





# Seasonal diets, trace minerals, heavy metals, and body condition: nutritional characteristics of barren ground caribou in Southwest Alaska

Robert G. Jespersen<sup>1</sup> , Renae Sattler<sup>2</sup> , Dominic Demma<sup>2</sup> , & Jeffrey Welker<sup>1,3</sup> 

*Collaborators: Federico Garrido-de León and Matteo Rizzuto*

<sup>1</sup> Department of Biological Sciences, University of Alaska Anchorage, Anchorage, Alaska, USA

<sup>2</sup> Alaska Department of Fish and Game, Palmer, Alaska, USA

<sup>3</sup> Ecology and Genetics Research Unit, University of Oulu, Oulu, Finland

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## Conflicts of Interest

The authors declare no conflicts of interest.

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## Corresponding Author

Robert G. Jespersen

Robert.Jespersen@usda.gov



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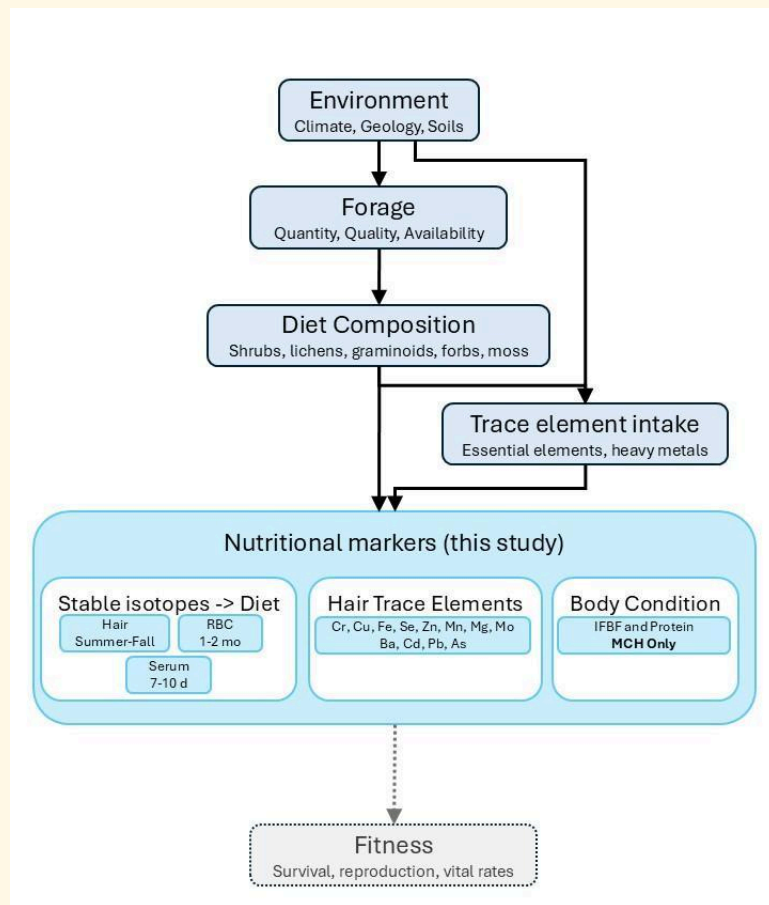
Wildlife Ecology

## Abstract

Barren-ground caribou (*Rangifer tarandus granti*) are a keystone species in tundra ecosystems experiencing rapid climate-driven habitat changes. Synchronous declines and persistent low numbers in many herds across the circumpolar north have raised concerns about the nutritional and demographic health of caribou populations. We sampled 170 animals from two recognized herds—the Mulchatna and Northern Alaska Peninsula herds—and three non-migratory groups in Southwest Alaska inhabiting areas around Goodnews Bay, Togiak, and Kukaklek Lake, analyzing stable



isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) and trace elements in tissues (hair, red blood cells, and serum). We also quantified body fat and protein in lactating and non-lactating females from the Mulchatna herd to assess body condition in the region's largest migratory herd. Using stable isotope mixing models and isotopic niche reconstructions—the first conducted for Southwest Alaska caribou—we quantified spatial and temporal differences in diet composition. We also assessed nutritional status using key markers such as  $\delta^{15}\text{N}$  and trace element concentrations along with body condition metrics. Our findings demonstrate significant spatiotemporal differences in dietary patterns and nutritional markers across groups. The Northern Alaska Peninsula herd exhibited the broadest isotopic niche and the highest consumption of deciduous shrubs (82% of summer-fall diet), while the Kukaklek Lake group displayed the narrowest niche, lowest  $\delta^{15}\text{N}$  levels, and highest levels of lead. Within the Mulchatna herd, the East subgroup showed elevated  $\delta^{15}\text{N}$  values (0.5-1‰ higher), improved mineral nutrition, and lower cadmium levels compared to the West subgroup. Redundancy analysis (RDA) revealed drivers of isotopic variation at two scales: at the regional scale caribou group was the dominant predictor, while within the Mulchatna herd, subgroup identity, lactation status, and several trace elements (barium, chromium, magnesium, lead) contributed additional fine-scale structure. A third RDA on the Mulchatna herd used body condition metrics—body fat and protein—as response variables and showed that only lactation status was a significant predictor, being negatively associated with body fat; subgroup, trace elements, and heavy metals did not explain variation in body condition within the Mulchatna herd. These results suggest that while subregional differences in forage quality and availability drive measurable variation in isotopic and trace elements in Southwest Alaska caribou, the fitness consequences remain unknown. This study highlights the importance of incorporating integrative dietary and physiological data into long-term monitoring to elucidate the nutritional consequences of environmental change in a rapidly shifting northern landscape.



**Abstract photo.** *Conceptual model illustrating the analytical approach to nutrition taken in this study. Environment shapes forage characteristics including nutritional quality and trace element content. Forage characteristics determine diet composition and trace element intake. Diet composition and trace element intake drive stable isotope variation in tissues, trace elements in hair, and body condition (assessed in the MCH only), the metrics we measured. Fitness outcomes were not directly measured.*

**Keywords:** Alaska, body condition, caribou, health indices, diet, isotopes, Mulchatna caribou herd, trace elements



## Introduction

Barren-ground caribou (*Rangifer tarandus granti*) are keystone herbivores in tundra ecosystems and a critical subsistence and cultural resource for many indigenous and rural northern communities (Bali and Kofinas, 2014, Borish et al., 2021, Fall, 2016). Recent declines and sustained low numbers in many herds are creating subsistence and conservation challenges across large parts of their range (Russell et al., 2024, Vors and Boyce, 2009). The synchronicity across populations suggests that climate-driven landscape changes (e.g., decreased tundra and increased shrub biomass, increased frequency of wildfire)—which are accumulating at an unprecedented rate across the Arctic (Box et al., 2019, Buchwal et al., 2020, Wenzl et al., 2024)—may be contributing factors. However, while climate change is undoubtedly impacting caribou (Joly et al., 2011, Mallory et al., 2018), the mechanisms remain uncertain. Other factors, such as density-dependent forage dynamics, anthropogenic development, disease, hunting, and predation, also influence caribou populations seemingly outside of “normal” fluctuations (Albon et al., 2002, Bergerud, 1996, Messier et al., 1988, Vors and Boyce, 2009). Likewise, concerns surrounding caribou resilience and best practices to support declining herds and maintain healthy populations vary widely among stakeholders. Increasingly, there is recognition that individual health and nutrition can help link environmental change to demography in northern ungulates (Rioux et al., 2022b).

As capital breeders, female caribou depend on enough high-quality forage during the warm season to replenish protein and fat reserves lost during the winter and support immune health, pregnancy, and lactation. Nutritional quality of the summer-autumn range is especially critical for female fecundity (Johnson et al., 2022, Mallory et al., 2018) through its influence on body condition (Cameron et al., 2011, Chan-McLeod et al., 1994), pre-winter fat accumulation (Adamczewski et al., 1987, Couturier et al., 2008, Crête and Huot, 1993), and mineral nutrition (Rioux et al., 2022b, Staal and White, 2001). Similar summer nutrition constraints affect other ungulates, limiting pregnancy rates and survival in elk (Proffitt et al., 2016), black-tailed deer (Parker et al., 1999), mule deer (Monteith et al., 2013), moose (Cook et al., 2021c), and bighorn sheep (Stephenson et al.,



2020), with trace mineral deficiencies linked to poor survival in moose (O'Hara et al., 2001) and black-tailed deer (Flueck, 1994). To meet these demands, barren-ground caribou rely on a seasonally dynamic diet that includes large quantities of vascular plants during the growing season and lichens during the snow-covered season (Webber et al., 2022). The abundance and phytochemical profiles of different plant functional types (PFTs; e.g. graminoids versus shrubs) shape range quality (Denryter et al., 2020, Johnstone et al., 2002, Richert et al., 2021). Simultaneously, ecological, environmental, and anthropogenic factors can influence foraging behaviour, predation (Gunn and Miller, 1986), insect harassment (Johnson et al., 2021), industrial infrastructure (Smith et al., 2023), and intraspecific competition (Ferguson et al., 2001) are known to impact foraging ground selection (Johnson et al. 2022).

The foraging landscape in the Arctic and subarctic is also changing rapidly. Tundra "greening" (Mekonnen et al., 2018) through the expansion of erect shrubs (Macander et al., 2022, Mekonnen et al., 2021), declines in graminoids, increases in the frequency of fires (Grabinski and McFarland, 2020) and rain-on-snow events (Pan et al., 2018, Hansen et al. 2019), and increasing moose abundance (Perry, 2023) are all impacting what is available and when it is accessible. Understanding how different herds meet their nutritional needs is therefore vital for effective conservation and management in a period of unprecedented ecological change.

A range of techniques has been employed to analyze caribou diets, including scat microhistology (e.g. Joly et al., 2007, Joly and Cameron, 2018), DNA-based methods (Mitchell et al., 2022, Nagati et al., 2024), direct observation (Denryter et al., 2017, Kuropat, 1984), and stable-isotope analysis of animal tissues (Hiltunen et al., 2026, Zhao et al., 2019). Stable isotopes offer the unique advantage of being time-integrated, such that values from tissues like serum, red blood cells (RBC), whiskers, and hair reflect nutrients assimilated over different temporal windows (Hilderbrand et al., 2011, Hiltunen et al., 2022, Schwertl et al., 2003). Crucially,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  also serve as proxies for an animal's trophic niche—the multidimensional space defined by its resource use and ecological role (Newsome et al., 2009, Shipley and Matich, 2020). In consumers  $\delta^{13}\text{C}$  values provide insight into the primary sources of dietary carbon, thus in herbivores  $\delta^{13}\text{C}$  values help distinguish between forage types, as  $\delta^{13}\text{C}$



values vary with photosynthetic pathway and water-use efficiency (e.g., lichens typically have much lower  $\delta^{13}\text{C}$  values than graminoids).  $\delta^{15}\text{N}$  values in consumers often reflect trophic level and may also reflect physiological condition, including nutritional stress (Gustine et al., 2011, 2012). In forage species  $\delta^{15}\text{N}$  varies with protein content and the nitrogen acquisition process employed by the forage species (e.g. mycorrhizal plants have lower  $\delta^{15}\text{N}$  than non-mycorrhizal species; Craine et al., 2009). Thus, major plant functional types (i.e. graminoids versus lichens) occupy distinct positions in  $\delta^{13}\text{C}$  -  $\delta^{15}\text{N}$  space, enabling inferences about trophic niche breadth, spatial variation in foraging, and dietary consistency across individuals or seasons.

Further, while trophic niche, digestible energy, and N content from forage are often the analytical focus in ungulate foraging ecology, essential trace elements such as chromium (Cr), cobalt (Co), copper (Cu), iron (Fe), manganese (Mn), molybdenum (Mo), selenium (Se), zinc (Zn), iron (Fe), magnesium (Mg) are also critical to metabolic health and reproductive success in ungulates (O'Hara et al., 2001, Puls, 1994), with low levels linked to poor individual health and recruitment (O'Hara et al., 2001). By contrast, non-essential heavy metals such as arsenic (As), barium (Ba), cadmium (Cd), and lead (Pb) are toxic (Puls, 1994), with high levels linked to reduced growth, reproductive impairment, and other health effects (Beest et al., 2023). Tissue levels of both essential and toxic elements are known to reflect dietary intake and the geochemical signatures of the landscape, which vary across ecozones and seasons (Gamberg et al., 2020, Oster et al., 2018, Staal and White, 2001). Thus, trace element profiles derived from caribou tissue can provide complementary ecological and nutritional information (Jutha et al., 2022a, Puls, 1994, Rioux et al., 2022b), allowing us to explore not only nutrient acquisition but also the potential environmental or physiological constraints on caribou foraging with implications for herd health and dynamics.

Here, we present the first stable isotope-based diet reconstruction and isotopic niche analysis for caribou in Southwest Alaska, a region containing the once-abundant Mulchatna herd (MCH)—which has declined ~90% since the 1990s—along with several smaller, less studied groups. We examined three linked components of nutritional ecology (Figure S1): (1) diet composition and foraging niche inferred from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in multiple

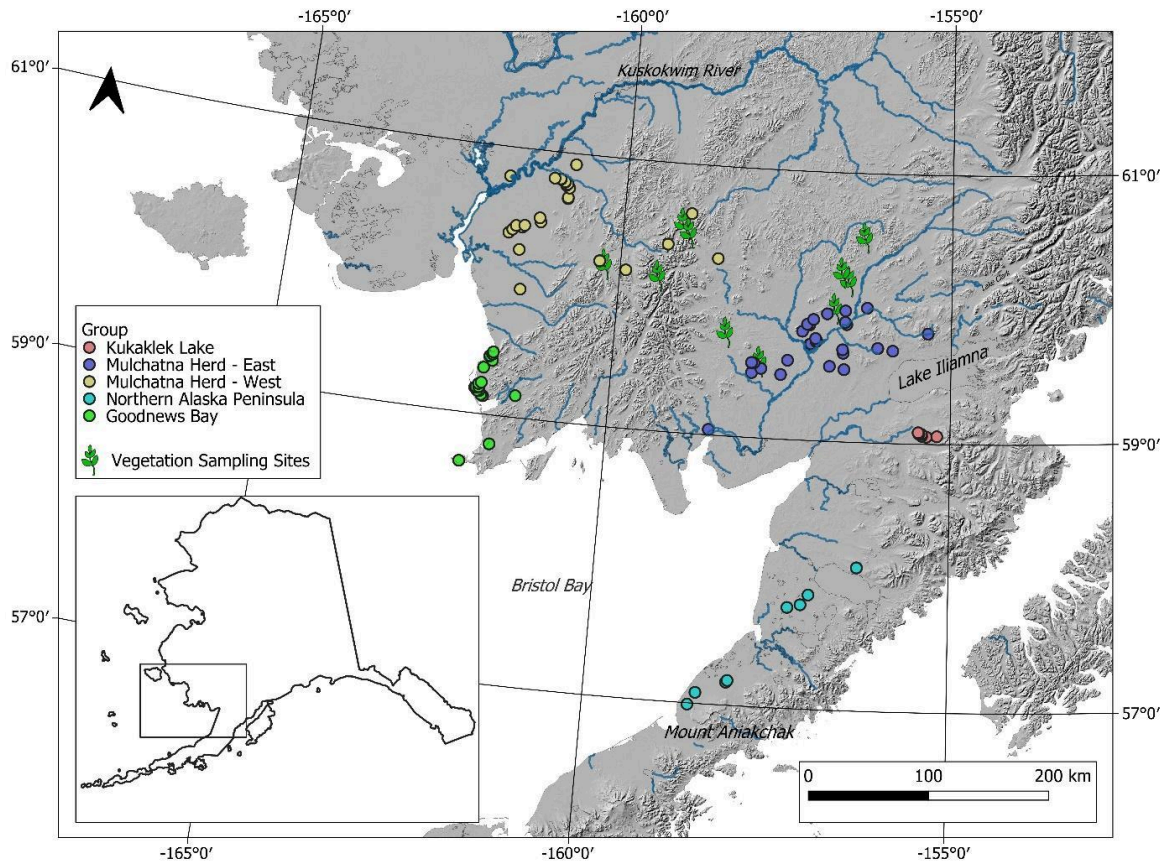


tissues representing distinct seasonal windows, (2) trace element and heavy metal levels measured in hair, which can reflect both access to micronutrients and exposure to potentially toxic elements, and (3) fall body composition in females from the MCH, integrating summer-fall foraging opportunity and lactation costs. We hypothesized that geographically discrete caribou groups would differ in these nutritional indicators, reflecting variability in forage quality across this vast landscape, and that the within-herd subgroups (MCH-East and West) would show corresponding differences in nutritional status. For the MCH specifically, we anticipated that nutritional indicators would correlate with body condition if subregional forage differences were substantial enough to affect individual performance. Such baseline data are urgently needed; understanding how caribou meet their nutritional needs in rapidly changing landscapes is essential for identifying habitat features that support population persistence and for guiding conservation in a warming Arctic.

## Methods and Materials

### Study area

Our study area encompassed much of Southwest Alaska and a portion of the northern Alaska Peninsula, including the lands bounded by the Kuskokwim River to the north, Bristol Bay to the west, Lakes Clark and Iliamna to the east, and Aniakchak National Monument to the south (Figure 1). The climate in this area is broadly subarctic with long, cold winters and short, cool summers with frequent precipitation; annual weather patterns are heavily influenced by proximity to the marine environment. Landscapes in Southwest Alaska are diverse and include extensive mountains, salmon-bearing streams and rivers, coastal deltas, boreal forest, tundra, peatlands, volcanoes, and large lakes. Likewise, vegetation across the region varies enormously, but generally is a mixture of wetlands, ribbon spruce forests, graminoid and shrub tundra, and lichen heath (Macander et al., 2022).



**Figure 1.** Sample locations in Southwest Alaska. Colored points represent caribou capture locations for individuals assigned to the Mulchatna caribou heard east and west subgroup (MCH-East, MCH-West), Northern Alaska Peninsula (NAP), Goodnews Bay (GB), and Kukaklek Lake (KL) area. Approximate herd boundaries are not available. Vegetation sampling locations are represented by green plant stems with leaves.

## Study populations

Caribou occur throughout the region, with state and federal management agencies recognizing three main herds (defined as female fidelity to a calving ground (Skoog, 1968) in the area; the MCH, Nushagak Peninsula, and the Northern Alaska Peninsula (NAP). The MCH is the largest and most historically significant (Murie, 1935, Skoog, 1968) but has declined by ~90% over the past three decades from ~200,000 animals in the late 1990s to ~13,000 animals (Lichwa and Landsiedel, 2024). As abundance declined the MCH's range contracted revealing spatial substructuring within the herd and two primary groups of migratory animals with spatially distinct calving grounds, divergent migration paths, and seasonal space use (referred to as



the East and West subgroups; Barten and Watine, 2020, Demma, 2019, Demma and Sattler, 2022). Despite hunting closures since 2019 and predator control efforts (Alaska Department of Fish and Game, 2016, 2023), MCH numbers have remained low since the early 2000's, raising questions on overall herd and range health (Demma and Sattler, 2022, Sattler, 2021).

Smaller groups of caribou occur (and calve) elsewhere in Southwest Alaska, but their ecological relationships with the MCH are poorly described. Local indigenous knowledge and collaring efforts over the past three decades indicate groups near Goodnews Bay (GB), Kukaklek Lake (KL), and NAP are resident and inhabit seasonal ranges of these groups mostly discrete from the East and West MCH groups (Valkenburg et al., 2003, Van Lanen et al., 2018). Despite their regional importance, Southwest Alaska caribou remain understudied (Colson et al., 2014) relative to other populations, with little data available regarding their diet, nutritional status, or behavior.

## Sample collection and analysis

### Caribou sampling

Between October 2020 and March 2023, 170 caribou were captured and sampled at several locations in Southwest Alaska (Figure 1). 116 female caribou were captured and sampled from the MCH, always in October, (60 in 2020, 16 in 2021 (due to equipment delays associated with COVID and severe weather patterns), and 40 in 2022). Smaller numbers of individuals were sampled from areas near GB (March 2023, n=23; April 2022, n=13), KL (February, 2023, n=8), and the NAP (February, 2023, n=10).

Caribou capture and handling was performed in accordance with the Alaska Department of Fish and Game (ADFG) Division of Wildlife Conservation protocol (Alaska Department of Fish and Game 2020) and approved by the ADFG Institutional Animal Care and Use Committee (IACUC Nos. 0102-2020-61, 0102-2021-51, 0102-2022-054). Because our study sought to evaluate seasonal diets and indices of health in mature females, we avoided capturing juvenile animals (< 2 year old), which are generally visually distinguishable from older animals, and confirmed this with dentition (Miller, 1972).



Caribou were chemically immobilized by aerial darting from a Robinson R-44 helicopter with 5.0 mg of thiafental (Wedgewood Pharmacy, USA) and 70 mg of xylazine hydrochloride (Wedgewood Pharmacy, USA) injected through a 1.5-cc barbed dart fired from a projector rifle (model 196, Pseudart, Williamsport, PA, USA). Immobilized caribou were placed in ventral recumbency, masked, given supplemental oxygen (1-1.5 liters/min), and heart rate, respiration rate, and rectal temperature monitored throughout sedation. Following sample collection, chemical immobilization was reversed by administering 10.0 mg of naltrexone (Wedgewood Pharmacy, USA) per 1.0 mg of thiafental injected intramuscularly, and 1.0 mg of atipamizole (Wedgewood Pharmacy, USA) per 10 mg of xylazine, one half given intravenously and one half intramuscularly.

For all caribou, hairs (including root) were plucked from the shoulders, and blood was drawn from the saphenous or jugular vein into a non-additive vacutainer blood tube and centrifuged (15 mins at 3000 - 3500 rpms) to separate serum and red blood cells. Spun blood tubes were frozen at -80 °C until stable isotope analysis. By sampling multiple caribou tissues at two capture periods (fall and late winter), diet estimation through isotopic signatures can be generated for multiple seasonal windows (Table 1).

**Table 1.** Conceptual diagram showing the general seasons the isotopic signatures from caribou hair, red blood cells, and blood serum represent depending on the timing of caribou sampling. For example, serum from winter captures reflects diet in March, whereas serum from fall captures represents diet in October. Caribou were sampled from the Mulchatna caribou herd (MCH), Northern Alaska Peninsula herd (NAP), and the Kukaklek Lake (KL) and Goodnews Bay (GB) areas, all in Southwest Alaska.

Sampling		Spring		Summer		Fall			Winter				
		May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	April
Winter (NAP, KL, GB)	Hair		■										
	RBC										■		
	Serum											■	
Fall (MCH)	Hair		■										
	RBC						■						
	Serum											■	

\*Mulchatna caribou were captured in mid-October, and caribou from the KL, GB, NAP animals were sampled late February to early April.



While under sedation Mulchatna caribou underwent additional sampling as part of a complementary study to estimate body condition (n=102) following protocols from Cook et al. (2021a). In brief, these caribou were placed in a net and weighed, assigned a body condition score based on palpation and prominence of skeletal features, and ultrasound-derived measurements of rump fat and loin thickness were collected (Ibex Pro ultrasound, 5-9 MHz linear probe, E.I. Medical Imagine, Loveland, CO, USA). Females were evaluated for evidence of lactation and were considered lactating if milk could be manually expressed from any teat and non-lactating if no milk could be expressed; calf presence near capture sites was also considered. Five caribou appeared to be ceasing lactation (4 in MCH-West, 1 in MCH-East) with a semi-clear fluid extractable from at least one teat, and were excluded from analysis. Caribou body condition metrics (i.e., weight, body condition score, ultrasound measurement of loin thickness and rump fat) were combined to calculate percent ingesta-free body fat (body fat, corrected for body size) and protein (kg) using published equations (Cook et al., 2021a).

### **Forage sampling**

Accurate estimates of the isotopic composition of potential diet items are critical to stable isotope-based diet analyses. At the time of the study, isotopic data from forage species in Southwest Alaska were unavailable. Thus, to improve the accuracy of our mixing models, forage samples were collected within the MCH range twice during the study. The first collection, in late May 2021, was opportunistic and occurred during green-up, and included six sites near the MCH calving grounds, where vegetative samples (new growth and previous year) of known forage species were collected (n=36 individual samples, Table S1).

We performed a more systematic collection between June 21 and June 23, 2022 to capture the full range of isotopic variability in potential forage species during the peak growing season. We manually selected four survey blocks in the west and east MCH summer range. Blocks were 40 m width and variable length, depending on considerations of terrain and vegetation heterogeneity, to constrain sampling logistics to feasible areas that captured a wide range of variation in plant community composition,



structure, and associated environment. Within each survey block, we selected three sites (12 total) according to a stratified random design where each site occurred within a different vegetation type according to classified foliar cover maps (Nawrocki, 2021). At each site, 12.5 m radius plots were established, and samples of each vascular plant species and forage lichen (leaves or lichen tissue) were collected within the plot, for a total of 147 individual samples. In total, our two sampling campaigns yielded 184 individual forage samples representing 101 species and 70 genera (Table S1).

### Sample processing

Initially, we analyzed hairs using two approaches: whole hairs (2020-2021) and segmented hairs (2022) split into proximal and distal segments to evaluate whether finer temporal resolution was achievable (Rogers et al., 2020, Schwertl et al., 2003). However, because the segmented hairs exhibited minimal intra-hair isotopic variation and caribou hair growth rates remain poorly characterized, we ultimately aggregated all samples to whole-hair values using mass-weighted means. All subsequent analyses use these whole-hair values, referred to simply as “hair.”

Hairs were cleaned in a 2:1 chloroform: methanol solution for 24 h and rinsed with deionized water 3-5 times to remove surface oils and debris. Cleaned hairs were oven-dried at 50 °C for 24 hours. Blood components were freeze-dried for 48 h and ground to a fine powder with a ball mill (Mini Beadbeater-16, Biospec Products Inc., Bartlesville, OK). Likewise, individual forage samples (n=183 total) from both sample campaigns were dried at 60°C for a minimum of two weeks, after which each sample was ground to a fine powder.

Subsamples of caribou hair, blood serum, red blood cells and forage were analyzed for N (%), C (%),  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$  with an elemental analyzer (model 4010, Costech Analytical, Valencia, CA, USA) linked to a continuous flow isotope ratio mass spectrometer (model DeltaPLUS XP, Thermo-Finnegan Scientific, Waltham, MA) at the University of Alaska-Anchorage.

A subset of hairs was cleaned according to Jutha et al. (2022b) and analyzed for the essential trace elements chromium (Cr), copper (Cu), iron



(Fe), molybdenum (Mo), magnesium (Mg), manganese (Mn), selenium (Se), and zinc (Zn) as well as the toxic heavy metals arsenic (As), barium (Ba), cadmium (Cd), and lead (Pb) at the University of Idaho's Analytical Science Laboratory (Moscow, Idaho).

## Statistical analysis

### Isotope status

We compared the isotope status ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values) among caribou groups in red blood cells, serum, and hair using one-way ANOVA models. Residuals were assessed for normality and homoscedasticity. All analyses were performed using R 4.5.0 (R Core Team, 2025). Post-hoc means separation was performed using the Tukey HSD test in the *emmeans* package (Lenth, 2021).

### Isotopic niche space

We quantified isotopic niche breadth and overlap among caribou herds for each isotopic time window using SIBER (Stable Isotope Bayesian Ellipses in R package version 2.1.9; Jackson et al., 2011). Bayesian posterior ellipse areas ( $\text{SEA}_B$ ) were estimated by fitting bivariate normal distributions to  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data using Markov Chain Monte Carlo (2 chains, 20,000 iterations, 1,000 burn-in, thinning = 10) with Inverse Wishart priors on covariance matrices and vague normal priors on means.  $\text{SEA}_B$  represents the posterior distribution of the standard ellipse area, containing approximately 40% of the data and representing the core isotopic niche. Pairwise niche overlap was calculated using the "bayesianOverlap" function with `p.interval = NULL` (40% core ellipses) and 100 posterior draws. We report 95% credible intervals for  $\text{SEA}_B$  and proportional overlap (overlap area / ellipse area  $\times$  100).

### Diet estimation

We estimated seasonal diet composition using three tissues (i.e., hair, red blood cells, serum) to capture different temporal windows (Table 1). In cervids, hair is shed at the end of the cold season and new growth occurs during the warm season, thus isotopic values of hair integrate caribou



diets from early summer through fall (Cuyler and Øritsland 2002, Table 1). Blood components reflect shorter windows: serum integrates forage consumed during the previous 7-10 days while red blood cells integrate the past 1-2 months (Lecomte et al., 2011, Rioux et al., 2020, Tieszen et al., 1983).

Diet source selection directly influences stable isotope mixing model (SIMM) predictions. Because plant functional types (PFTs) in this landscape share biochemical traits that shape their isotopic profile (Jespersen et al., 2018, Welker et al., 2005), we aggregated our forage isotope data by PFT (Figure S2) and sampling period (May, 2021 or late June, 2022). May 2021 PFT groups were fungi, lichen, graminoid, and deciduous shrubs + moss. June 2022 PFT groups were lichen, graminoid, shrub, forb, and spore-bearer (e.g. *Equisetum* spp. and ferns). We did not collect fungi during June 2022 sampling, but because fungi are a known caribou food item (Druckera et al., 2010) we used plausible values from fruiting body samples collected in a similar landscape in Finland (T.M. Hiltunen, unpublished data) in our mixing models.

Mixing models assume isotopic values primarily reflect diet, but physiological and environmental factors can also influence isotopes—for example, lactation status (Gustine et al., 2012), sampling year, and trace-element or heavy-metal levels (Rioux et al., 2022b; see below). Modern Bayesian techniques can accommodate some of these additional variance sources, but because our primary interest was group-level dietary differences we first evaluated whether lactation and year might confound interpretation. We tested for differences in isotope values among years and between lactating and non-lactating MCH females using additive linear models with year and lactation status treated as categorical predictors. Although a few comparisons reached statistical significance, the modeled effect sizes were generally small compared with background variation in diet sources and population isotope values (Figures S2 and S3). Also, because we lacked repeated measures on individuals, we could not separate individual-level from interannual variation or definitively attribute isotopic shifts to lactation versus diet. Consequently, we pooled years and lactation status for diet analyses.



Dietary proportions were estimated using concentration-dependent Bayesian stable isotope mixing models in MixSIAR (Stock et al., 2018). Models were fit using generalist priors. We evaluated the use of informative priors from West Arctic Herd diet estimates (Joly et al., 2015, Joly and Cameron, 2018) but those priors matched our data poorly, used different forage categories, and produced poor convergence (Gelman-Rubin and Geweke diagnostics), so we retained generalist priors. Tissue-specific isotope discrimination factors (TDFs) were: hair,  $\delta^{13}\text{C} = 2.61\text{‰}$  and  $\delta^{15}\text{N} = 4.23\text{‰}$  (Rioux et al., 2020); RBC,  $\delta^{13}\text{C} = 3.7\text{‰}$  and  $\delta^{15}\text{N} = 2.5\text{‰}$  (Halley et al., 2010); serum,  $\delta^{13}\text{C} = 3.34\text{‰}$  and  $\delta^{15}\text{N} = 5.02\text{‰}$  (Rioux et al., 2020).

For each tissue collected we estimated diet proportions using caribou group (KL, NAP, GB, MCH-East, and MCH-West) as a random effect, allowing us to simultaneously estimate at the population and group levels. Posterior distributions and the Gelman-Rubin and Geweke diagnostics were all used to confirm model convergence.

### **Trace elements and heavy metals**

We compared hair trace element and heavy metal levels among Southwest Alaska groups using ANOVA models for censored data (datasets with non-detects) from the *NADA2* R package (“*cenanova*” function; Julian and Helsel, 2021) followed by a Tukey's multiple comparison test for means separation. To evaluate potential biological relevance, values were compared with published values from mountain and woodland caribou (Jutha et al., 2022a, Rioux et al., 2022).

### **Factors influencing isotopic variation and body condition**

While our mixing models (above) estimate dietary proportions from isotopic signatures, substantial variation in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values can remain among individuals with similar inferred diets due to physiological state, environmental context, and nutritional status. To identify factors contributing to isotopic variation beyond isotope-inferred dietary composition, we used redundancy analysis with hair samples (RDA; following methods in Rioux et al., 2022b) at two spatial scales: 1) an all-groups analysis to evaluate broad-scale geographic patterns, and 2) a



MCH-only analysis to examine finer scale variation in this herd. We conducted an additional RDA within the MCH to test whether the same predictors explained variation in body composition (body fat and body protein). Both analyses were performed using the *vegan* package (Oksanen et al., 2022) in R.

For the all-groups RDA, we included geographic group (KL, NAP, GB, MCH-East, and MCH-West) and trace element concentrations as predictors of hair  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . For the MCH-only isotope RDA we included subgroup (East vs. West) and lactation status (lactating vs. non-lactating), and the same suite of trace elements as predictors; the response variables were again  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . The MCH-only body condition RDA used the same predictor set but with IFBF and total body protein as response variables. For all RDAs, trace elements with high levels of non-detects were excluded from the analysis; these were As, Cd, and Mo. All predictor variables were centered and standardized prior to analysis. Multicollinearity among predictors was assessed using variance inflation factors (VIF); in the all-groups RDA only Manganese exceeded 5 and was excluded from the final model. In both MCH-only RDAs no variables exceeded VIF = 5. The significance of the overall model, individual axes, and predictor variables was assessed via permutation tests ( $n = 999$  permutations).

### **Body condition**

Using published equations in Cook et al. (2021a), we combined body condition indices (i.e., weight, body condition score, ultrasound measurement of loin thickness and rump fat) to calculate body fat (%) and protein (kg). Individuals where body mass was not collected were assigned the mean mass from females captured in the same year to allow full calculation of body composition metrics. We evaluated differences in body fat and protein using two-way ANOVA models with lactational status (lactating vs. non-lactating) and herd subgroup (MCH-East vs. MCH-West) as fixed effects, including their interaction. Model assumptions were assessed using residual diagnostics, and body fat was log-transformed to meet ANOVA assumptions regarding residual normality and homoscedasticity. We compare our measures of caribou body fat estimates to categories of nutritional limitations ranging from severe (< 6%), moderate (6-9%), mild (> 9 - 12%), or little-to-none (>12%) developed from captive elk nutritional



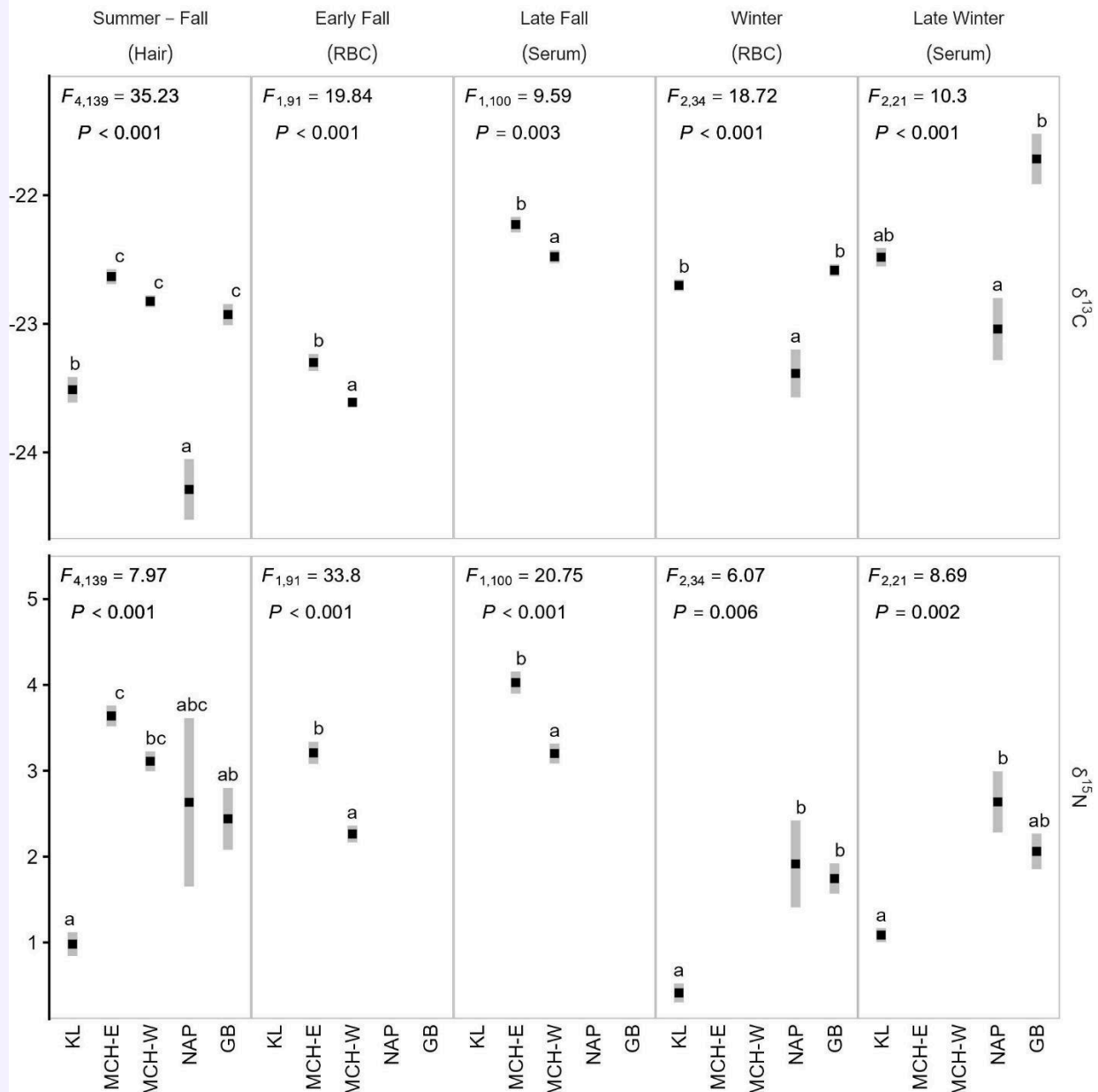
studies that linked body composition metrics to fitness performance measures (Cook et al. 2004) and have been used to describe the nutritional condition of free-ranging moose (Cook et al. 2021a).

## Results

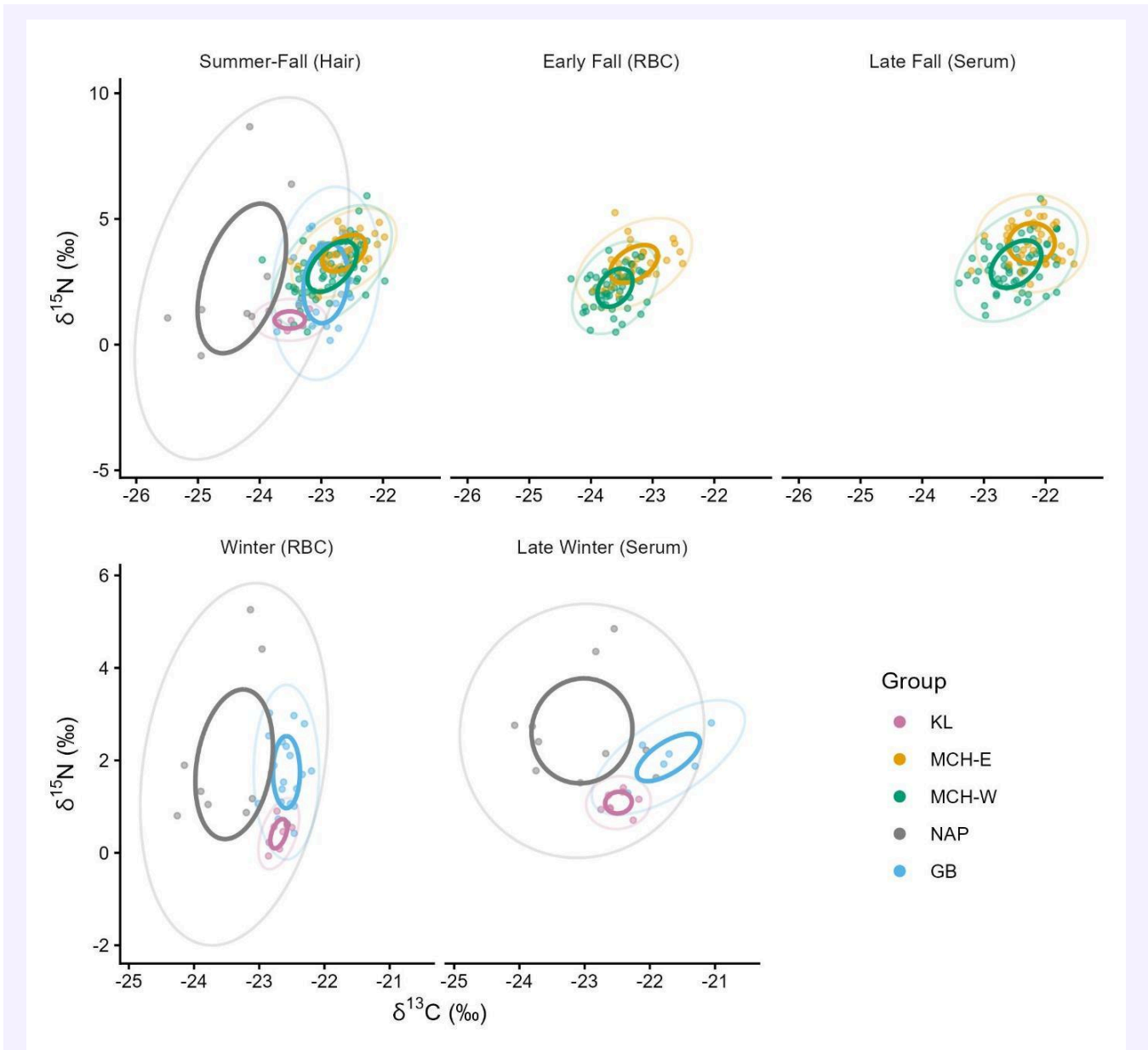
### Group isotope status and niche space

Caribou groups differed in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  status in all tissues and sampling periods (Figure 2). Caribou from the NAP group tended to be lowest in  $\delta^{13}\text{C}$ , while caribou from the KL displayed the lowest  $\delta^{15}\text{N}$  values. During all seasons where data was available the MCH-East displayed higher  $\delta^{15}\text{N}$  (0.5-1 ‰) values than the MCH-West.

The isotopic niche breadths of Southwest Alaska caribou varied across groups and seasons (Figures 3 and S4). The NAP consistently exhibited the broadest isotopic niche, with median  $\text{SEA}_b$  values ranging from 2.7 to 6.4, while the KL group maintained the narrowest niches (0.11–0.28). Niche breadth tended to be lowest during the winter and higher in the summer-fall. The MCH-East and West groups' isotopic niche breadths were indistinguishable during all seasons.



**Figure 2.** Stable isotope levels ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) in red blood cells (RBC), serum, and hair from the Mulchatna caribou herd east and west subgroups (MCH-E and MCH-W), Northern Alaska Peninsula herd (NAP) and Goodnews Bay (GB), and Kukaklek Lake (KL) area. Values are displayed as mean  $\pm$  SE. ANOVA statistics are inset at the top of each panel. Different letters indicate significant differences among groups at the  $P < 0.05$  level.



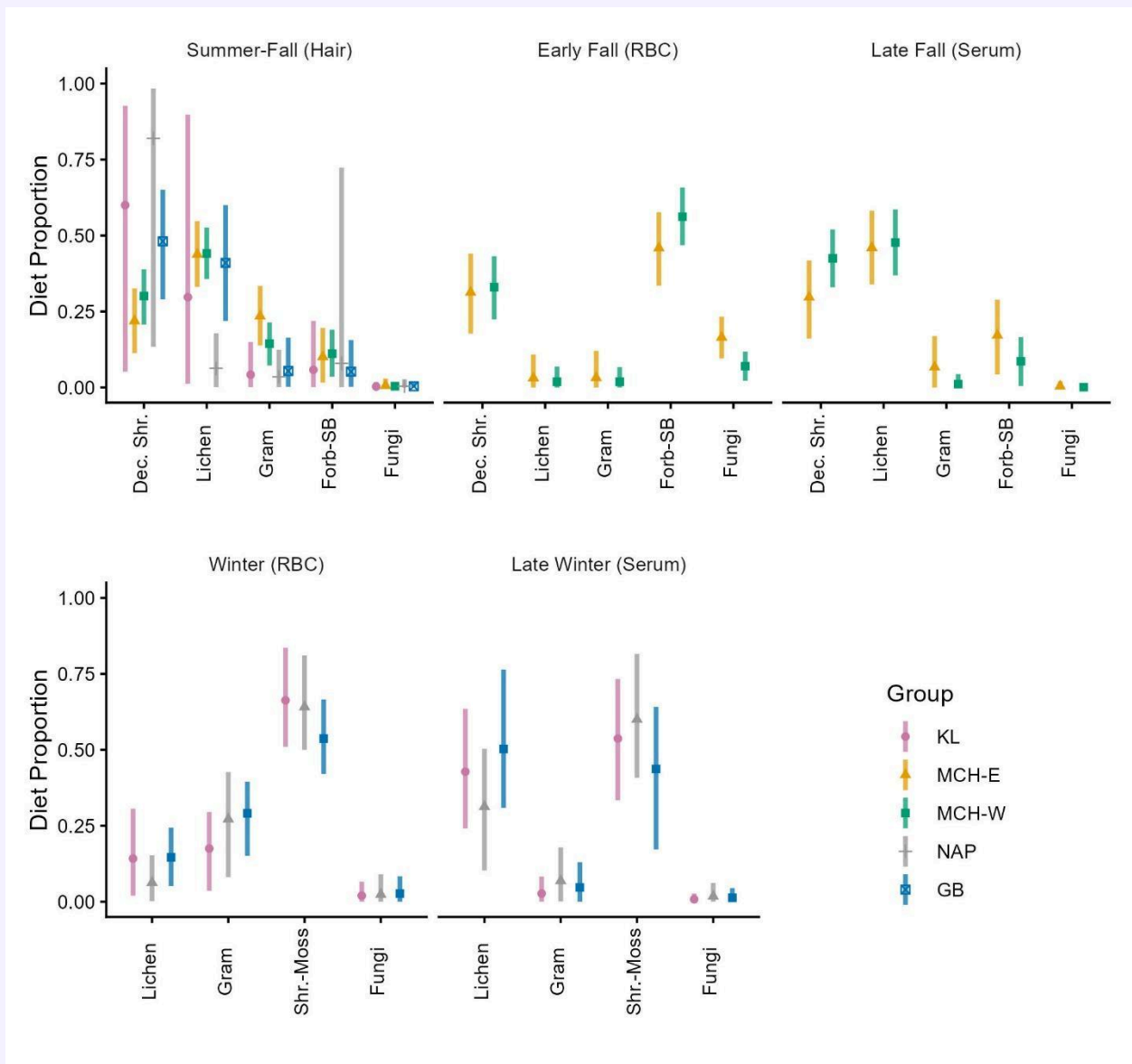
**Figure 3.** Isotopic niche spaces of Southwest Alaska female caribou 2020 – 2023 by season from 2020 - 2023, including individuals from the Mulchatna caribou herd east and west subgroups (MCH-E and MCH-W), Northern Alaska Peninsula herd (NAP), and Goodnews Bay (GB), and Kukaklek Lake (KL) areas. Points show individual  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (‰). Solid ellipses denote corrected standard ellipse areas (SEAc, 40% probability), representing the core isotopic niche. Faint ellipses show 95% prediction ellipses for context. Ellipse areas are expressed in permille squared (‰<sup>2</sup>), reflecting the dispersion of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values.



Isotopic niche overlap among the groups varied between groups and seasons (Figure 3). Overlap of the core ellipses was negligible in winter, with median values near zero, but increased during summer and fall. In the summer through fall period, the strongest overlap occurred among GB, MCH-E, and MCH-W, with median overlap proportions reaching 36%, indicating substantial similarity in isotopic space. In contrast, NAP's broad niche showed little overlap with other herds, and KL's narrow niche overlapped minimally with other groups.

### **Diet**

Diet estimates from MixSIAR indicated that Southwest Alaska caribou groups shifted their diet substantially throughout the year, differed in their dietary preferences during some seasons, and consumed unequal proportions of diet items during all periods (Figure 4). We describe diets by broad seasons across tissue types (Table 1).



**Figure 4.** Group-level diet estimates for Southwest Alaska caribou, 2020-2023. Bars are median  $\pm$  95% credible interval for proportional contribution of each diet item estimated in MixSIAR. Bars are colored by group. Summer through fall estimates are derived from hair, late summer through early fall estimates from red blood cells, and late fall estimates from serum from October sampling. Winter and late winter diet estimates are derived from blood and serum from late February through early April sampling.

### Summer - Fall

During summer and early fall (reflected by hair, Table 1), deciduous shrubs dominated caribou diets, comprising 46% (95% CI: 19–71) of the assimilated diet, followed by lichens (32%, 95% CI: 11–58), graminoids



(12%, 95% CI: 2–30), and forbs and spore-bearers (11%, 95% CI: 2–31); fungi were negligible (<1%, Figure 4). Group-specific estimates revealed strong dietary differences during this period but all included considerable amounts of lichen during the growing season. The NAP herd consumed markedly more deciduous shrubs (82%) relative to other groups, although high individual variation led to high uncertainty (95% CI: 13–98), while GB displayed a balanced diet of deciduous shrubs (48%, 95% CI: 29–65) and lichens (41%, 95% CI: 22–60). KL also relied primarily on deciduous shrubs (60%, 95% CI: 5–93) followed by lichens (30%, 95% CI: 1–90), albeit with high uncertainty in estimates for both items. In contrast, the MCH subgroups showed more balanced diets: MCH-East consumed modest amounts of deciduous shrubs (22%), yet with more lichens (44%) and slightly more graminoids (24%), whereas MCH-West consumed more deciduous shrubs (30%), but with more lichens (44%) and less graminoid input (14%). No consumption of fungi was detected in any caribou groups in the summer-fall period (Figure 4).

### **Fall**

In early fall (represented by RBC from the MCH subgroups), forbs and spore bearers became the dominant diet items, constituting 42% (95% CI: 10–67) of the overall (both subgroups) assimilated diet, followed by deciduous shrubs (32%, 95% CI: 8%–59%, Figure 4). Diet composition was similar in the MCH-East and MCH-West, except that the MCH-East subgroup consumed more fungi (17% and 7%, respectively). By late fall (reflected in serum from the MCH subgroups), there were no detectable dietary differences between the subgroups, and lichens and deciduous shrubs were again the primary diet items, comprising 35% (95% CI: 5–67) and 31% (95% CI: 5–63) of the overall assimilated diet, respectively.

### **Winter**

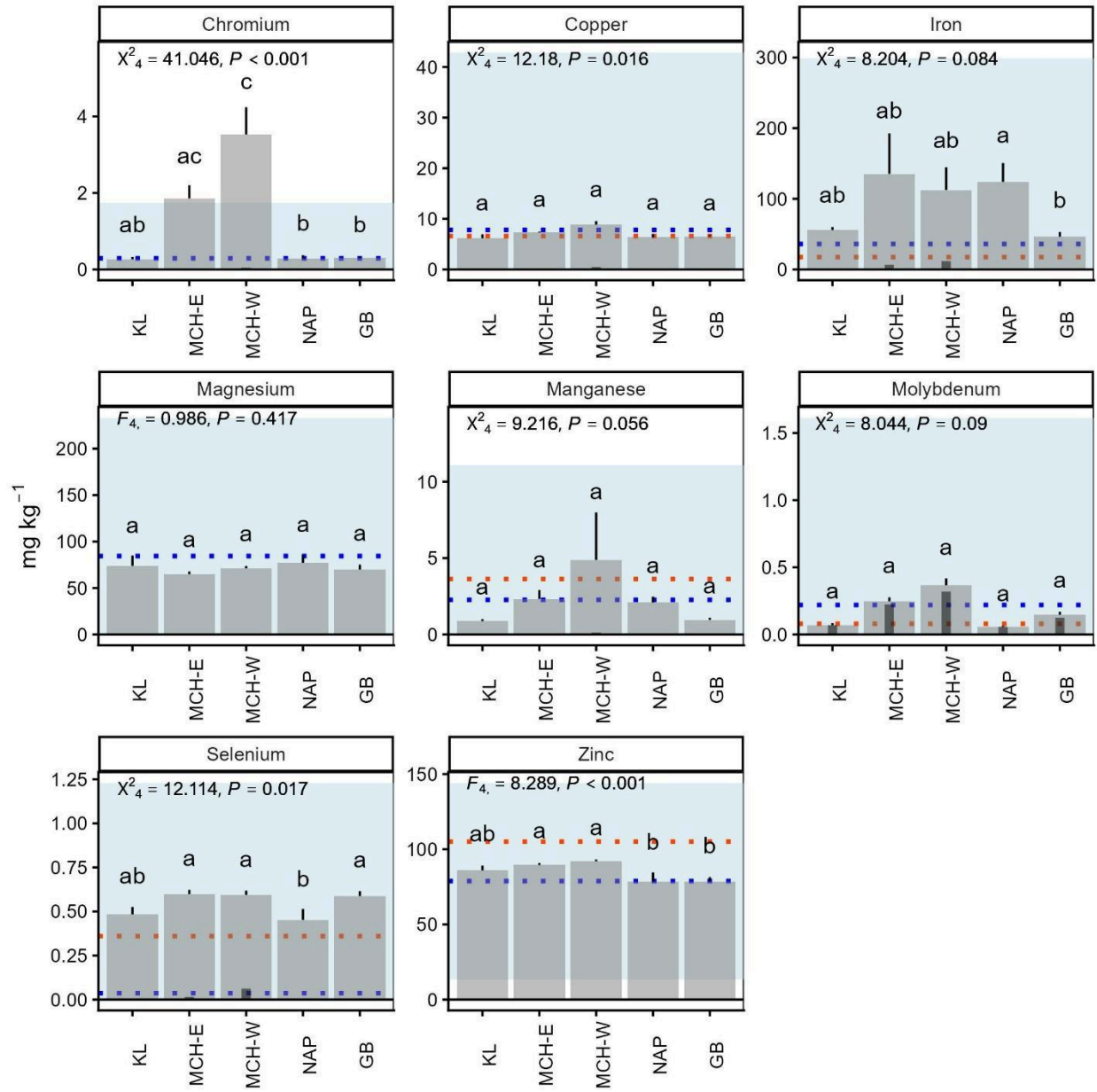
During winter (reflected by RBC from caribou captured in late February - early March, 2022, Table 1), shrub-moss dominated diets of KL, NAP, and GB caribou, comprising 56% (95% CI: 23–76) of the assimilated diet, followed by smaller quantities of graminoids (27%, 95% CI: 9–52) and lichens (14%, 95% CI: 3–35, Figure 4). In late winter (reflected by serum from the same captures), lichens became more prominent, constituting



41% (95% CI: 14-69) of the assimilated diet, although shrub-moss remained the single largest diet component, constituting 49% (95% CI: 16-74). No measurable differences in dietary preference were detected across caribou groups during winter.

### **Trace elements and heavy metals**

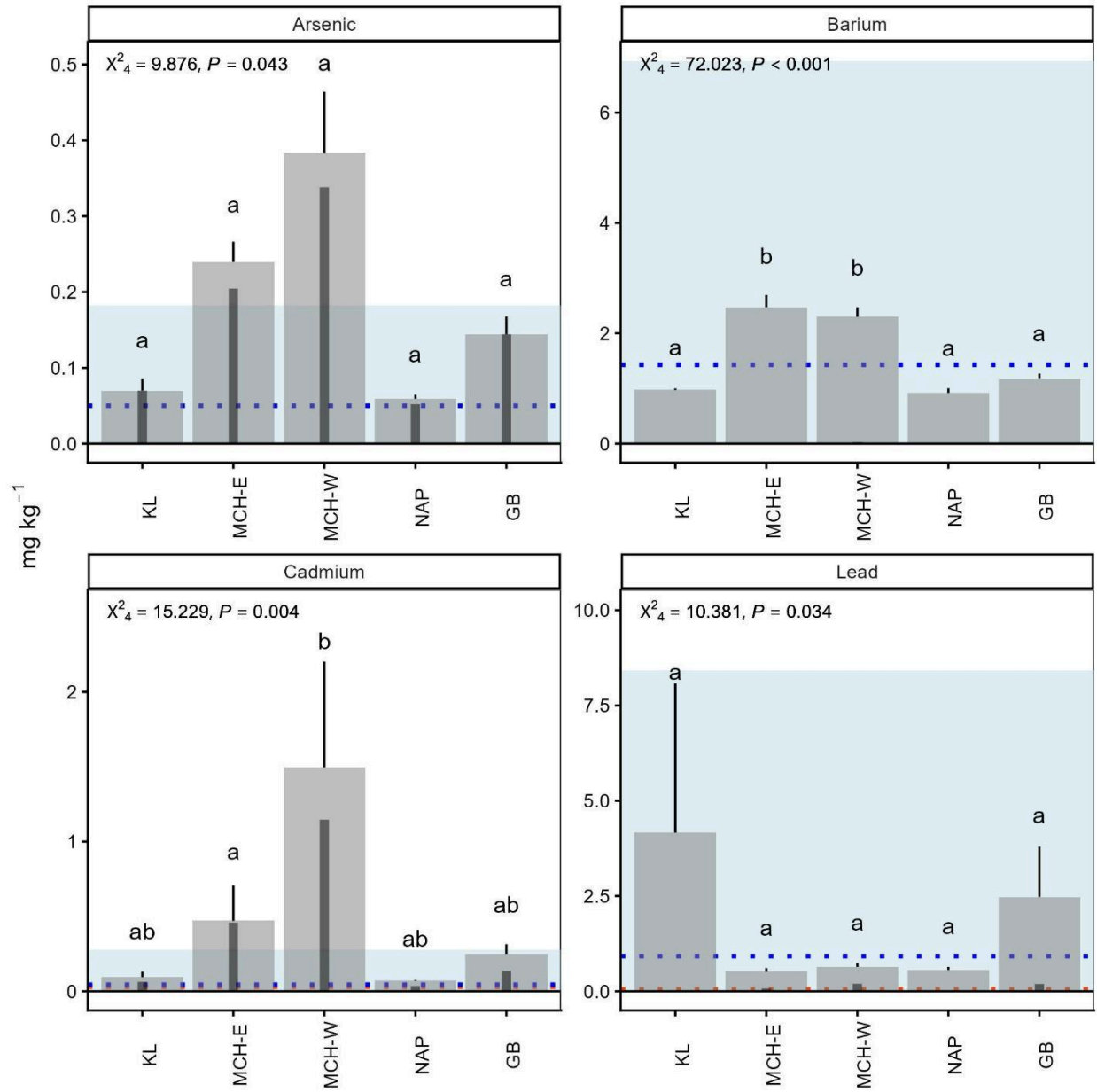
Trace element concentrations differed significantly among the Southwest Alaska caribou groups for Cr, Cu, Fe, Se, Zn, and Mg (Figure 5). The most pronounced group difference was in Cr, which was more than two times higher in the MCH-West than MCH-East and three times higher than in the KL, NAP, and GB groups. Differences in Cu, Fe, Se, Zn, and Mg between some groups were smaller in magnitude but still statistically supported. Trace element levels in Southwest Alaska caribou generally fell within ranges reported from hair samples in other caribou populations (Jutha et al., 2022, Rioux et al., 2022).



**Figure 5.** Comparison of trace mineral levels in hair from adult female caribou from the Mulchatna caribou herd east and west subgroups (MCH-E and MCH-W), Northern Alaska Peninsula herd (NAP), and Goodnews Bay (GB), and Kukaklek Lake (KL) area in Southwest Alaska. Large grey bars display as mean + SE. The inset darker bars represent the proportion of values that fell below detection limits, where the height of the larger bar represents a proportion of 1, thus bars without any inset bars (e.g. Mg) did not have any values below detection limits. Groups with different letters are significantly different at the  $P < 0.05$  level. Test statistics (F-ANOVA,  $\chi^2$ -ANOVA for censored data) are inset. The blue dashed line and shaded area represent mean  $\pm$  SD from Rioux et al. (2022) for mountain caribou (note: the lower limit for the shaded area is zero). The orange dotted line is the mean value reported in Jutha et al. (2022) for woodland caribou.



We found significant differences in levels of Ba, Cd, and Pb among groups (Figure 6). Cd levels in the MCH-West group were exceptionally high, exceeding other groups' levels by at least 2x; although there were large proportions of animals that fell below detection limits in all groups. Likewise, there was high intergroup variation in Pb levels; the KL group displayed the highest Pb levels, followed by the GB group. Detectable levels of As were found in all caribou groups, although there was a large proportion of non-detects and no differences between groups were observed. Heavy metal concentrations showed substantial variation relative to levels reported in other caribou populations (Jutha et al., 2022a, Rioux et al., 2022) with MCH-West Cd levels elevated compared to published values.

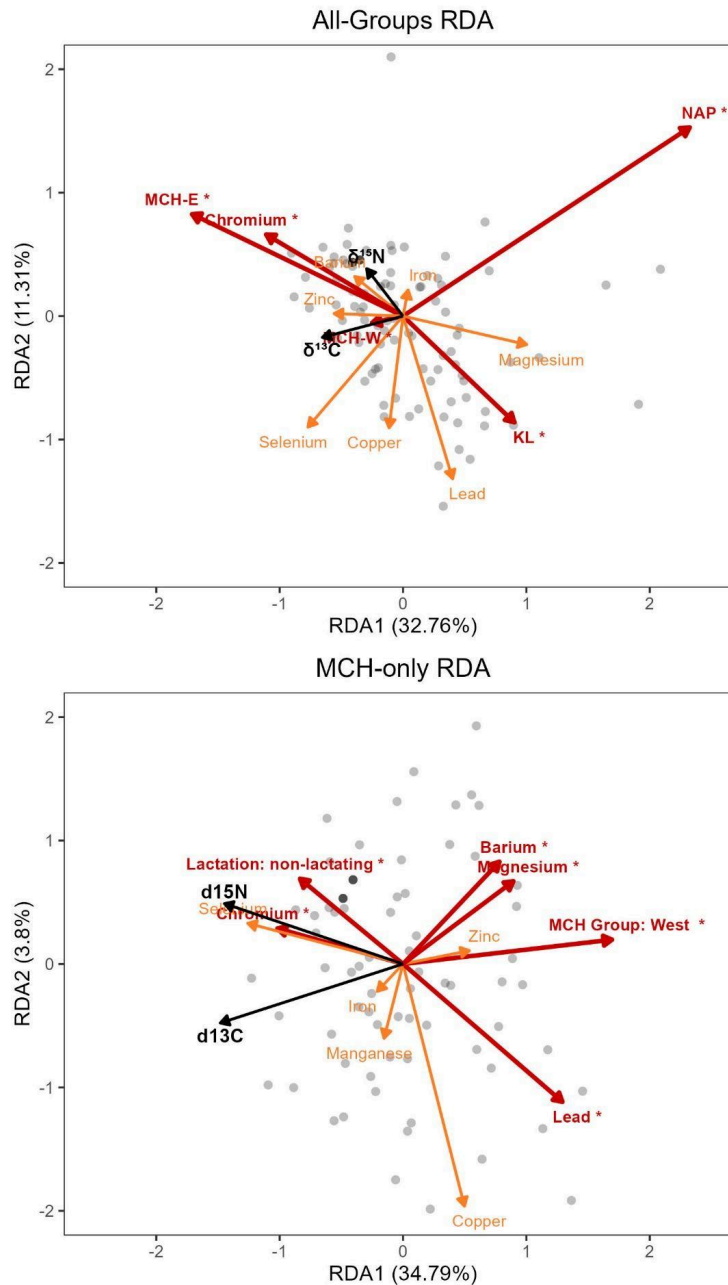


**Figure 6.** Comparison of heavy metal levels of arsenic, barium, cadmium, and lead in hair from adult female caribou from the Mulchatna caribou herd east and west subgroups (MCH-E and MCH-W), Northern Alaska Peninsula herd (NAP), and Goodnews Bay (GB), and Kukaklek Lake (KL) area in Southwest Alaska. The inset darker bars represent the proportion of values that fell below detection limits, where the height of the larger bar represents a proportion of 1, thus bars without any inset bars (e.g. Ba) did not have any values below detection limits. Groups with different letters are significantly different at the  $P < 0.05$  level. Test statistics (F-ANOVA,  $\chi^2$ -ANOVA for censored data) are inset. The blue dashed line and shaded area represent mean  $\pm$  SD from Rioux et al. (2022) for mountain caribou (note: the lower limit for the shaded area is zero). The orange dotted line is the mean value reported in Jutha et al. (2022) for woodland caribou.



### Factors influencing isotopic variation in the MCH

The RDA revealed a clear hierarchical structure in the drivers of isotopic variation. At the broadest scale, the all-groups RDA showed a strong multivariate relationship between isotopic composition and the set of explanatory variables (Figure 7, overall model:  $F = 7.52$ ,  $P = 0.001$ ), with the overall model explaining 44.1% of the total constrained variance. RDA1 accounted for most of the explained variation (eigenvalue = 0.659), whereas RDA2 contributed a smaller proportion (eigenvalue = 0.223). Among the predictors, group showed the strongest association with isotopic variation (Table S2;  $F = 3.29$ ,  $P = 0.059$ ), driven by MCH-East animals aligning with higher  $\delta^{15}\text{N}$  values, while the KL and NAP groups aligned with lower  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values, respectively. Only Cr approached significance at this scale ( $F = 3.28$ ,  $P = 0.051$ ), but it explained minimal variance (~4%). All other elements (Ba, Cu, Pb, Se, Zn, Fe, Mg) had low F-values and high P-values, indicating limited explanatory power relative to group.



**Figure 7.** Redundancy analysis (RDA) ordination tri-plots relating carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotopes to ecological, lactation, and nutritional covariates in female caribou from the Mulchatna caribou herd east and west subgroups (MCH-E and MCH-W), Northern Alaska Peninsula herd (NAP), and Goodnews Bay (GB), and Kukaklek Lake (KL) area. Top: All-groups RDA tri-plot relating  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to trace mineral levels and group. Bottom: MCH-only RDA tri-plot relating  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to trace mineral levels, caribou group, and lactation status. Dots represent individual caribou hair samples. Black arrows indicate the response variables ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), and covariate predictors are shown as orange lines, with red lines indicating statistically significant predictors ( $P < 0.05$ ). The lengths of all covariate lines have been multiplied by 3 for visual clarity.

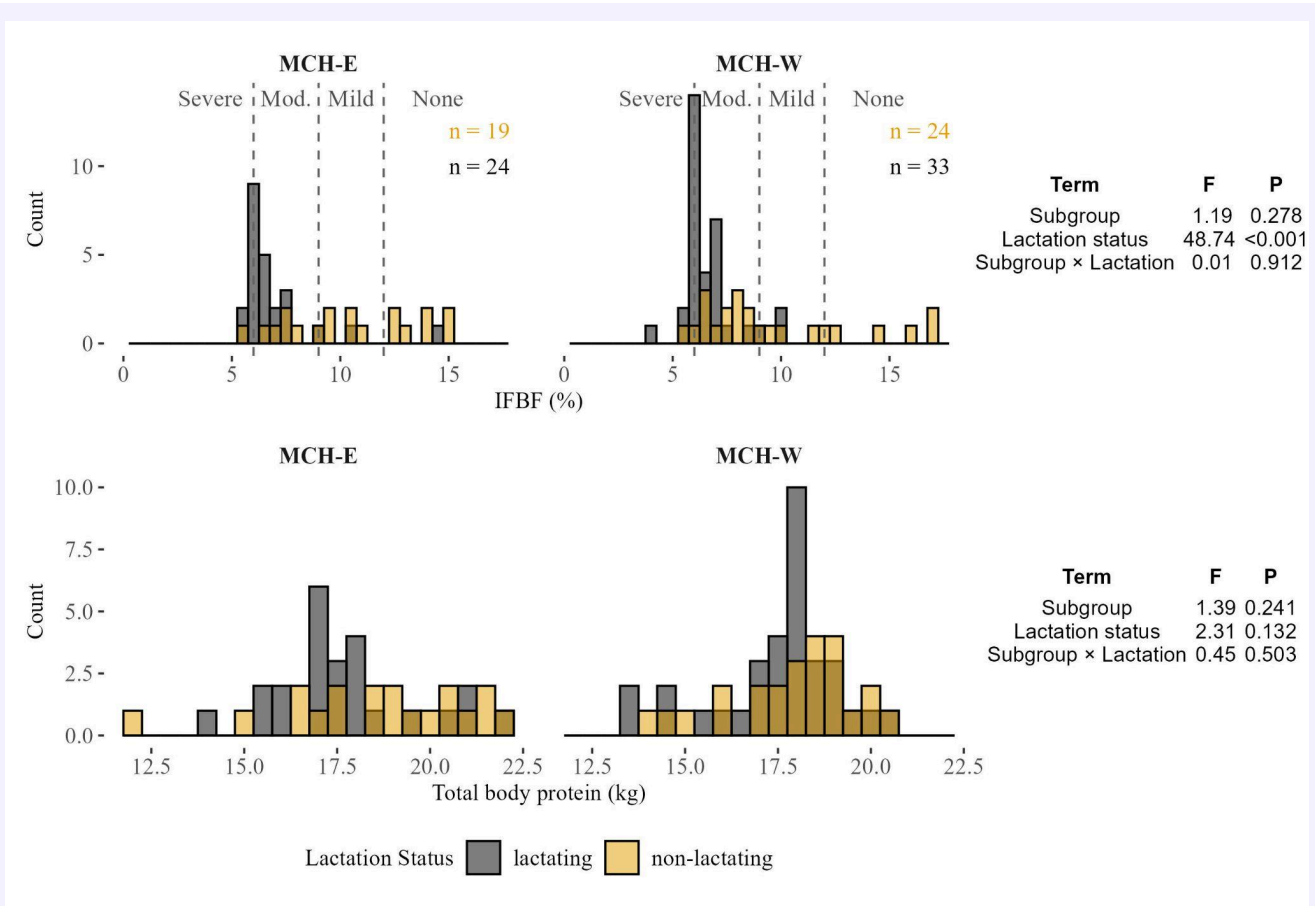


The MCH-only isotope RDA revealed additional fine-scale structure (Figure 7, overall model:  $F = 3.71$ ,  $P = 0.001$ ) in drivers of isotopic variation and explained 39% of the total constrained variance. Subgroup was the strongest predictor of isotopic variation (Table S3;  $F = 11.76$ ,  $P = 0.001$ ), with MCH-East animals aligning with higher  $\delta^{15}\text{N}$  values. Lactation status also contributed significantly ( $F = 4.22$ ,  $P = 0.031$ ), with lactation associated with lower  $\delta^{15}\text{N}$ . Several trace elements—Ba, Cr, Mg, and Pb—were significant predictors within MCH (all  $P \leq 0.046$ ), each explaining variance comparable to or slightly below that of lactation. Notably, Pb approached significance ( $P = 0.51$ ) and was associated with lower  $\delta^{15}\text{N}$ , while Cr was linked to higher  $\delta^{15}\text{N}$ .

In contrast, the MCH-only body condition RDA was significant ( $F = 2.74$ ,  $P = 0.003$ ) but explained less of the total constrained variance (32%) and showed that only lactation status significantly predicted variation in body fat and body protein (Table S3;  $F = 16.99$ ,  $P = 0.001$ ). Subgroup was not a significant predictor of body condition ( $F = 0.05$ ,  $P = 0.955$ ), nor were any of the trace elements or heavy metals (all  $P > 0.07$ ).

### **Body condition**

Overall the mean mass of adult females from the MCH was  $108.7 \text{ kg} \pm 9.4 \text{ SD}$ . Median body fat was 6.81% (interquartile range (IQR): 3.54-10.08%) and mean total body protein was  $17.85 \text{ kg} (\pm 1.9 \text{ SD})$ . Body composition varied with lactational status but showed little difference between MCH-East and MCH-West (Figure 8). Lactating females had substantially lower body fat (mean  $6.77 \% \pm 1.6 \text{ SD}$ ) but not protein (mean  $17.63 \text{ kg} \pm 1.7 \text{ SD}$ ) than non-lactating females (mean  $10.07 \% \pm 3.5 \text{ SD}$ ,  $18.13 \text{ kg} \pm 1.6 \text{ SD}$ ), a pattern supported by a strong effect of lactation status in the two-way ANOVA ( $F = 40.9$ ,  $P < 0.001$ ). Subgroup membership and the subgroup  $\times$  lactation interaction did not influence body fat. Body protein did not differ significantly by lactational status, subgroup, or their interaction. Although females in the MCH-East tended to have slightly higher body fat and protein than those in the MCH-West, these differences were not statistically supported (Figure 8).



**Figure 8.** Frequency distributions of ingesta-free body fat (IFBF, %) and total body protein (kg) of lactating and non-lactating Mulchatna herd (MCH) female caribou across the two herd subgroups (MCH-East and MCH-West). Bars show frequency of each value bin (bins are 0.5 wide). ISBF thresholds are from Cook et al. (2021) for the Porcupine Herd. Embedded tables report two-way ANOVA results for each response variable. Sample sizes (n) are shown inset and colored by lactation status.

## Discussion

Regional variation in caribou nutrition offers critical insights into the ecological and conservation dynamics of populations. Our findings revealed consistent and meaningful differences among discrete caribou groups in dietary patterns, levels of trace elements and heavy metals, and body condition between lactating and non-lactating females in the fall. Group differences in nutritional indices measured (e.g.  $\delta^{15}\text{N}$ ) or estimated (e.g. diet) at multiple time points tended to persist, suggesting differences in the quantity and/or quality of forage available to different Southwest Alaska caribou groups or differences in forage selection. On the other



hand, some indicators, such as fall body condition—assessed in the MCH—showed limited geographic differentiation despite differences in several nutritional markers, underscoring the complexity of linking nutritional markers to performance outcomes.

### **Dietary patterns and methodological considerations**

Our SIMM-based diet and niche reconstructions, the first conducted for caribou in Southwest Alaska, revealed substantial dietary flexibility within and across groups (Figure 4). Overall, our diet estimates also differed somewhat from microhistology-based diet estimates for adjacent herds (Boertje, 1984, Joly and Cameron, 2018), particularly in the reduced contributions of lichens in the early fall and late winter-spring periods yet increased contributions during summer, and the increased prominence of shrubs and moss during the late winter period. Before concluding that landscape differences drove the observed dietary patterns, we acknowledge that methodological differences between these techniques could substantially contribute to the divergent estimates. SIMMs integrate longer-term dietary signals and are sensitive to metabolic routing and tissue-specific fractionation (Ben-David and Flaherty, 2012, Gannes et al., 1997). In contrast, microhistology provides direct identification of plant fragments but is limited to recently consumed forage and may be biased toward more identifiable and/or less digestible plant structures (Bergerud and Russell, 1964, see review in Garnick et al., 2018, Norbury, 1988).

Regardless of methodological caveats, the temporal and group diversity in diet is consistent with recent meta-analyses (Webber et al., 2022) and underscores the species' remarkable adaptability as a generalist forager with dietary preferences. The greater shrub prominence relative to microhistology-based estimates in adjacent herds could reflect the enhanced availability of shrubs in this region (Macander et al., 2022, Mekonnen et al., 2021), the continued slow recovery of lichens from the MCH peak abundance in the late 1990s, or a relative lack of browsers in the system (Webber et al., 2022). However, estimated declines in macrolichen cover in the region between 1985 and 2020 were relatively modest compared to the substantial increases in shrub cover (Macander et al., 2022) and lichens remained prominent in our warm-season diet estimates.



The nutritional implications of the group and seasonal dietary variation we observed (Figure 4) depend on forage quality. Deciduous shrubs generally provide higher crude protein and digestible energy than mosses and lichens (Johnstone et al., 2002, Richert et al., 2021), though nutritional quality varies considerably among shrub species and plant parts (Thompson and Barboza, 2014). Graminoids offer intermediate quality that varies seasonally (Staalnd et al., 1988), while forbs can be highly nutritious when available (Chapin et al., 1986). Lichens provide readily digestible carbohydrates but are relatively low in protein (Garmo, 1986). Groups consuming higher proportions of deciduous shrubs, forbs, and graminoids likely access superior forage quality, potentially affecting performance, though the fitness consequences remain unknown. The substantial lichen consumption we observed across groups during summer-fall (mean=32%, 95% CI: 12-58) may thus represent a tradeoff during this critical period—accessing reliable energy at the cost of protein intake—if higher quality forage is limited, patchily distributed, or difficult to access for other reasons.

### **Body condition**

Fall body condition provides an integrated measure of summer-fall foraging success relative to energetic demands. Median body fat for MCH females in fall was 6.81% (IQR: 3.54-10.08%) overall, and 9.3% (IQR: 4.28-14.3%) for non-lactating females, values that fall within the range reported for other North American barren-ground herds during this season, including both expanding and contracting populations (Cook et al., 2021a, Cook et al., 2021b). The strong negative effect of lactation on body fat (Figure 8) was consistent across subgroups but expected given the energetic costs of lactation. While non-lactating females were dispersed across moderate, mild, and little-to-no nutritional limitation categories, the majority of lactating females from the Mulchatna herd had body fat levels indicative of animals experiencing moderate nutritional limitation—a category associated with reduced pregnancy rates, slow juvenile growth, and increased mortality in captive elk trials (Cook et al. 2004)—and consistent with a growing body of literature pointing to deficits in summer-autumn nutrition as a contemporary challenge of many ungulate populations (Cook et al. 2013, Monteith et al. 2014, Cook et al. 2017,



Proffitt et al. 2016, Stephenson et al. 2020, Cook et al. 2021c). However, future efforts to interpret these body condition patterns and their probable effects on pregnancy, offspring growth, and survival in the MCH is complicated by the substantial seroprevalence (>30%) of *Brucella suis*, a pathogen capable of reducing reproductive performance through late-term abortion, stillbirth, infertility, and weak calves (Nielsen and Duncan 1990, Aguilar et al. 2022), that has been documented in the herd (Sattler 2021, Demma and Sattler 2022). We note that our non-lactating category likely included females that recently lost calves; if calf mortality occurred late in summer when lactating females typically show maximum depletion, this could reduce the apparent difference between lactation groups, though the strong statistical signal we observed suggests this effect was limited.

Although females in the MCH-East group tended to have slightly higher fat and protein reserves than those in the West, neither the two-way ANOVA nor the MCH-focused RDA detected significant effects of subgroup on body condition—only lactation status was significant (Figure 8, Table S3). In the MCH, the decoupling between isotopic/trace element markers and body condition could reflect several possibilities: (1) the dietary and trace element differences we detected may not be large enough to translate into meaningful body condition differences by October, (2) behavioral or physiological compensation may allow MCH-West females to maintain similar body reserves despite apparently poorer nutritional indicators, or (3) both subgroups experience similar overall nutritional constraints despite differing in specific markers. Unfortunately, we lacked body condition assessments for non-MCH caribou groups, which prevents us from determining whether the patterns we observed in the MCH are representative of Southwest Alaska populations generally.

### **Geographic patterns in isotope status**

Our analyses of seasonal diets, trace minerals, heavy metals, and body condition indicate that geographic group—reflecting differences in spring, summer, and autumn range quality—is a strong predictor of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in Southwest Alaska caribou, while physiological state and specific trace elements introduce additional structure within groups. At the broad scale, caribou group explained significantly more isotopic variation ( $F = 14.7$ ,  $P =$



0.001) than any trace element, none of which were significant (Figure 7, Tables S2 and S3). Within the MCH, subgroup (East versus West) remained the strongest predictor of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  ( $F=11.76$ ,  $P=0.004$ ), with East group females exhibiting higher values by 0.5-1‰ and 0.3‰, respectively, across tissues (Figure 2). While lactation also contributed significantly to isotopic variation within the MCH ( $F = 4.22$ ,  $P = 0.019$ ), its effect (estimated in the univariate ANOVA models) was smaller, averaging 0.52‰ and 0.13‰ in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , respectively (Figure S3). Several trace elements—Barium, Chromium, Magnesium, and Lead—were also significant predictors within the MCH (all  $P \leq 0.046$ ), each explaining variance comparable to or slightly below that of lactation.

The biological significance of the 3‰ difference in  $\delta^{15}\text{N}$  observed between caribou groups during summer-fall is challenging to interpret, but similar-magnitude differences in  $\delta^{15}\text{N}$  have been associated with variation in nutritional status and body condition in other caribou populations (Found et al., 2022). In the context of Southwest Alaska forage isotopic profiles (Figure S2), this level of  $\delta^{15}\text{N}$  variation is consistent with dietary shifts between forage types with different protein content (Brenning et al., 2024). Accordingly, the observed group isotopic differences—including the 0.5-1‰ MCH East-West difference—could reflect meaningful variation in forage quality and nutritional status. In the MCH-East we observed tendencies towards higher graminoid consumption than other groups during summer-fall (reflected in hair) and higher fungi consumption during late fall (reflected in serum, Figure 4), both of which corresponded with higher  $\delta^{15}\text{N}$  values (Figure 2). In contrast, the KL group consistently exhibited the lowest  $\delta^{15}\text{N}$  values, yet diet estimates did not reveal a clear dietary explanation, suggesting that other factors—such as physiological state or environmental conditions—may be influencing isotopic signatures in this group.

### **Trace elements, heavy metals, and potential performance consequences**

Considerable variation in trace element and heavy metal concentrations across caribou groups—particularly elevated Cr and Cd in MCH-West as well as generally higher Pb in the KL and GB groups—raises questions about the environmental sources. Because hair trace element content



reflects dietary intake and environmental exposure (Gamberg et al., 2020, Oster et al., 2018), these patterns may indicate underlying differences in geochemical landscapes or forage composition. Indeed, the observed spatial variation aligns with irregular concentrations of several trace elements (Pb, Zn, Ag, As, Cu, Mo) documented in the subsurface geology and soils of the region (Perryman et al., 2020, Riehle, 1994). However, most soil samples from the broader ranges of the MCH-West and KL groups did not return elevated Cr or Pb (Perryman et al., 2020), leaving the mechanism behind these elevated levels unresolved.

Assessing the biological relevance of these trace element differences remains challenging, as caribou-specific reference values linked to fitness outcomes are lacking. Moreover, the relationship between hair trace element levels and circulating concentrations or tissue stores—and ultimately, animal performance—is incompletely understood for free-ranging caribou, although Jutha et al. recently reported strong relationships for some elements (2022). Recent work by Rioux et al. (2022) found higher survival in caribou with elevated Zn and Na and lower Cs and Mn concentrations in hair samples, suggesting that such markers may reflect demographically relevant variation. Broader ungulate literature provides additional context: Cr deficiency is linked with impaired immune function, reduced growth rates, and reproductive problems, while excesses can cause organ damage (Puls, 1994, see Rioux et al., 2022 and references therein). In contrast, Pb and Cd, both non-essential and toxic, are associated with multiple adverse effects including reduced growth and immune function, reproductive impairment, and increased mortality (Beest et al., 2023, Puls, 1994). In the MCH-West the higher Cr, Cd, and Ba may create a challenging physiological scenario, as toxic levels of these trace elements can increase mortality, reduce pregnancy rates, impact calf growth rate, and compromise immune function (Puls 1988, Barboza and Parker 2006, Sparling 2016, Rioux et al. 2022). These effects are particularly relevant given the variability in age-specific pregnancy and survival rates observed over the last two decades among MCH subgroups and recent elevation in *B. suis* seroprevalence (Barten and Watine 2020, Sattler 2021, Demma and Sattler 2022), as compromised immunity could increase disease susceptibility. However, neither the ANOVA or RDA analyses detected relationships between subgroup, trace element levels, and body condition (Table S3), suggesting that in this herd any influence these trace



elements exert on body condition may—at the observed levels of exposure—be buffered by other aspects of nutrition or behavioral compensation.

### **Management implications and knowledge gaps**

The persistent variation we documented in diet composition, tissue chemistry, trace element, and heavy metal status among caribou herds in Southwest Alaska has potential implications for population dynamics and conservation. If these nutritional differences translate to fitness—a connection we could not establish with our data—we might expect variation in vital rates (pregnancy rates, calf survival, adult survival) that could drive asynchronous population trends even within a single herd. However, nutritional deficits seldom present as obvious or catastrophic events. More frequently they accumulate over years, and act subtly, altering individuals susceptibility to disease, predation, and resilience to stochastic weather events (Bender et al. 2008, Bastille-Rousseau et al. 2016, Johnson et al. 2019), without manifesting in commonly monitored herd performance metrics like pregnancy and adult survival (Cook et al. 2004, Simard et al., 2008, Monteith et al., 2014), underscoring the value of integrating isotopic and trace element markers into long-term monitoring frameworks.

For management, these findings suggest that large caribou herds managed as homogeneous units may contain important internal ecological structure (Paez et al. 2026). Areas supporting better nutritional indicators may warrant conservation attention as potential source habitats, while identifying specific factors limiting nutrition in other areas and could guide targeted habitat management or other interventions. However, we emphasize a critical limitation: without corresponding individual fitness data—pregnancy rates, calf recruitment, adult survival—we cannot conclusively link the nutritional patterns we observed to population-level consequences, as the differences we documented may or may not exceed thresholds necessary to affect individual performance and population dynamics over the longer-term.

This limitation extends to our interpretation of dietary flexibility and climate resilience. Our data, collected from five caribou groups across a



region exceeding 400,000 km<sup>2</sup> in size, demonstrate the capacity of caribou to adapt their dietary patterns and acquire essential nutrients in the face of extreme spatiotemporal diversity in resource availability. Whether this dietary flexibility confers resilience during rapid climate-driven vegetation changes—particularly the widespread expansion of shrubs and decline of lichens documented across caribou ranges and Southwest Alaska—remains a critical unanswered question. The prominence of deciduous shrubs in most groups' diets indicates a capacity to exploit shrub-dominated landscapes, but whether further shrub expansion leads to adequate nutrition, especially during energetically demanding periods like late winter gestation and neonatal period—when lichens have been traditionally thought to be critical—is unknown.

Addressing these questions requires moving beyond the baseline description our study provides to integrated monitoring that simultaneously tracks diet composition, body condition, trace element status, and demographic vital rates across multiple years, varying herd densities, and changing environments. Only through such comprehensive, long-term monitoring can we determine whether the nutritional patterns we observed represent adaptive foraging in productive habitats or constrained choices within degrading landscapes. For the Mulchatna herd—which remains at historically low abundance despite hunting closures and predator control efforts—and for other northern caribou populations facing similar challenges, establishing these linkages between nutrition and population performance is essential for evidence-based conservation in a rapidly changing North.

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## Author Contributions

Robert G. Jespersen: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review and editing

Renaë Sattler: Conceptualization, Funding acquisition, Project administration, Resources, Data collection and curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review and editing

Dominic Demma: Conceptualization, Funding acquisition, Data collection, Methodology, Writing – review and editing

Jeffrey M. Welker: Conceptualization, Resources, Project administration, Methodology, Writing – review and editing

## Data Availability

All data and code [can be found here](#).

## Supplementary Information

Supplementary information [can be found here](#).



## Transparent Peer Review

Results from the Transparent Peer Review [can be found here](#).

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