cdot LWG^{-1}$	$1.56 \cdot MY^{-1}$
	Goat	0.9	$(2.6\ g \cdot DMI^{-1}) + (0.05\ g \cdot BW^{-1})$	$2.4 \cdot LWG^{-1}$	$1.56 \cdot MY^{-1}$
	Dairy Cattle	0.9	$(2.6 \cdot DMI^{-1}) + (0.038\ g \cdot BW^{-1})$	$1.6 \cdot LWG^{-1}$	$1.56 \cdot MY^{-1}$
	Horse	0.75	$0.048 \cdot BW^{-1}$	$1.5 \cdot LWG^{-1}$	$1.56 \cdot MY^{-1}$

Table 2.2. Factorial relationships for requirements of Fe, Mn, Cu, and Zn in sheep, goats, beef cattle, dairy cattle and horses. BW = Body Weight (kg), MW = Mature Weight (kg), DMI = Dry matter Intake (kg), LWG = Live Weight Gain (kg), LMG = Lean Mass Gain (kg), MY = Milk Yield (kg), and AC = Absorption Coefficient

Element	Factorial Requirement	AC $(g \cdot g^{-1})$	Maintenance $(mg \cdot d^{-1})$	Body mass change $(mg \cdot d^{-1})$	Lactation $(mg \cdot d^{-1})$
Fe	Sheep	0.1	$0.014 \cdot BW^{-1}$	$55 \cdot LWG^{-1}$	$0.007 \cdot MY^{-1}$
	Dairy Cattle	0.1	$0 \cdot BW^{-1}$	$34 \cdot LWG^{-1}$	$0.007 \cdot MY^{-1}$
Mn	Sheep	0.0075	$0.002 \cdot BW^{-1}$	$0.47 \cdot LWG^{-1}$	$0.0008 \cdot MY^{-1}$
	Goat	0.0075	$0.002 \cdot BW^{-1}$	$0.7 \cdot LWG^{-1}$	$0.0008 \cdot MY^{-1}$
	Dairy Cattle	0.01	$0.002 \cdot BW^{-1}$	$0.7mg \cdot LWG^{-1}$	$0.0008 \cdot MY^{-1}$
Cu	Sheep	0.06	$0.004 \cdot BW^{-1}$	$1.06 \cdot LWG^{-1}$	$0.0008 \cdot MY^{-1}$
	Dairy Cattle	0.04	$0.0071 \cdot BW^{-1}$	$1.15 \cdot LWG^{-1}$	$0.0008 \cdot MY^{-1}$
	Horse	0.35	$0.069 \cdot BW^{-1}$	$1 \cdot LWG^{-1}$	$0.0008 \cdot MY^{-1}$
Zn	Sheep	0.15	$0.076 \cdot BW^{-1}$	$24 \cdot LWG^{-1}$	$1.13 \cdot MY^{-1}$
	Goat	0.15	$0.045 \cdot BW^{-1}$	$25 \cdot LWG^{-1}$	$1.13 \cdot MY^{-1}$
	Dairy Cattle	0.15	$0.045 \cdot BW^{-1}$	$24 \cdot LWG^{-1}$	$1.13 \cdot MY^{-1}$

Table 2.3. Relationships between the minimum dietary concentration of mineral (Y) mg•kg^{-1} of Ca, P, Mg, Na, K, Fe, Mn, Cu, or Zn) required for zero body balance of female caribou and time from birth (B; days).

Element	Requirement Phenology Regression	Adjusted r^2
Ca	$Y = -25.32x+0.2375x^2-0.00056x^3+4719.26$	0.20
P	$Y = -11.92x +0.0399x^2+0.00019x^3+3732.65$	0.11
Mg	$Y = -11.31x +0.1407x^2-0.00055x^3+829.89$	0.64
Na	$Y = -12.8x +0.1656x^2-0.00068x^3+840.15$	0.14
K	$Y = -28.08x +0.3377x^2-0.00134x^3+4108.27$	0.03
Fe	$Y = -0.16x +0.0065x^2-0.00003x^3+1.7$	0.81
Mn	$Y = -0.19x +0.0034x^2-0.00002x^3+6.99$	0.71
Cu	$Y = -0.1x +0.0016x^2-0.00001x^3+4.12$	0.14
Zn	$Y = -0.25x +0.0047x^2-0.00002x^3+12.13$	0.61

Table 2.4. Estimated requirements of female caribou (mean ± SD) from parturition through 120 days of lactation based on factorial relationships for selected domestic ungulates. Estimates for early lactation were averaged from parturition to peak lactation (28 days from parturition). Estimates for late Lactation are averaged from 29 to 120 days from parturition. S = sheep model projection, G = goat model projection, D = dairy cattle model projection, C = beef cattle model projection, and H = horse model projection.

Element	Incorporated Models	Peak Dietary Requirement (mg • kg DMI^{-1})	Day of Peak Requirement	Early Lactation Requirement (mg • kg DMI^{-1} ± SD)	Late Lactation Requirement (mg • kg DMI^{-1} ± SD)
Ca	S,G,D,H	4694	120	4406 ± 484	3999 ± 397
P	S,G,D,H	3721	1	3567 ± 696	3202 ± 499
Mg	S,G,C,D,H	819	1	719 ± 42	570 ± 40
Na	S,G,D,H	828	1	691 ± 267	535 ± 194
K	S,G,D,H	4653	1	3775 ± 1213	3364 ± 1285
Fe	S,D	21.74	120	1.03 ± 1.46	12.43 ± 5.26
Mn	S,G,D	7.02	110	5.1 ± 0.81	5.56 ± 0.79
Cu	S,D,H	4.02	1	3.04 ± 1.46	2.6 ± 1.02
Zn	S,G,D	14	115	9.67 ± 2.48	11.22 ± 1.72

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CHAPTER III

THE MINERAL CONSTRAINTS OF ARCTIC CARIBOU: A SPATIAL AND

PHENOLOGICAL PERSPECTIVE

Introduction

The spatial and temporal distribution of mineral nutrients on the landscape can influence the movement and productivity of ungulate populations. Yet, much of the literature on what drives ungulate populations has focused on energy and nitrogen (N) availability in forages. 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). Spatial heterogeneity in forage nutrients are driven primarily by plant community composition, which is regulated by environmental variation in precipitation, temperature and soil fertility (Skarpe and Hester 2008). The transfer of soil minerals to plants and to ungulates is affected by soil pH and by interactions among minerals and organic matter. For example, apparent copper (Cu) deficiencies in moose have been associated with increased availability of sulfur (S) and molybdenum (Mo) in regions affected by acid rain (Suttle 1991, Frank et al. 1994).

Concentrations of nutrients in plants vary with developmental stage from emergence to senescence and with local environmental conditions (soil nutrients, temperature, light and water). Nitrogen concentrations decline from a peak at or shortly after emergence as proportions of fiber and other structural components increase to senescence (VanSomeren 2014). Proteins are 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

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trends to N or fiber depending on their function in structure and metabolism plants: P, K, and Cu are associated with photosynthetic parts of plants and decline to senescence, while Ca, Fe, Zn and other trace mineral may be tied to structural components and tend to increase to senescence (Suttle and Underwood 2010).

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 plants secondary metabolites. Graminoids contain higher concentrations of fiber than leaves of browse but are relatively free of plant secondary metabolites. Phenological differences in minerals between the 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 species depending on the landscape physiognomy, 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). Spatial variation in rainfall and forage phosphorus (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 1988b, Hopcraft et al. 2010, Pretorius et al. 2011). Similarly, sodium (Na) distributions on the landscape have been associated with ungulate movements in North America (Jones and Hanson 1985, Ayotte et al. 2006, Slabach et al. 2015).

Constraints of available Na in forages may also significantly impact the movements Eurasian caribou (Staaland and White 2001).

Caribou in Alaska's arctic undergo the longest land migration of any ungulate (~5000 km) (Fancy et al. 1989b, Nicholson et al. 2016, Fullman et al. 2017). Female caribou in the Central Arctic and Western Arctic herds move between the wintering grounds in and/or south of the Brooks Range and the calving grounds on the Coastal Plain (Cameron and Whitten 1979a, Joly et al. 2009, Nicholson et al. 2016). Winter diets of arctic caribou are primarily composed of lichens with smaller proportions of senescent vegetation and bryophytes. Overall, arctic caribou in Alaska survive the long arctic winter on a diet that contains marginal concentrations of N and mineral nutrients (Staaland et al. 1986b). Consequently, caribou rely on using and conserving body stores of minerals and protein during the summer growing season to survive the winter (White et al. 1984). Timing of movements in summer is affected by thawing of snow packs and ice, and emergence of new vegetation. Males migrate behind parturient females by 2-3 weeks and tend to stay off the Arctic Coastal Plain (Cameron and Whitten 1979b).

Here we describe the seasonal variation in mineral nutrients for arctic caribou in Alaska during the summer by comparing forages in the ranges of the Central Arctic herd (CAH) and the Western Arctic herd (WAH). We examined seven species including 3 browse, 3 graminoids and one forb over a combined total of 5 transect years to describe the phenology of 9 minerals. We tested the hypothesis that the migration and the life history of arctic caribou is constrained by regional differences in minerals by comparing available minerals over space and time with estimated requirements of reproductive females.

Methods

We studied forage biomass and characteristics of forage and soil on two transects bisecting the summer ranges of the migratory CAH and WAH spanning the three northernmost arctic ecoregions of Alaska. At the start of regular monitoring in 1975, the CAH increased from 5,000 animals to 70,000 by 2010 but since then has declined to 22,000 individuals (Lenart 2016). The WAH declined in the 1970s to a population near 70,000 animals and slowly increased to become the largest caribou herd in Alaska at 490,000 animals by 2003. Since 2003, the herd has declined to approximately 200,000 animals. The CAH transect extended north from the Brooks Range Ecoregion, through the Arctic Foothills to the Arctic Coastal Plain over 200 km along the Dalton Highway (Gustine et al. 2017), while the WAH transect spanned the same ecoregions over 150 km in Northwestern Alaska (Figure 3.1).

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 bigelowii, Carex aquatilis, Eriophorum vaginatum*) and forbs of the genus *Pedicularis*. We estimated biomass by completely sampling all study species in 5 randomly selected ½ m by ½ 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. Weather permitting in 2011−2014, forage samples were collected from each transect every 2 weeks from ordinal days 149 - 273. 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 5 locations at each sampling site.

Forage samples were dried at 55°C and homogenized through a 1 mm mesh in a centrifugal mill (Retsch ZM 200, Verder Scientific, Haan Germany) for analyses of ash, carbon and nitrogen (Gustine et al. 2017). Samples for each macroplot and forage species were separated into 3 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). 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 Corp., Mathews NC) at 200ºC for 10 min. Each digest rack of 40 included duplicates of a reference material with known concentration (NIST; National Institute Standards and Technology; US Department of Commerce, Gaithersburg MD) and 2 method blanks (no sample). Sample digests and method blanks were diluted with 60 mL of deionized water (-18 MΩ·cm^{-1}; Thermo-Scientific Gen-CAD, Waltham, MA) 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 (1000µg·ml^{-1}; Specpure, Alfa Aesar, Ward Hill, MA). 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; Mg-Ca, Fe-P, 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 DPTA 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, TX 77845. Total nitrogen (N) was estimated using an elemental analyzer (CNS2000, LECO, St. Joseph, Michigan, USA). Assays of plant secondary metabolites (PSM) were completed using a reaction of extracted phenolics with Folin-Ciocalteu reagent expressed as gallic acid equivalents, while acid detergent fiber 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, NY) (Thompson and Barboza 2014).

We used mixed effects regression to model the phenology of minerals in forages (STATA 14.0; StataCorp, College Station TX). The full phenological model for each forage mineral (Y) included the fixed effects of ecoregion (ECO), transect (TRAN), species (SPEC), ordinal day (OD) and ordinal day^2 (OD^2): $Y = ECO + TRAN + SPEC + OD + OD^2 + SPEC*OD + SPEC*OD^2 + \varepsilon$. Mixed effects models were also used to examine drivers of forage mineral concentration (Y) in soil (minerals [SOIL] and pH) and forage components (total nitrogen content (N) and acid detergent fiber (ADF): $Y = SPEC + SOIL + ADF + N + pH + \varepsilon$. Soils 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

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the phenology models to retain only those coefficients that differed significantly from zero (p ≤ 0.05). Model predictions of mineral concentrations in forages were compared with estimated requirements of caribou at early and late lactation derived in Chapter II. Post hoc tests of fixed effects included pairwise comparisons of predicted margins ($\bar{X} \pm SE$) with Bonferroni's adjustments for multiple comparisons (Rabe-Hesketh and Skrondal 2010, Mitchell 2012).

Results

We collected 1296 samples of caribou forages over transects bisecting the summer ranges of the Central Arctic and Western Arctic caribou herds in northern Alaska (Figure 3.1); of those, 585 samples were included in phenologically representative subsets. Concentrations of Ca, P and Mg differed among species of forage over the season and between transects. Concentrations of Ca increased with ordinal day in all species and were greater in browse than graminoids with especially high concentrations in *S. richardsonii* and *Pedicularis spp.* (Figure 3.2a and 3.2b). In contrast, concentrations of P declined over the growing season and were lower in graminoids than browse and the forb (Figure 3.2c and 3.2d). Ranges of Ca in soil were greater in the CAH transect than on the WAH transect (Table 3.1), which corresponded with greater soil pH on the CAH than the WAH transect (5.8 ± 0.4 vs. 4.7 ± 0.2; z = -1.99 *P* = 0.046). Soil pH was positively related to forage Ca (Table 3.2), which was greater on the CAH than the WAH (7120 ± 520 vs. 4720 ± 260 mg•kg^{-1}; z = -4.69 *P* = 0.000). Concentrations of P in forages increased with forage N (Table 3.2) but only 10% of the forage samples contained sufficient P to meet the estimated requirement of caribou (Table 3.3). Increased soil pH and soil Ca (Table 3.2) were associated with decreases in forage P between the CAH and the WAH transects (1690 ± 80 vs. 1990 ± 50 mg•kg^{-1}, z = 3.33 *P* = 0.001). The lowest concentrations of P coincided with the highest concentrations of Ca (Figure 3.2), that is 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) than

either graminoids or the forb (1–42). 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 = 0.000) even after removing Ca-rich species (*S. 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 = 0.000). Ratios of Ca:P in graminoids were low and accompanied by more available P than browse (56 % ± 1 vs. 43 % ± 4; z = 2.86 P = 0.004; Table 3.4) even though availabilities of Ca were similar among plant groups (80 ± 2%). Availabilities of Ca and P varied widely among species with the lowest availabilities for *B. nana* (Table 3.4). Availability of Ca declined between early and late season for *B. nana* but increased over the season for three other species. (Table 3.4).

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 3.3; Supplement Figure 1a and 1b). Soil concentrations of Mg were higher on the WAH than on the CAH transect (Table 3.1). 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 3.2).

Forage concentrations of Na were much lower than those for K throughout the growing season (Figure 3.3). The ranges of concentrations for Na in forage and soil were greatest on the Coastal Plain (Tables 3.1 and 3.3). Forage Na was positively associated with soil Na (Table 3.2) and only exceeded the estimated requirement of caribou on the Coastal Plain (Table 3.3) in 1% of all samples. Conversely, K concentrations exceeded the estimated requirement of caribou in 94% of samples (Table 3.3) even though K concentration declined through the season (Figure 3.3) with the concentration of N and with decreases in soil pH (Table 3.2).

Concentrations of Cu in forages declined through the season in both browse and graminoid species (Figure 3.4). Forage Cu was positively associated with N and fiber (Table

3.2), and with concentrations of Cu in soil that were greater on the WAH transect than the CAH transect (2.5 ± 0.4 vs. 1.3 ± 0.2; z = 2.96 P = 0.003). Concentrations of Cu in forages were adequate early in the season but marginal at the end of the season (Figure 3.4). Forage Zn was highly available in both early and late season (Table 3.4) and present in much greater concentrations than those for Cu especially among browse species (Figure 3.4). Although forage Zn was negatively associated with fiber (Table 3.2), Zn concentrations were greater than the estimated requirement for caribou (Table 3.3).

Forage concentrations of Fe increased with soil pH and were greater on the CAH than the WAH (170.9 ± 27.8 vs. 108.1 ± 10.2; z = -2.63 P = 0.009; Table 3.2). Availabilities of Fe in forages were lower than those of all other minerals and less than 21% for Fe in *B. nana* (Table 3.4). In contrast, the availability of Mn in forages was high and ranged from 68–97%. Forage concentrations of Mn were negatively associated with soil pH, forage N and fiber and were also positively associated with phenolic activity (Table 3.2). Concentrations of Mn in forage were highest in the Brooks Range and lowest on the Coastal Plain (Table 3.3). Concentrations of Fe and Mn in forages were well above the dietary requirements estimated for lactating caribou (Table 3.3).

Discussion

Variation in forage minerals among ecoregions and transects was primarily driven by soil pH and secondarily by soil mineral concentrations (Table 3.2). Slow decomposition of organic matter in arctic soils releases humic acids that reduce soil pH. 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 but lower concentrations of P and Mg in forages on the CAH transect than the WAH transect (Table 3.1 & 3.2). 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 3.1) (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 (Table 3.1 & 3.2).

Concentrations of minerals in forages vary over time according to the role of the element in the metabolism and structure of plants (Clárk 1983). Minerals that decline in plants as they mature are typically associated with plant proteins in photosynthetic parts while those that increase with maturity are likely associated with fiber matrices. Concentrations of P, K, and Cu were positively associated with forage N (Table 3.2) all of which declined from emergence to senescence (Figures 3.2c, 3.2d, 3.3c, 3.3d, 3.4a, 3.4b). However, the concentration of Ca, Mn, and Zn in forages increased over the season (Figures 3.2a, 3.2b, 3.4c, 3.4d, A.1e & A.1f) but decreased with increasing concentrations of N and also fiber in plants (Table 3.2). 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 plant secondary metabolites (Garten 1978, De Silva et al. 1996, Millaleo et al. 2010) which are consistent with seasonal changes in cuticular waxes (Carnahan 2011) and plant toxins of arctic forages (Dormann 2003).

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Contrasting phenologies of minerals indicated large imbalances in supplies of Ca, P, Zn, and Cu. 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). 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. Interactions of Ca and P have the potential to limit mass gain and movement of lactating caribou and their calves because P concentrations declined below requirements in all forage species after emergence (Figure 3.2). Greater concentrations of P coincided with lower Ca content and hence lower Ca:P ratios of forages on the WAH transect, which may partially explain differences in size between WAH and CAH caribou herds. Annual and regional variation in the availability of Ca and P has been associated with population cycles of brown lemmings (*Lemmus* sibricus) in arctic Alaska (Barkley et al. 1980, Pitelka and Batzli 2007). 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, Morrison et al. 2016). Likewise,

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concentrations of P in forages may constrain arctic caribou populations and, therefore, unrestricted migration may be integral to maintaining large population sizes of arctic caribou herds.

Development of mineral 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 with their annual migration (Bergerud et al. 1984, Nicholson et al. 2016). Roads perpendicular to migration routes may have a greater effect on the migration routes of WAH caribou thereby limiting foraging time on autumn ranges of some caribou (Wilson et al. 2016). Road dust blown from roads and trucking carrying mining ore have also been shown to contaminate vegetation in Western Alaska 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 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 days of the summer, but the adequate period was extended on the Coastal Plain for 70 days from parturition. High concentrations of P and low concentrations of Ca early in the growing season could support bone deposition but late in the summer, but without supplementation (e.g., geophagy, 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 (Grasman and Hellgren 1993) but female caribou are more likely to be limited by P because they must deposit P in both milk and

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antlers (Luick et al. 1974, Moen and Pastor 1998). Consequently, females that lose a calf early in the summer may be better able to replenish body stores and reproduce the following year(Cameron et al. 1993, Cameron 1994). Those that suckle a calf all summer may not be able to produce a calf the following year due to limited body stores of protein and minerals such as Ca and P.

Arctic caribou probably emerge from winter with limited stores of Na that are likely to be depleted by high concentrations of K in emergent vegetation (White et al. 1984) (Figure 3.3). Previous studies have reported limitation of Na for caribou in interior Alaska and Eurasia with adequate concentrations only found on Eurasian coastal plains but did not report data for the Coastal Plain of Alaska (Staaland and White 2001). Our data in Alaska supports 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 3.3). Even though high concentrations of Na are present in soil on the Coastal Plain (Table 3.1) forages concentrations are not adequate for caribou until mid-summer because plants appear to accumulate Na through the start of the growing season (Figure 3.3, Table 3.3). If forage concentrations of Na are inadequate when needs are greatest, caribou may use spring brine pools caused by freeze thaw cycles of permafrost or brackish water to meet sodium requirements (Osterkamp and Romanovsky 1997).

Cu may not limit lactating caribou in Arctic Alaska but could limit the recruitment of their calves in late season, 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 (Figure 3.4a and 3.4b). Limitations on late summer feeding

due to early snow fall may limit uptake of Cu for calves and further increases their vulnerability to winter (Hendrichsen and Tyler 2014).

Mineral licks are used by migratory caribou but the use may be limited to only small portions of the large herds observed in Alaska's arctic (Calef and Lortie 1975). Soils at lick sites are rich in Na, which is potentially limiting to caribou (Calef and Lortie 1975, Ayotte et al. 2006). However, migratory ungulates such as caribou are often less constrained by lick soil than those of resident populations (Jones and Hanson 1985). However, our results show that Na in forages is not available in adequate concentrations early in the season when needs are greatest, but concentrations of Na in soil are higher on the Coastal Plain than inland ecoregions. Soil Na or brackish water on the Coastal Plain may therefore serve as a primary source of Na for arctic caribou in early summer. Calcareous and clay rich lick soils may also 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).

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. Although fires on the arctic tundra are rare, the frequency of burning is projected to increase with warming

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(Bret-Harte et al. 2013). The long terms effects of fire on the arctic tundra has yet to be clearly established but fires may benefit caribou foraging in summer even though fires adversely affect their winter supplies of lichen (Rickbeil et al. 2017).

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). Increased temperatures and subsequent changes to permafrost, active soil layers, snow cover, hydrology, and soil mineralization all have the potential to alter the distribution and availability of mineral for 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 *C. aquatilis*, *E. vaginatum*, *S. pulchra* and *Pedicularis spp*. (Whitten and Cameron 1980). However the N concentrations of these forages were not significantly different between 1977 and 2011-2013 (Gustine et al. 2017). The uniform positive bias observed for minerals indicates this comparison may be confounded by differences in analytical methods. Simulated changes to warming and hydrology may increase the prevalence of the shrub *B. 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 3.4) (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) produce 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.
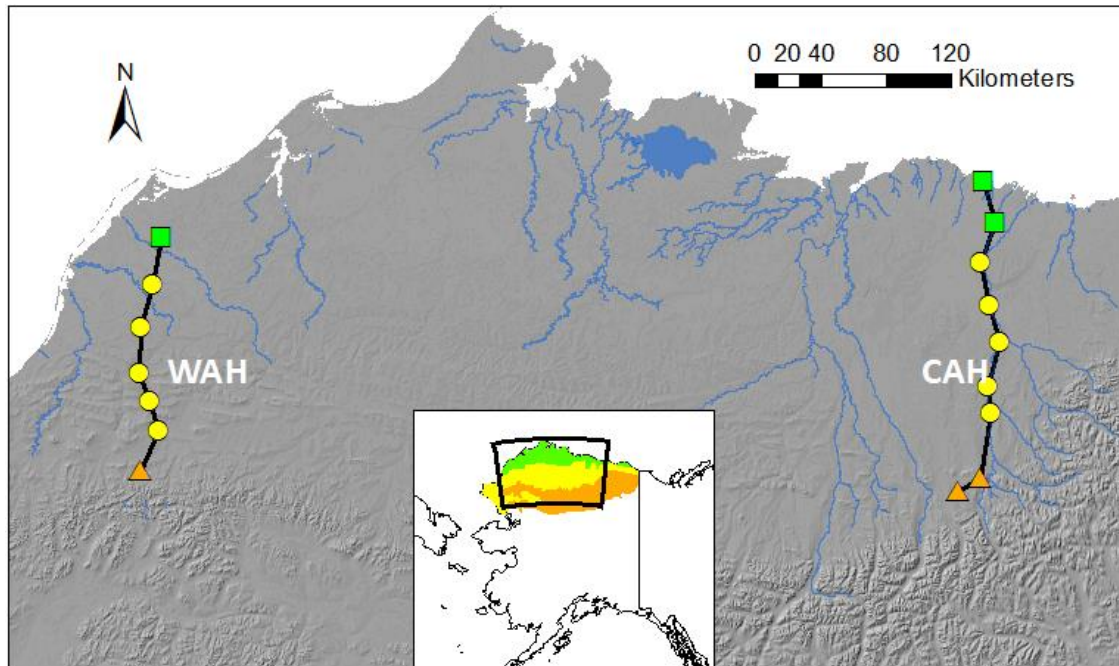
Figure 3.1. Transects and sites for sampling forages used by two herds of arctic caribou in Alaska: Western Arctic Herd (WAH) and Central Arctic Herd (CAH). Solid shadings on inset map indicate ecoregions from the Brooks Range (orange) through the Arctic Foothills (yellow) to the Coastal Plain (green). Site marker colors correspond to the ecoregion each site lies in.
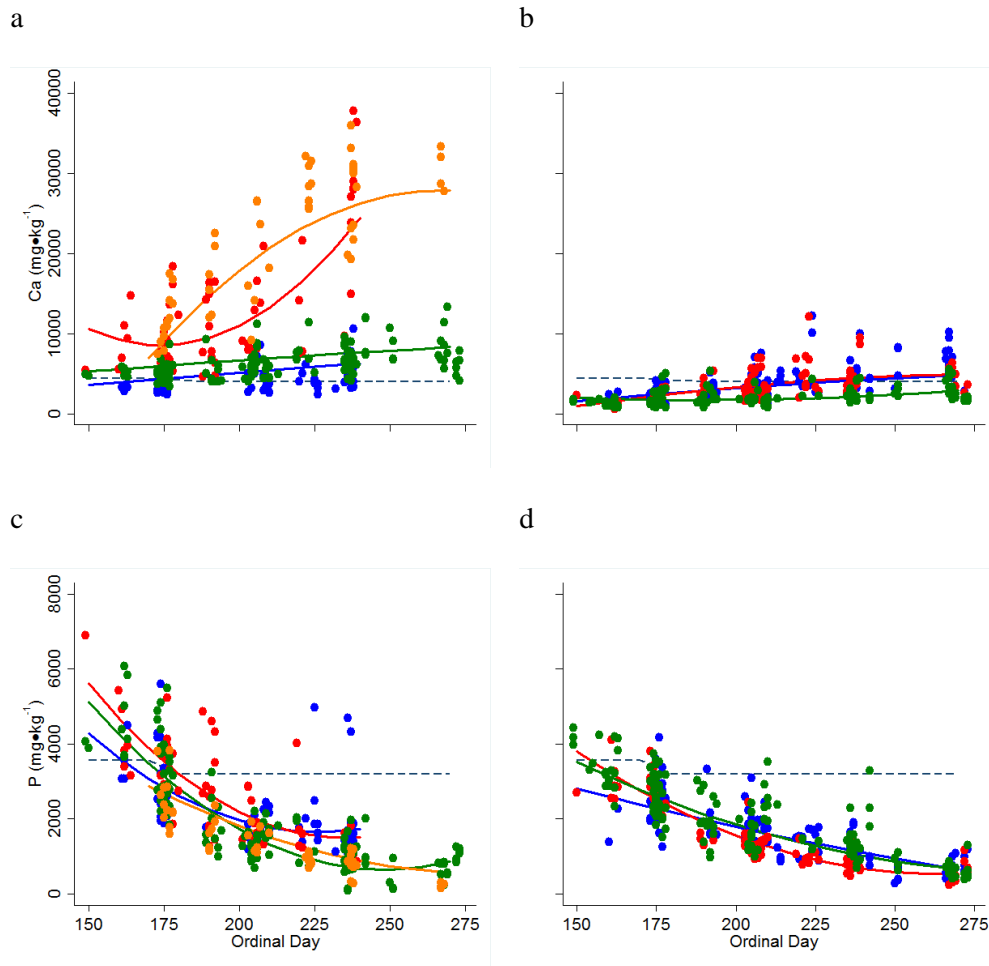
Figure 3.2. Concentrations (mg • kg^{-1} dry matter) of Ca (a & b) and P (c & d) in forages used by arctic caribou in Alaska. Dashed lines represent estimated dietary requirements of lactating caribou. Browse (a & c): *B. nana* (blue), *S. pulchra* (green), *S. richardsonii* (orange) and forb *Pedicularis spp.* (red). Graminiods (b & d): *C. aquatilis* (blue), *C. bigelowii* (red), and *E. vaginatum* (green).

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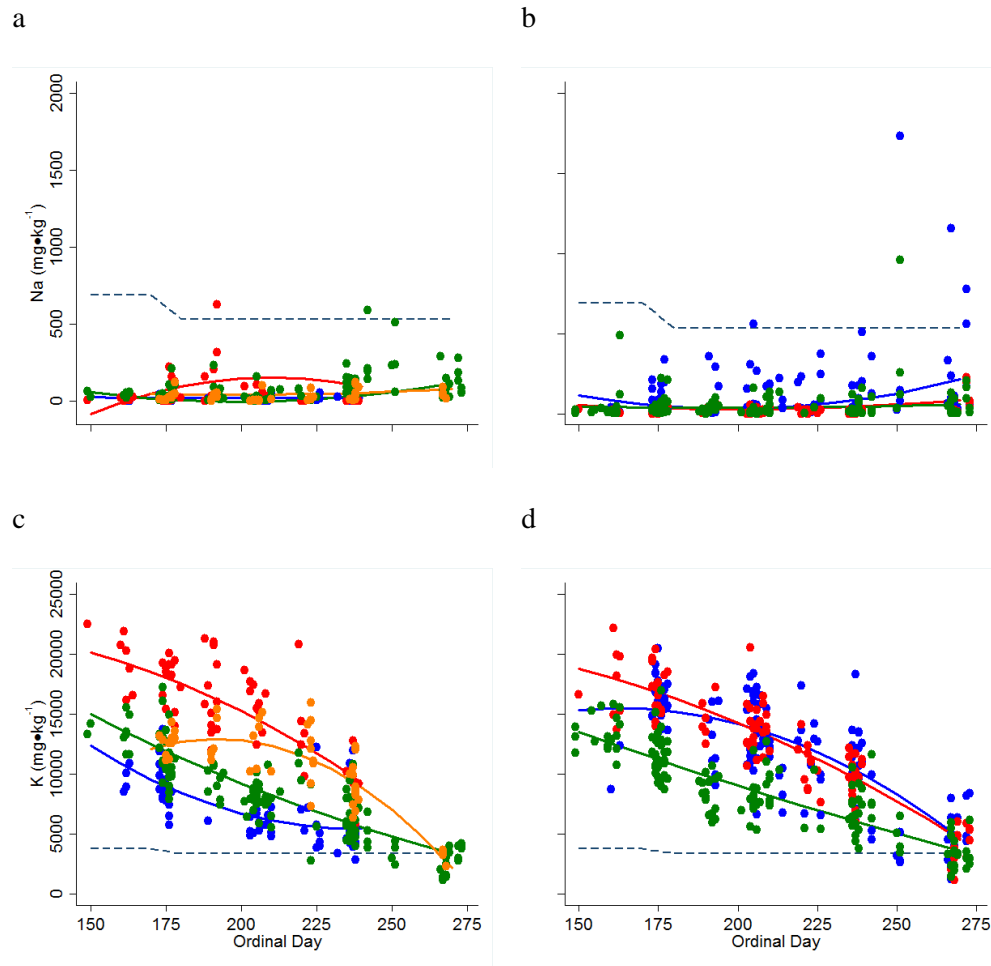
Figure 3.3. Concentrations (mg • kg⁻¹ dry matter) of Na (a & b) and K (c & d) in forages used by arctic caribou in Alaska. Dashed lines represent estimated dietary requirements of lactating caribou. Browse (a & c): *B. nana* (blue), *S. pulchra* (green), *S. richardsonii* (orange) and forb *Pedicularis spp.* (red). Graminiods (b & d): *C. aquatilis* (blue), *C. bigelowii* (red), and *E. vaginatum* (green).
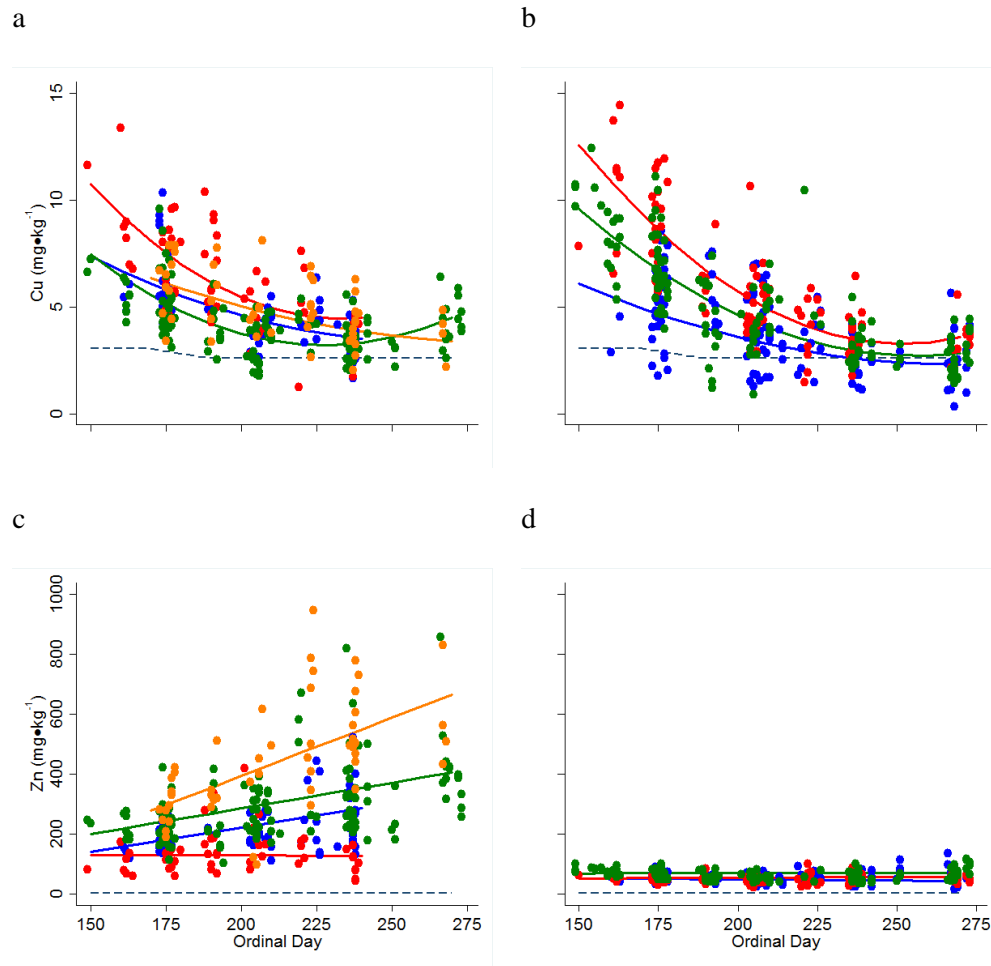
Figure 3.4. Concentrations (mg • kg^{-1} dry matter) of Cu (a & b) and Zn (c & d) in forages used by arctic caribou in Alaska. Dashed lines represent estimated dietary requirements of lactating caribou. Browse (a & c): *B. nana* (blue), *S. pulchra* (green), *S. richardsonii* (orange) and forb *Pedicularis spp.* (red). Graminiods (b & d): *C. aquatilis* (blue), *C. bigelowii* (red), and *E. vaginatum* (green).

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Table 3.1. Observed concentrations (mg • kg^{-1} dry mass) of available minerals and pH in soils by ecoregion and transect ($\bar{X} \pm SD$). Different letters indicate significant pairwise differences between groups within each mineral ($P < 0.05$).

| 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]	50	5.9 ± 1.5[ab]
	Coastal Plain	0	-	20	6.7 ± 1.1[b]
Ca	Brooks Range	6	430 ± 260[a]	20	1140 ± 900[a]
	Arctic Foothills	20	950 ± 460[a]	50	5630 ± 6620[a]
	Coastal Plain	0	-	20	6290 ± 5620[a]
P	Brooks Range	6	6.7 ± 4.4[c]	20	14.9 ± 9.2[d]
	Arctic Foothills	20	5.1 ± 1.8[ab]	50	8.5 ± 5.2[c]
	Coastal Plain	0	-	20	5.9 ± 3.7[bc]
Mg	Brooks Range	6	116 ± 36[bc]	20	81.0 ± 37.8[a]
	Arctic Foothills	20	201 ± 85[c]	50	96.1 ± 39.2[ab]
	Coastal Plain	0	-	20	84.2 ± 20.9[a]
Na	Brooks Range	6	8.7 ± 3.1[b]	20	5.8 ± 1.4[a]
	Arctic Foothills	20	8.9 ± 2.5[b]	50	4.8 ± 6.6[a]
	Coastal Plain	0	-	20	23.0 ± 23.9[ab]
K	Brooks Range	6	22.0 ± 8.4[a]	20	37.5 ± 13.0[a]
	Arctic Foothills	20	48.8 ± 22.4[a]	50	25.9 ± 11.9[a]
	Coastal Plain	0	-	20	21.7 ± 13.7[a]
Fe	Brooks Range	6	409 ± 113[a]	20	206 ± 105[a]
	Arctic Foothills	20	313 ± 122[a]	50	213 ± 154[a]
	Coastal Plain	0	-	20	150 ± 123[a]
Mn	Brooks Range	6	9.6 ± 5.3[a]	20	50.2 ± 44.9[a]
	Arctic Foothills	20	41.2 ± 43.3[a]	50	22.9 ± 23.5[a]
	Coastal Plain	0	-	20	17.3 ± 13.8[a]
Cu	Brooks Range	6	1.9 ± 0.6[c]	20	1.5 ± 0.7[ab]
	Arctic Foothills	20	2.2 ± 1.0[b]	50	1.1 ± 0.7[ac]
	Coastal Plain	0	-	20	1.4 ± 0.8[abc]
Zn	Brooks Range	6	1.0 ± 1.0[a]	20	2.8 ± 3.2[a]
	Arctic Foothills	20	0.8 ± 0.5[a]	50	2.6 ± 2.8[bc]
	Coastal Plain	0	-	20	2.2 ± 1.8[c]

Table 3.2. Linear effects of composition of forage and soil on minerals in forages used by arctic caribou in Alaska based on a mixed model regression with sample site as a random effect. Plus and minus signs indicate the direction of significant effects ($P < 0.05$).

	Independent Variables			
Element	N	ADF	Soil	pH
Ca	−	−		+
P	+			−
Mg		−		−
Na			+	+
K	+			+
Fe				+
Mn	−	−		−
Cu	+	+	+	
Zn	−	−	+	

Table 3.3. Observed concentrations (mg • kg⁻¹ dry mass) of minerals in forages used by caribou in arctic ecoregions of Alaska. Dietary requirements for each mineral are listed with the proportion of samples above requirement (adequate) and the range of days where at least one sample exceeded the respective requirement.

Mineral	Ecoregion	N	Range (mg • kg⁻¹)	Requirement (mg • kg⁻¹)	Adequate (%)	Adequate (days)
Ca	Brooks Range	125	530 – 21609		40%	149 – 269
	Arctic Foothills	410	752 – 37798	4406	47%	162 – 273
	Coastal Plain	160	740 – 31977		53%	174 – 268
P	Brooks Range	125	78 – 6904		9%	149 – 175
	Arctic Foothills	410	135 – 6068	3567	7%	149 – 177
	Coastal Plain	160	150 – 5498		10%	157 – 219
Mg	Brooks Range	125	511 – 3930		96%	149 – 273
	Arctic Foothills	410	310 – 7335	719	92%	149 – 273
	Coastal Plain	160	338 – 4279		96%	154 – 272
Na	Brooks Range	125	0 – 151		0%	-
	Arctic Foothills	410	0 – 558	691	0%	-
	Coastal Plain	160	3 – 1981		4%	203 – 272
K	Brooks Range	125	2291 – 22491		94%	149 – 273
	Arctic Foothills	410	1133 – 20470	3775	91%	149 – 273
	Coastal Plain	160	2010 – 21293		94%	154 – 272
Fe	Brooks Range	125	39 – 365		100%	149 – 273
	Arctic Foothills	410	14 – 1044	12.43	100%	149 – 273
	Coastal Plain	160	40 – 2681		100%	154 – 272
Mn	Brooks Range	125	104 – 3164		100%	149 – 273
	Arctic Foothills	410	35 – 2775	5.56	100%	149 – 273
	Coastal Plain	159	46 – 1721		100%	154 – 272
Cu	Brooks Range	125	0 – 14		78%	149 – 273
	Arctic Foothills	410	1 – 14	3.04	72%	149 – 273
	Coastal Plain	160	1 – 12		87%	154 – 268
Zn	Brooks Range	125	15 – 503		100%	149 – 273
	Arctic Foothills	410	23 – 778	11.22	100%	149 – 273
	Coastal Plain	159	30 – 945		100%	154 – 272

Table 3.4. Availability ($\bar{X} \pm SD$) of minerals in forages used by arctic caribou in Alaska at early and late season. 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 ($P < 0.05$).

Mineral	Species	N	Early	N	Late	Comparison	
Ca	B. nana	5	68 ± 10.4	5	35 ± 13.7	c	(-)
	S. pulchra	6	86 ± 1.8	6	92 ± 1.1	b	(+)
	S. richardsonii	2	95 ± 1.6	4	94 ± 1.4	d	
	Pedicularis spp.	2	94 ± 3.1	0	—		
	C. aquatilis	5	74 ± 7.7	7	83 ± 4.7	a	
	C. bigalowii	4	65 ± 8.5	5	90 ± 2	a	(+)
	E. 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	

CHAPTER IV

CONCLUSIONS

Minimum dietary concentrations of minerals required by caribou varied with the physiological demand (e.g. milk production) and with changes in intake over the course of the growing season. Requirements of macrominerals Ca, P, Mg, Na and K were greatest at parturition and declined through the summer while requirements of trace minerals Fe, Mn, Cu and Zn increased through the summer with gains in mass. In either case, this is in contrast to previous studies which assumed requirements for minerals in caribou were greatest at peak lactation (Staaland and White 2001). However, it is unclear what factors (e.g., intake, mass gain, milk composition) were used in previous literature to determine absolute mineral requirements of caribou.

Caribou from the Western Arctic Herd and Central Arctic Herd do not appear to be limited or influenced by spatial or temporal trends in forage concentrations of Mg, Fe or Mn. Cu does not appear to be limiting to lactating caribou in Arctic Alaska but may limit the recruitment of juveniles to adult age classes as calves transition to forages through the end of summer. Juvenile Cu limitation may also be exacerbated by the divergent phenologies of Cu and Zn as Cu approaches marginal concentrations late in the summer. Interactions of Na and K have the potential to influence the movements and productivity of caribou populations in Alaska. Inland ecoregions (Brooks Range and Arctic Foothills) are limited in Na in forages. High concentrations of K in emergent vegetation are likely to exacerbate the Na limitation of arctic caribou.

Concentrations of P on the Brooks Range and Arctic Foothills ecoregions were only adequate for 30-40 days of the summer, yet concentrations on the Coastal Plain extended the adequate period through 70 days of the roughly 120 day growing season. In order to alleviate constraints of P and Cu in forages, caribou also may exploit variation in plant emergence along gradients of elevation, snow melt and with micro-topographical differences in hydrology, slope and aspect.

The difference in number of caribou between the WAH and CAH may be associated with differences in P and Cu between the summer ranges. Higher concentrations of Cu and P with lower ratios of Ca:P coincided with the range of the larger WAH herd. High Ca in calcareous soils are likely to form insoluble complexes with P thereby reducing the availability of P to forage plants in the Arctic Foothills and Coastal Plain of the CAH. Adsorption of P in soil may explain lower concentrations of P in forages even though concentrations of P in soils were greater on the CAH transect.

Warmer conditions on the WAH transect may also explain higher concentrations of P in forages despite lower soil P. Warming temperatures in the arctic have been associated with increased shrub biomass and increased mineralization rates of N and P (Schmidt et al. 2002, Welker et al. 2005). The summer range of the WAH lies within a region of high summer warming index where higher rates of vegetative growth is projected (Raynolds et al. 2008). Even though available phosphorus concentrations in soil are lower in the range of the WAH herd, the warmer summers experienced there may increase phosphorus mineralization rates and therefore increase phosphorus availability to plants despite the lower soil P concentrations. Weather cycles that

increase summer temperatures and thus forage growth may also enhance P supplies for caribou and thus drive cycles of population growth. Caribou in the WAH appear to benefit from positive phase of the Pacific Decadal Oscillation which coincides with warmer temperatures and increased biomass production over their summer range (Joly et al. 2011). Population trends of the CAH are influenced by phases of the Arctic Oscillation rather than the Pacific Decadal Oscillation. Although the positive phase of the AO is also associated with warmer temperatures and increased summer biomass, the population trends of the CAH are negatively associated with this phase (Joly et al. 2011). If CAH forages contain higher phosphorus concentrations in positive AO years, any benefit to CAH caribou may be counteracted by limitation of the availability of P in forages on calcareous soils.

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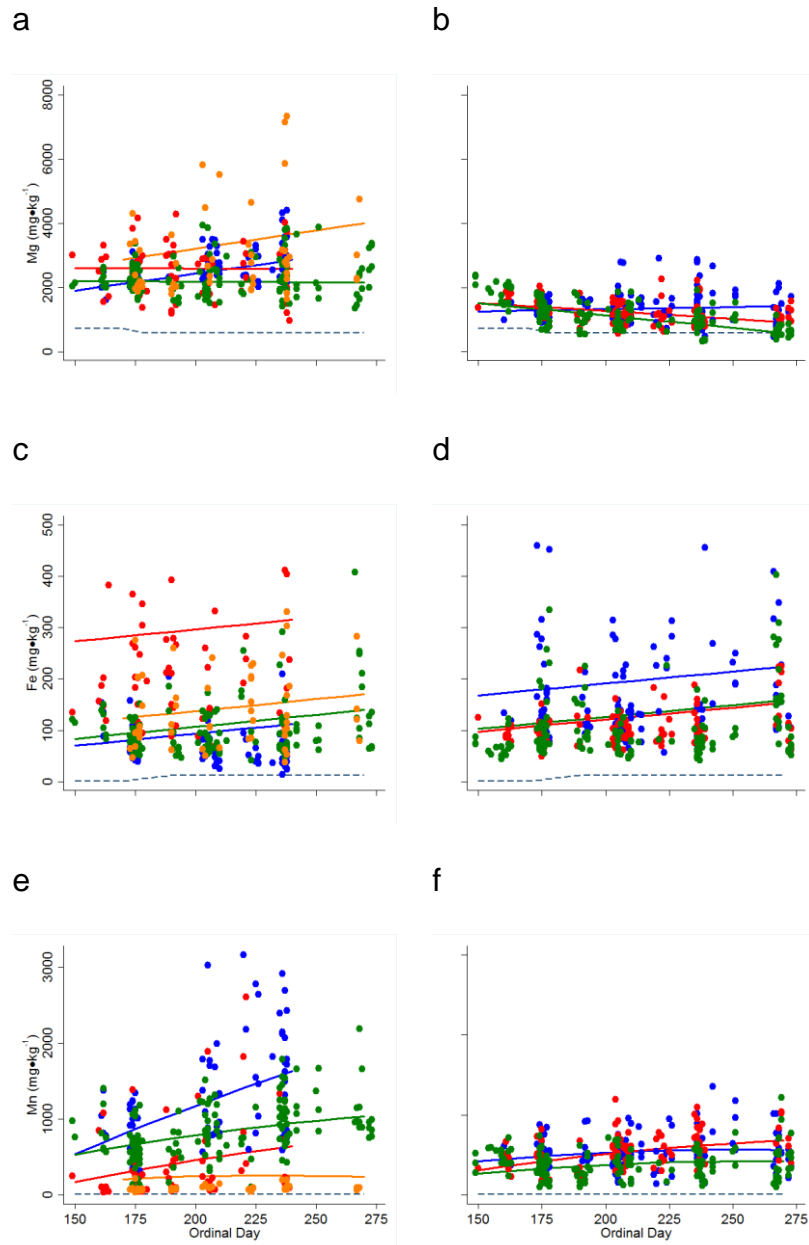
Figure A.1. Concentrations (mg • kg^{-1} dry matter) of Mg (a & b), Fe (c & d) and Mn (e & f) in forages used by arctic caribou in Alaska. Dashed lines represent estimated dietary requirements of lactating caribou. Browse (a & c): *B. nana* (blue), *S. pulchra* (green), *S. richardsonii* (orange) and forb *Pedicularis spp.* (red). Graminiods (b & d): *C. aquatilis* (blue), *C. bigelowii* (red), and *E. vaginatum* (green).

Table B.1. Effects of the composition of forage and soil on minerals (mg • kg^{-1}) in forages used by arctic caribou in Alaska. Regression coefficients are derived from a mixed model with nitrogen, fiber (ADF) and soil concentration as main effects, and sample location as a random effect. Underlined coefficients are significantly different from zero at $P < 0.05$. The range of values for each element available in soil (mg • kg^{-1}) is listed in the table. Corresponding ranges for nitrogen were 0.6−4.8 g • 100g^{-1} dry matter, 0.2 to 0.5 g • g^{-1} dry matter for fiber and 4.0−7.7 for pH

Element	N	ADF	Soil	pH	Soil Range
Ca	-3241	-32361	0.2	1846	289 – 16036
P	1147	417	-8.6	-170	2.9 – 18.5
Mg	-53	-5434	-0.3	-247	54.4 – 348.6
Na	-7.2	175	7.4	12.8	0.9 – 38.1
K	4134	5172	18.2	814	11.8 – 75.2
Fe	-7.4	122	0	17.9	52.9 – 446.1
Mn	-141	-1480	0.4	-188	2.9 – 79
Cu	2.1	5.8	0.4	0.1	0.5 – 3.8
Zn	-29.3	-769	1.6	5.6	0.3 – 5.5