Arctic herbivore diet can be inferred from stable carbon and nitrogen isotopes in C_3 plants, faeces, and wool

D.K. Kristensen, E. Kristensen, M.C. Forchhammer, A. Michelsen, and N.M. Schmidt

Abstract: The use of stable isotopes in diet analysis usually relies on the different photosynthetic pathways of C_3 and C_4 plants, and the resulting difference in carbon isotope signature. In the Arctic, however, plant species are exclusively C_3, and carbon isotopes alone are therefore not suitable for studying arctic herbivore diets. In this study, we examined the potential of both stable carbon and nitrogen isotopes to reconstruct the diet of an arctic herbivore, here the muskox (*Ovibos moschatus* (Zimmermann, 1780)), in northeast Greenland. The isotope composition of plant communities and functional plant groups was compared with those of muskox faeces and shed wool, as this is a noninvasive approach to obtain dietary information on different temporal scales. Plants with different root mycorrhizal status were found to have different $\delta^{15}N$ values, whereas differences in $\delta^{13}C$, as expected, were less distinct. As a result, our examination mainly relied on stable nitrogen isotopes. The interpretation of stable isotopes from faeces was difficult because of the large uncertainty in diet–faeces fractionation, whereas isotope signatures from wool suggested that the muskox summer diet consists of around 80% graminoids and up to 20% willows. In conclusion, the diet composition of an arctic herbivore can indeed be inferred from stable isotopes in arctic areas, despite the lack of C_4 plants.

Résumé : L'utilisation des isotopes stables dans l'analyse des régimes alimentaires se base ordinairement sur les voies photosynthétiques distinctes des plantes C_3 et C_4 et des différences qui en résultent dans la signature des isotopes de carbone. Cependant, dans l'arctique, les espèces de plantes sont toutes de type C_3 et les isotopes de carbone seuls ne suffisent pas pour étudier le régime alimentaire des herbivores arctiques. Notre étude examine le potentiel des isotopes stables de carbone et d'azote pour reconstituer le régime d'un herbivore arctique, le bœuf musqué (*Ovibos moschatus* (Zimmermann, 1780)), dans le nord-est du Groenland. Nous avons comparé la composition isotopique de la communauté végétale et des groupes fonctionnels de plantes à celle des fèces et de la laine perdue durant la mue chez les bœufs musqués, car il s'agit d'une méthode non invasive d'obtenir des informations sur la régime à différentes échelles temporelles. Les plantes qui possèdent des arrangements différents de mycorhizes dans leurs racines ont des valeurs distinctes de $\delta^{15}N$, alors que les différences de $\delta^{13}C$, comme prévu, sont moins marquées. C'est pourquoi, notre recherche s'est basée surtout sur les isotopes stables d'azote. L'interprétation des isotopes stables dans les fèces est difficile à cause de l'incertitude élevée associée à la fractionation régime-fèces, alors que les signatures isotopiques de la laine indiquent que le régime alimentaire des bœufs musqués en été consiste d'environ 80 % de graminoïdes et de jusqu'à 20 % de saules. En conclusion, la composition du régime alimentaire d'un herbivore arctique peut être déduite des isotopes dans les régions arctiques, malgré l'absence de plantes C_4.

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Introduction

The use of stable isotope analysis in mammal ecology is widespread (Crawford et al. 2008), and a variety of questions regarding diet have been addressed using this technique. Inference from stable isotopes has, for example, shed light on dietary shifts (e.g., Darimont and Reimchen 2002; Cerling and Viehl 2004; West et al. 2004) and diet composition of both predators (e.g., Roth and Hobson 2000; Fox-Dobbs et al. 2007) and herbivores (e.g., Jones et al. 1979; Cerling and Harris 1999; Sponheimer et al. 2003*a*; Codron et al. 2007). When studying the diet of terrestrial herbivores, the technique usually relies on the different photosynthetic pathways of C_3 and C_4 plants, which results in different carbon isotope signatures ($\delta^{13}C$) (for review see Koch 2007). Almost all C_4 species are native to warmer climates, whereas C_3 species

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dominate in colder regions (Osborne and Beerling 2006). In the Arctic, plants are exclusively C_3 species (Öpik and Rolfe 2005), and thus stable carbon isotopes alone are not suitable for analysis of herbivore diets within these regions. Arctic plant species, however, differ with respect to ^{15}N natural abundance (Michelsen et al. 1998), and thus analyses of stable nitrogen isotopes may give important additional insights into arctic herbivore diets (see Drucker et al. 2010). We address this topic by investigating the composition of carbon and nitrogen isotopes in the wool and faeces of muskox (*Ovibos moschatus* (Zimmermann, 1780)) and its plant forage at Zackenberg, northeast Greenland.

The muskox is the only large herbivore in northeast Greenland and therefore central to the reciprocal plant–herbivore interactions there. However, although the population dynamics of muskox have been examined in several studies (e.g., Forchhammer et al. 2005; Berg et al. 2008), only limited information exist on their foraging ecology within this area, and thus of the potential feedbacks between the two trophic levels. Across high-arctic populations, muskox diets consist primarily of graminoids and willow (genus *Salix* L.) (e.g., Thing et al. 1987; Ihl and Klein 2001; Larter and Nagy 2004). Graminoids make up the dominant food source throughout most seasons, whereas willow is the main forage early in the plant growing season (Thing et al. 1987; Klein and Bay 1994; Larter and Nagy 2004). Other shrubs and forbs are quantitatively unimportant for muskox but may be qualitatively important, especially during early summer when young shoots and flowers are high in nutrients (Thing et al. 1987).

The purpose of this study was to examine the stable carbon and nitrogen isotope signatures in arctic plants and their potential to reconstruct the diet of an herbivore, here the muskox. We compared isotope compositions of plant communities and different functional plant groups at Zackenberg with those of muskox faeces and shed wool, as this is an easy noninvasive approach to obtain dietary information on different temporal scales. To estimate the source partitioning of the diet, we used the Bayesian stable isotope mixing model (SIAR) (Jackson et al. 2009; Parnell et al. 2010).

Materials and methods

Study area

The study was carried out in the Zackenberg Valley, northeast Greenland (74°28′N, 21°33′W). The valley has a high-arctic climate with an annual mean air temperature around –9 °C and total precipitation of about 260 mm (Hansen et al. 2008). As part of the on-going ecosystem monitoring at Zackenberg (Meltofte et al. 2008), the muskox population is monitored in a 45 km^2 designated area, embracing the valley lowland to approximately 600 m above sea level. The census area consists of a mosaic of different vegetation types (Bay 1998; Fig. 1). During summer, the muskox mainly forage in grasslands, fens, and *Salix* snowbeds (Thing et al. 1987; D.K. Kristensen, personal observations), covering 36%, 6%, and 17% of the area, respectively. Grasslands are widely distributed and are found on mesic–wet areas that dry out during the growing season. Besides a dense layer of moss, the vegetation is dominated by a variety of graminoids (Cyperaceae, Juncaceae, and Poaceae), especially wideleaf polargrass (*Arctagrostis latifolia* (R. Br.) Griseb.), tall cottongrass (*Eriophorum angustifolium* ssp. *triste* (Th. Fr.) Hultén), and alpine foxtail (*Alopecurus magellanicus* Lam.). Fens are located in the wet lowland where soils are water-saturated throughout the growing season. The grass *Dupontia fisheri* ssp. *psilosantha* (Rupr.) Hultén and the white cottensedge (*Eriophorum scheuchzeri* Hoppe) dominate this vegetation type together with a complete layer of moss. Different forbs and the dwarf-shrub arctic willow (*Salix arctica* Pallas) are scattered throughout both grasslands and fens. *Salix* snowbeds are mainly situated on sloping sites with a prolonged snow cover. The dominant species is *S. arctica*, but different forbs and graminoids are present as well. The remaining part of the study area is dominated by dwarf-shrub heaths, abrasion plateaus, and fell fields (see Elberling et al. 2008).

Plant samples

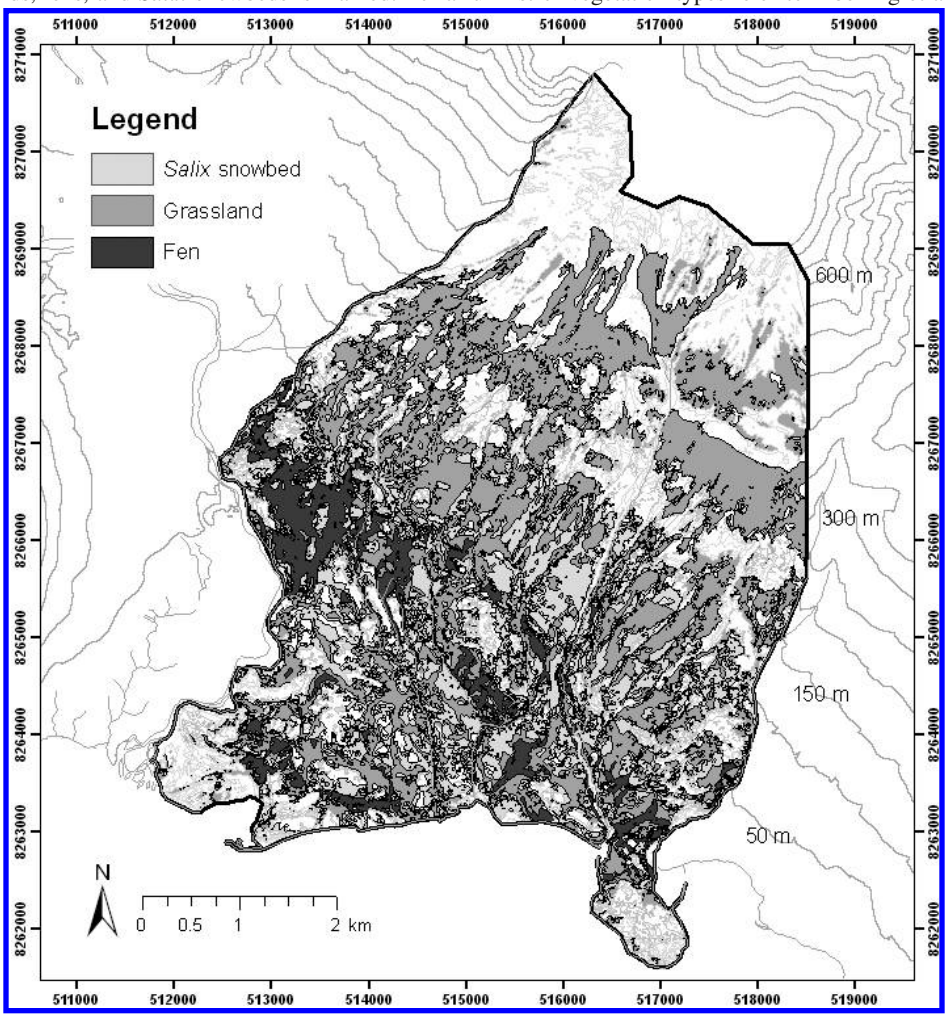
To obtain the isotope composition of the muskox forage, we collected vegetation samples from three vegetation types: grasslands, fens, and *Salix* snowbeds. As the visual distinction between grasslands and fens is not clearcut, these were treated as one vegetation type and termed graminoid-dominated areas. Harvesting was performed by imitating the foraging technique of muskox, which differs markedly between graminoid-dominated areas and *Salix* snowbeds (Forchhammer and Boomsma 1995). When muskox feed on graminoids, they press the lower incisors against the pad and pull by the head. When feeding on willow shrubs, muskox use a sharp upward head movement to peel leaves and catkins free of the stems (Forchhammer and Boomsma 1995; D.K. Kristensen, personal observations). Muskox are known to be efficient bulk feeders (Klein 1992), and therefore more or less consume biomass proportional to its availability. To mimic such foraging behaviour, we sampled the vegetation at the community level, thereby producing two specific types of mixed plant samples. In the graminoid-dominated areas (GRAM), plants were cut with scissors about 3–5 cm above ground, causing samples to be almost exclusively composed of graminoids, as shrubs and forb species often are lower than the grazing depth. In *Salix* snowbeds (SAL), leaves and catkins were peeled off willow stems by hand, while forbs and graminoids were cut at the lower stalk. Sampling was performed from a minimum of 30 randomly distributed plots (~0.5 m^2) within each of the two vegetation types. In addition to the mixed samples, we also harvested plant specimens belonging to the dominant functional groups: graminoids, forbs, and *S. arctica*. Ten replicate samples were collected for each plant group in GRAM and SAL, respectively.

All plant materials were sampled in the period 19–23 August 2008. Upon collection, the plant material was oven-dried at 70 °C for 24 h and ground-milled into a homogenous powder.

Muskox samples

Faeces were collected to describe the short-term dietary intake of muskox. Faeces are assumed to integrate the diet over a weekly time scale, based on faecal turnover time in other similar-sized ruminants (Jones et al. 1979; Sponheimer et al. 2003*b*). We collected at least 30 separate faecal samples from each of the three vegetation categories: graminoid-dominated areas, *Salix* snowbeds, and other vegetation types, where the latter was defined as all remaining vegetation types within the census area. All samples were representative subsamples

Fig. 1. Map showing the central part of the Zackenberg Valley, northeast Greenland, in which the sampling for this study was focused. The distribution of grasslands, fens, and *Salix* snowbeds is marked. For a full list of vegetation types refer to Elberling et al. (2008).



of recently deposited faeces, e.g., within a few days. Faeces were collected in late August 2008, parallel with the collection of plant materials.

Shed muskox wool was collected from the entire valley in late August 2008. To minimize the risk of sampling wool from the same individual more than once, all samples were collected from spatially separated hair stacks. In contrast to faeces, wool integrates the diet over a longer temporal scale, as the stable isotope composition of wool represent the entire period of hair growth, i.e., approximately April to November (Flood et al. 1989). Seasonal growth rates of wool are unknown, but we expect the main growth to take place during summer, when food is abundant.

Faeces and wool were immediately oven-dried at 70 °C to complete dryness (2–5 days). The outer layer of the dried faeces was peeled off to avoid contamination from soil particles. The wool was cleaned by removing all visible contaminants with tweezers, washed several times in 96% ethanol, and re-dried at 60 °C for 24 h. Subsequently, faeces were ground-milled into a homogenous powder, whereas wool was cut into fine bits with scissors.

Elemental and stable isotope analysis

Subsamples of the ground material were weighed (~5 mg plant, ~4 mg faeces, ~0.7 mg wool) and packed into tin capsules. Analyses for elemental concentrations and $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios were performed at the Department of Biology, University of Copenhagen, with an Isoprime isotope ratio mass spectrometer (Micromass-GV Instruments, Manchester, UK) coupled to a Eurovector CN elemental analyser (Eurovector, Milan, Italy) using continuous flow. Natural abundances of isotopes are expressed in the δ notation relative to international standards (Vienna Pee Dee Belemnite for C and atmospheric N_2 for N): δX_{sample} (‰) = 1000 × [($R_{sample}/R_{standard}$) − 1], where R is the molar ratio of heavy X / light X. Samples were analysed with reference gas calibrated against international standards IAEA C5, CH6, CH7, N1, N2 and USGS 25, 26, 32, and drift corrected using peach leaves (NIST) as internal standard. The standard deviation of isotope measurements of the standards was ±0.2‰ for $\delta^{15}N$ and ±0.1‰ for $\delta^{13}C$ (Clemmensen et al. 2006).

Mixing models

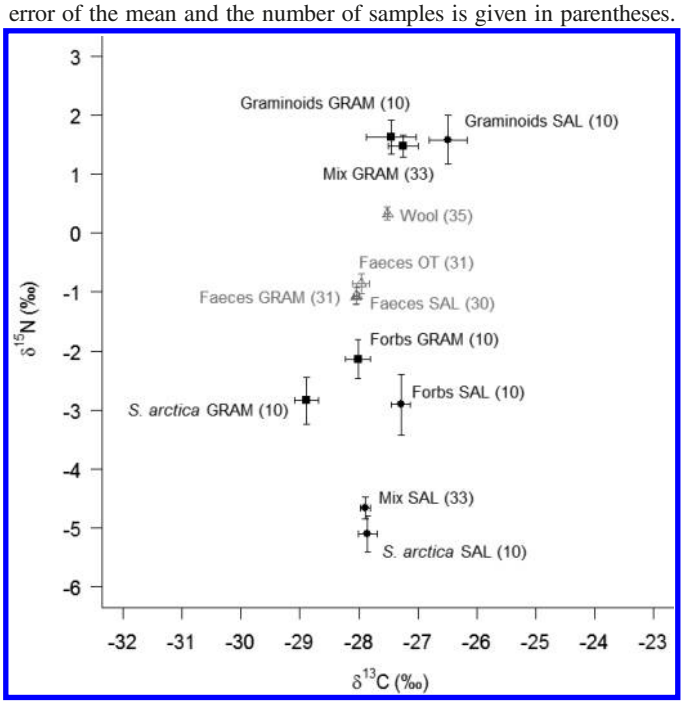
The diet compositing of muskox was examined using the Bayesian multisource SIAR (Parnell et al. 2008, 2010). SIAR offers a great advantage over earlier mixing models (e.g., IsoSource; Phillips and Gregg 2003) in that it can incorporate the variability of input parameters, i.e., consumer values, sour-

Table 1. C and N elemental concentrations of plants species and functional groups collected from graminoid-dominated areas (GRAM) and *Salix* snowbeds (SAL) in the Zackenberg Valley during summer 2008.

		Concentration (%)			
		C		N	
Vegetation	Sample	Mean	SD	Mean	SD
GRAM	Graminoids	43.1	0.9	1.7	0.4
GRAM	Mix	42.9	0.9	1.6	0.4
SAL	Graminoids	42.1	0.5	1.6	0.3
SAL	Arctic willow (*Salix arctica*)	44.7	0.8	2.1	0.3
SAL	Forbs	42.3	0.6	2.1	0.3
SAL	Mix	44.8	0.8	2.2	0.3

Note: Mix samples represent the forage intake of muskox (*Ovibos moschatus*).

Fig. 2. Mean $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures of plants (species and functional groups) and wool and faeces of muskox (*Ovibos moschatus*) collected from graminoid-dominated areas (GRAM), *Salix* snowbeds (SAL), and other vegetation types (OT) in the Zackenberg Valley during summer 2008. Mix samples represent the muskox forage intake. Wool and faeces have been corrected for trophic enrichment before plotting (see text for details). Bars indicate the standard error of the mean and the number of samples is given in parentheses.



ces, and trophic enrichment factors (TEF), as well as elemental concentration dependence. Moreover, the model outputs represent true probability density functions, from which probability intervals and other statistics can be derived (for further details on the SIAR method see Parnell et al. 2010).

To estimate the proportion of GRAM and SAL in the muskox diet, the model was run on the mixed plant signatures with either wool or faeces (see below) as proxies for the consumer tissue. Since no TEFs (noted with Δ) currently exist for muskox, we used published data on domestic cattle because of similarities in body mass and digestive system (Hofmann 1989, 2000). However, we are aware of the risk of error associated with the use of nonspecific TEFs (e.g., Caut et al. 2009). The values of $\Delta^{15}N$ (mean ± SD) for hair and faeces were set at 2.5‰ ± 1.7‰ (low-protein diet; Sponheimer et al. 2003*c*) and 1.9‰ ± 0.3‰ (Steele and Daniel 1978), respectively. Similarly, $\Delta^{13}C$ values for hair and faeces were 2.7‰ ± 0.4‰ (low-protein diet; Sponheimer et al. 2003*b*) and –0.9‰ ± 0.2‰ (Sponheimer et al. 2003*b*), respectively. Elemental concentrations were corrected for by incorporating the observed C and N concentrations of the plant sources into the mixing models (see Table 1). No priors were included in the SIAR models.

Moreover, SIAR was run on the isotope signatures of individual plant groups to investigate if the muskox diet could be reconstructed at the plant functional level as well. The models were simplified by including only four potential food sources, based on knowledge of the foraging behaviour of muskox (Forchhammer and Boomsma 1995; Oakes et al. 1992; D.K. Kristensen, personal observations). The four sources were *S. arctica*, forbs, and graminoids from the *Salix* snowbeds, as well as graminoids from the graminoid-dominated areas.

Results

Stable isotope signatures

Mean $\delta^{13}C$ in plants were quite consistent and only ranged about 2.5‰. *Salix arctica* from the graminoid-dominated areas (–28.9‰) was the most ^{13}C-depleted group, whereas graminoids from *Salix* snowbeds (–26.5‰) was the most enriched (Fig. 2). Within functional groups, the $\delta^{13}C$ values were in general around 1‰ higher in the *Salix* snowbeds than in the graminoid-dominated areas. In comparison, mean $\delta^{15}N$ values were much more variable and ranged almost 7‰. The lowest $\delta^{15}N$ value was found in *S. arctica* from the graminoid-dominated area (–5.1‰), whereas the highest was found in graminoids (1.6‰ for both vegetation types). Mean $\delta^{15}N$ of the *S. arctica* differed with 2.3‰ between the two vegetation types, with the highest value in the graminoid-dominated areas. A similar but less pronounced tendency was seen for forbs, with the $\delta^{15}N$ values of graminoids from the two vegetation types being very similar (Fig. 2). The mixed samples from the *Salix* snowbeds (mix SAL) and the graminoid-dominated areas (mix GRAM) had comparable $\delta^{13}C$ mean values (–27.9‰ and –27.3‰, respectively), unlike their $\delta^{15}N$ values that varied considerably between the two vegetation types (–4.7‰ and 1.5‰, respectively) (Fig. 2).

Variations in $\delta^{13}C$ and $\delta^{15}N$ of faeces were very small and no significant differences among samples from the three vegetation types were found (one-way ANOVA; C: $P = 0.760$; N:

Fig. 3. Proportions of food sources in the muskox (*Ovibos moschatus*) diet derived from the graminoid-dominated areas (GRAM) and the *Salix* snowbeds (SAL). Predictions are from stable isotope analysis in R (SIAR) with (*a*) wool or (*b*) faeces as proxies for consumer tissue. Boxes indicate 50%, 75%, and 95% Bayesian probability intervals.

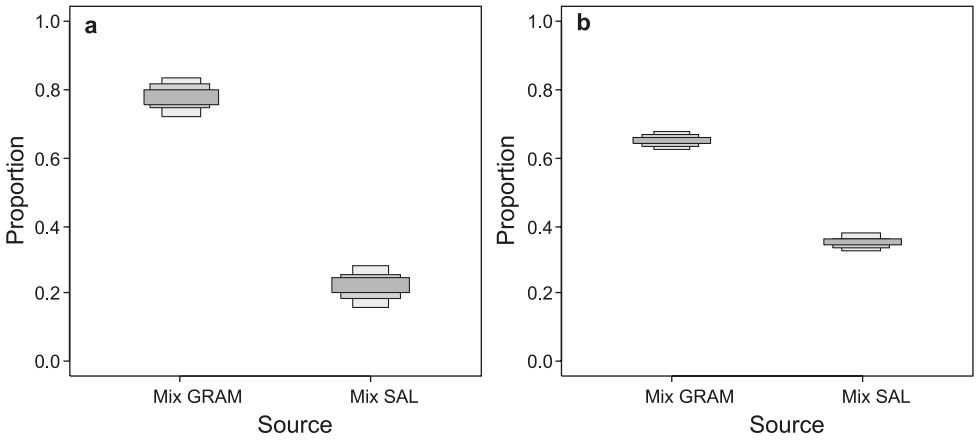
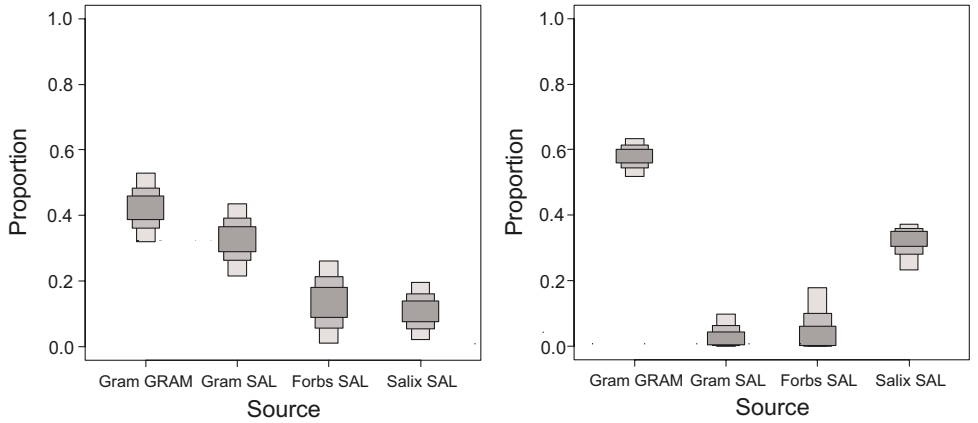


Fig. 4. Proportions of functional plant groups (graminoids, forbs, and arctic willow (*Salix arctica*)) in the muskox (*Ovibos moschatus*) diet from the graminoid-dominated areas (GRAM) and the *Salix* snowbeds (SAL). Predictions are from stable isotope analysis in R (SIAR) with (*a*) wool or (*b*) faeces as proxies for consumer tissue. Boxes indicate 50%, 75%, and 95% Bayesian probability intervals.



$P = 0.544$) (Fig. 2). Hence, in the following diet analyses, faeces from the three vegetation types were pooled. Compared with faeces, wool was enriched in both ^{13}C and ^{15}N, having mean values of –24.8‰ and 2.8‰, respectively (Fig. 2).

Dietary composition

The mixing models on mixed plant samples clearly showed that the main proportion of the muskox diet was derived from the graminoid-dominated areas, whether inferred from wool (95% probability interval; 71%–85%) or faeces (62%–67%) (Figs. 3*a,* 3*b*). The diet composition predicted from the models on functional groups were, on the other hand, less clear because the probability intervals of most groups were very large, especially for wool as consumer tissue (Figs. 4*a*, 4*b*). However, although the predictions from the two models differed to a large extent, they both indicated that graminoids from the graminoid-dominated areas were the most important food source, accounting for around 45%–60% of the muskox diet (Figs. 4*a*, 4*b*).

Discussion

Isotope signatures in plants, faeces, and wool

As expected, the observed range in stable isotope signatures of the examined arctic plants was indeed larger for nitrogen than for carbon (Fig. 2). Although nitrogen isotope signatures generally were consistent with those reported by Michelsen et al. (1998) from the Zackenberg Valley, this study revealed that $\delta^{15}N$ not only vary among functional plant groups but also spatially within some groups. The effect was most pronounced for *S. arctica* where individuals from the graminoid-dominated areas, on average, were more than 2‰ enriched in ^{15}N compared with individuals from *Salix* snowbeds. Michelsen et al. (1998) demonstrated that plant ^{15}N is strongly related to the presence and type of symbiotic fungi in roots (mycorrhiza) and suggested that different $\delta^{15}N$ values partly arise from variable nitrogen sources; i.e., high uptake of organic N such as amino acids (with low $\delta^{15}N$; Yano et al. 2010) in mycorrhizal plants versus solely inorganic N uptake (high $\delta^{15}N$) in nonmycorrhizal plants. Unlike graminoids, both *S. arctica* and the dominant forb, alpine bistort (*Bistorta vivipara* (L.) Delarbre), are colonized by ectomycorrhizal fungi at Zackenberg (Michelsen et al. 1998). As ammonium is more available in the nutrient-rich fens and grasslands than in the drier *Salix* snowbeds (Elberling et al. 2008), the ^{15}N enrichment observed for *S. arctica* and forbs in the graminoid-dominated vegetation types may be attributed to a proportionally larger uptake of inorganic N. This

also explains why graminoids, relying solely on inorganic N, had similar $\delta^{15}N$ values in all vegetation types (Fig. 2).

The $\delta^{13}C$ values of the examined plants were within the range of that previously reported for C_3 plants (–22‰ to –35‰; Koch 2007). Despite the lack of different photosynthetic pathways, a small differentiation in ^{13}C abundance was observed within and between plant groups (Fig. 2). Plants from the *Salix* snowbeds were in general 1‰ more enriched in ^{13}C than their counterparts from the graminoid-dominated areas (Fig. 2). This tendency may be caused by relatively higher water-use efficiency in plants from the drier *Salix* snowbeds, as drought-tolerant plants in general have high water-use efficiencies and thus higher $\delta^{13}C$ values (reviewed by Marshall et al. 2007).

The signatures of the mixed plant sampled were generally very close to those of the dominant plant groups in the two vegetation types. Bay (1998) estimated that graminoids and *S. arctica* make up more than 80% of the aboveground biomass in the graminoid-dominated areas and *Salix* snowbeds, respectively. Our mixed samples thus reflect the biomass composition in the two vegetation types directly, and therefore most likely also reflect the muskox forage intake of the nonselective bulk-feeders (Klein 1992).

Carbon and nitrogen isotope signatures of muskox faeces (mean (±SD) of all vegetation types; $\delta^{13}C$: –28.9‰ ± 0.5‰; $\delta^{15}N$: 0.9‰ ± 0.8‰) are comparable with values of muskox faeces sampled in northeastern Alaska ($\delta^{13}C$: –27.8‰ ± 0.7‰; $\delta^{15}N$: 1.3‰ ± 1.1‰; Barboza and Reynolds 2005). We are not aware of any data on stable isotopes in muskox wool; however, Barboza and Reynolds (2005) analysed guard hair from wild muskox ($\delta^{13}C$: –24.0 ± 0.3‰; $\delta^{15}N$: 2.4 ± 0.5‰) and found signatures similar to our wool estimates ($\delta^{13}C$: –24.8 ± 0.2‰; $\delta^{15}N$: 2.8 ± 0.7‰).

Diet composition of muskox inferred from stable isotopes

Differences in nitrogen signatures between mycorrhizal and nonmycorrhizal plants found at Zackenberg were sufficiently large to infer muskox diet at the plant community level. SIAR produced narrow probability densities, clearly separating the diet from the two vegetation types (Figs. 3*a*, 3*b*). The mean contribution from *Salix* snowbeds was estimated to be 22% and 35%, based on wool and faeces, respectively. As faeces represent the muskox diet in August and wool the entire summer season, our results are in conflict with previous microhistological studies indicating that muskox primarily consume *Salix* sp. during early summer, i.e., June (Thing et al. 1987; Klein and Bay 1994; Larter and Nagy 2004). Although this might be a consequence of unequal digestibility of willow and graminoids (Thing et al. 1987), Sponheimer et al. (2003*b*) argued that differential digestibility is unlikely to significantly bias faecal isotope signatures of wild ruminants. Hence, we do not consider the faeces composition to be strongly biased compared with the actual diet. Instead, the main factor responsible for the observed discrepancy between diet inferred from wool and faeces stable isotopes is probably due to the use of inappropriate TEFs. In general, animal faeces are enriched in ^{15}N compared with diet owing to the presence of endogeneous tissue and gut fauna (Sponheimer et al. 2003*d*). However, the enrichment varies greatly among and within species and is strongly affected by the study approach. Among ruminants alone, diet–faeces $\Delta\delta^{15}N$ values range from 0.4‰ to 3.0‰ (Steele and Daniel 1978; Sutoh et al. 1987, 1993; Sponheimer et al. 2003*d*). In contrast, the enrichment between diet and hair seems less variable, as the majority of studies on mammals have reported consistent $\Delta\delta^{13}C$ values of 2‰–3‰ (Sponheimer et al. 2003*c*; Nardoto et al. 2006; Caut et al. 2009). Thus, we consider the food partitioning inferred particularly from wool to be a realistic approximation of the muskox summer diet at Zackenberg. Such partitioning is indeed supported by other studies carried out in high-arctic regions (e.g., Thing et al. 1987; Klein and Bay 1994; Larter and Nagy 2004).

The attempt to run SIAR at the level of plant functional groups failed to give an unambiguous picture of the muskox diet. Even though the mean signatures of both carbon and nitrogen do vary among the different plant groups, the differences are too small for the model to differentiate between several plant groups, causing a very high sensitivity towards the TEFs. Nevertheless, the model outputs on both wool and faeces indicate that graminoids from graminoid-dominated areas is the most important food source in the muskox diet (Figs. 4*a*, 4*b*).

In conclusion, the diet composition of an arctic herbivore, here the muskox, can indeed be inferred from stable isotopes despite the fact that arctic plants are exclusively C_3 species. However, the resolution can only be obtained at the plant community level, as the differences in isotope signatures among functional plant groups generally are too small to support a more detailed examination of the muskox forage. The use of wool and faeces constitutes an easy and noninvasive approach to examine herbivore diet in protected areas such as Zackenberg, but species-specific TEFs especially for muskox faeces are needed. Stable isotopes may thus be very useful in examinations of arctic herbivore diets.

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