Mineral nutrition and alimentary pools in muskoxen and caribou on the Angujaartorfiup Nunaa range in West Greenland

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Abstract: Minerals (Na, K, Cl, Ca, P, Mg) and crude protein concentrations as well as total contents were measured throughout the alimentary tract of muskoxen and caribou from Angujaartorfiup Nunaa range, Søndre Strømfjord area in West Greenland. The muskoxen had significantly higher K concentrations in the caecum and proximal colon than the caribou. Caribou collected during the summer season had the highest Mg concentrations throughout the alimentary tract. In both species water, Na, K and Cl concentrations decreased through the distal part of the alimentary system whereas Ca, Mg, P and crude protein concentrations increased. The muskoxen had relatively larger mineral pools and total content in the omasum than the caribou, and the caribou relatively larger mineral pools (except K and Cl) and total content in the caecum. Higher concentrations of Mg in the alimentary tract of the caribou than the muskoxen during the summer could also indicate that the caribou feed more on herbs with high concentrations of Mg. The data does also indicate that both the caribou and the muskoxen are living in an area where high intakes of minerals from both vegetation and mineral licks are possible. Based on the present study the muskoxen is apparently a typical grazer whereas the caribou is more like a concentrate selector.

Key words: *Ovibos moschatus, Rangifer tarandus groenlandicus,* alimentary tract, minerals, omasum, caecum, grazing strategy.

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Introduction

Twenty seven muskoxen, *Ovibos moschatus,* introduced to the Angujaartorfiup Nunaa range, West Greenland in 1962 and 1965 multiplied to about 3000 animals in 1990. During the same period caribou, *Rangifer tarandus groenlandicus,* population decreased from about 40 000 to 2000 animals (Olesen, 1993). The caribou then abandoned winter grazing in the coastal regions and spent all year on the steppe like areas closer to the inland glacier where muskoxen had been introduced. In this area both muskoxen and caribou seemed to have adopted similar feeding habits and year around mainly fed on grasses (Thing, 1984; Olesen, 1990; 1993). In other high arctic regions where both species are living the caribou appears to be more like a browser and the muskoxen more like a grazer (Thomas & Edmonds, 1984; Staaland *et al.,* 1997). However in the high arctic Svalbard, reindeer has apparently adapted to a grass diet with very little lichens (Staaland & White, 1991) and may have competed out introduced muskoxen (Klein & Staaland, 1984).

Table 1. Examples of mineral concentrations of forage plants and soils from mineral licks and controls from West Greenland [mmol kg^{-1} DM (standard deviation)]

Species/season			Na	K	Cl	P	Mg	Ca
Betula nana	Summer	(7)	8 (3)	114 (25)	5 (3)	66 (20)	101 (41)	90 (18)
	Winter	(4)	8 (3)	59 (9)	13 (11)	41 (3)	70 (15)	87 (37)
Salix glauca	Summer	(12)	13 (7)	327 (83)	31 (25)	144 (68)	159 (76)	180 (41)
	Winter	(9)	10 (6)	158 (10)	23 (28)	70 (47)	75 (10)	116 (15)
Kobresia	Summer	(12)	11 (14)	119 (52)	31 (30)	41 (14)	91 (21)	88 (16)
myosuroides	Winter	(9)	9 (5)	54 (9)	17 (10)	23 (13)	108 (27)	111 (39)
Mixture of grass	Summer	(7)	28 (14)	140 (40)	49 (32)	36 (8)	80 (5)	137 (14)
	Winter	(4)	15 (9)	96 (46)	29 (9)	14 (5)	67 (29)	107 (44)
Calamagrostis	Summer	(1)	6	84	123	23	66	82
langsdorfii	Winter	(1)	7	91	29	6	65	89
Eriophorum	Summer	(1)	6	71	33	48	79	69
scheuzeri								
Hippurus	Summer	(1)	230	423	-	91	213	321
vulgaris								
Mixture of	Summer	(1)	21	163	24	78	248	299
mosses								
Salt licks	Water soluble	(6)	369 (340)	5 (2)	408 (369)	0 (0)	47 (17)	22 (17)
	Acid soluble	(6)	411 (313)	78 (16)		17 (2)	489 (71)	316 (32)
Controls	Water soluble	(3)	12 (17)	2 (1)	11 (18)	0.1 (0.0)	3 (1)	2 (0)
	Acid soluble	(3)	67 (48)	65 (46)		14 (9)	390 (255)	248 (168)

Based on alimentary tract structure as well as observations of feeding habits the muskoxen, a typical grazer, should be better adapted to these West Greenland ranges than caribou, a possible concentrate selector (Wilkinsson *et al.*, 1976; Vincent & Gunn, 1981; Thomas & Edmonds, 1984; Ferguson, 1987; Hofmann, 1989; Staaland & Thing, 1991; Staaland & Olesen, 1992). A question to ask: Do we have special adaptations in the alimentary system of different subspecies and/or populations of muskoxen and caribou/reindeer to different feeding strategies and available food in different regions?

In a previous paper (Staaland & Olesen, 1992) we examined the organic components of the forage as well as its relation to alimentary structure and size in muskoxen and caribou collected on the Angujaartorfiup Nunaa range in West Greenland. In the present study emphasise is put on macrominerals in forage and the alimentary system of caribou and muskoxen to observe possible adaptations relative to different grazing strategies.

Material and methods

Forage plants; *Kobresia myosuroides, Salix glauca, Betula nana* and a mixture of different species of monocotyledons were collected in the area around Søndre Strømfjord from early May to late August 1990. Occasional samples of the same plants were also collected during the winter season. Plants collected in the period from greenup in June until late August were evaluated as summer samples, and plants collected in other periods of the year as winter samples. The plants were air dried in paper bags. Soil samples from 6 locations used as "mineral licks" by muskoxen and 3 control samples were collected within the study area. Seven muskoxen (*O. moschatus*) and 5 caribou (*R. t. groenlandicus*) were collected in the Angujartorfiup Nunaa range of West Greenland in the summer (July-August 1989-91). In the same area 8 muskoxen and 3 caribou were collected in the winter (late October to early May 1988-91, see Fig.1 and Table 2).

All animals were eviscerated as soon as possible after being shot. The gastrointestinal tract was laid out on the ground and sampled according to Staaland *et al.* (1979) and Staaland & Olesen (1992). In 5 muskoxen and 5 caribou collected in the summer (August) the content of every section of the alimentary tract was weighed and representative samples taken for chemical analyses (Table 2). Animals collected during the winter and 2 one year old

muskoxen collected during the summer were sampled similarly, but the weight of the alimentary content could not be accurately measured (because of weather conditions), and data from these animals could only be used to estimate concentrations of different elements in the alimentary tract (Fig. 1). Samples were taken from the rumen, reticulum, omasum, abomasum, three successive samples from the small intestine, caecum, proximal colon and three successive samples from both the coiled and distal colon to the anus. The samples were transferred to sealed plastic vials and added 5 ml 40% formalin as a preservative. The samples were frozen as soon as possible and stored at -20 °C until analysed.

All samples were freeze dried to constant weight and the difference between wet and dry weight was assumed to be equal to the water content. Quantities of formalin added were subtracted from the total content.

Nitrogen in gastrointestinal samples were determined by the Kjeldahl-N method. For mineral analyses samples of plants and alimentary content were ashed at 550 °C and the ash dissolved *in aqua regia.* Soil samples were either dissolved in deionized water or in hydrochloric acid (0.7%). Sodium, K, Ca, Mg and P were analysed by Inductively Coupled Plasma Spectrometry (ICP). Chloride was determined by an autoanalyzer from ash added sodium carbonate and dissolved in nitric acid, using $Hg(SCNH)_2$ and Fe^{3+} as reagents. All chemical analyses were carried out at Chemical research laboratory of the Agricultural University of Norway, Ås. Statistical analyses includes the *t*-test and the Duncan multiple range-test.

Results

The concentrations of Na in the terrestrial forage plants were in the order of 6-28 mmol kg^{-1} DM. One aquatic plant, *Hippurus vulgaris,* analysed had a Na concentrations of 230 mmol kg^{-1} DM. Only small seasonal variations in Na concentrarions were observed. The concentrations of K, Mg and P were usually higher in summer than in winter. The "salt licks" examined had Na concenttations about 30 times higher than the controls. Also Ca, Mg and Cl concentrations appeared higher than controls. Levels of P was low both in aquatic solution and acid soluble solutions (Table 1).

Body mass in muskoxen ranged from 149-347 kg and in caribou from 54-146 kg (Fig. 1). In both muskoxen and caribou Na concentrations in the alimentary tract decreased from rumen to abomasum and increased again into the proximal part of the small intestine. Caribou collected during the winter had significantly higher Na concentrations in the caecum and the proximal part of the large intestine than caribou collected in the summer and muskoxen from both the winter and summer season (Fig. 1A). In the same section of the alimentary tract muskoxen (winter and summer) and caribou collected during the summer had high concentrations of K (Fig. 1B). Chloride concentrations were low in rumen/reticulum and reached its highest concentrations in the abomasum and proximal small intestine (Fig. 1C). From caecum to anus the concentrations of Na, K and Cl decreased.

Calcium concentrations remained relatively stable (highest concentrations in omasum) from rumen to the proximal part of the small intestine and from then on Ca concentrations increased continuously to the anus. Large individual variations in Ca concentrations were observed throughout the alimentary tract (Fig. 1D). Phosphorous concentrations decreased from the rumen to the caecum (highest concentrations in omasum), and had a small increase in concentration through the large intestine. Seasonal or interspecific variations between the two species were small and mostly not significant (Fig. 1E). Caribou collected in the summer had throughout the alimentary tract the highest Mg concentrations. The concentrations of Mg in all animals, winter and summer, increased from the distal section of the small intestine to the anus (Fig. 1F). The highest concentrations of crude protein were observed in the duodenum (S1) and the lowest concentrations in the caecum. From caecum to anus the crude protein concentrations increased (Fig. 1G). Water percentages were highest in the abomasum and small intestine, and decreased continuously through the large intestine (Fig. 1H).

The total alimentary pools could only be calculated for 5 caribou and 5 muskoxen collecred during the summer season (Table 2). The rumen-reticulum contained 60-84% of the total alimentary content of all elements analysed with the exception of Cl which had only 34-47% of the total alimentary Cl content in the rumen-reticulum.

For all elements as well as for total content the omasum contained a larger proportion of the alimentary fill in the muskoxen than in caribou. The abomasum and small intestine usually had nutrient pools of relatively similar size in both species, but

the caecal pools (except for K and Cl) was relatively smaller in the muskoxen than in the caribou (Table 2).

Discussion

Analyses of mineral concentrations in plants showed large seasonal variations and differences between different species, but the concentrations were more or less similar to observations from other regions with reindeer grazing (Staaland *et al.*, 1983; Staaland & Sæbø, 1993). But much more mineral analyses are needed to give more exact and detailed comparison of mineral content of plants in different regions grazed by reindeer/caribou and muskoxen. Relative to the concentrations of other minerals analysed, the Na concentrations (except the aquatic plant) was low (Table 1). However, reindeer forage plants in some other regions like the interior region of Finnmark county in Norway, have Na concentrations in the order of 3-4 mmol kg^{-1} DM against 6-28 mmol kg^{-1} DM in the present study (Staaland &

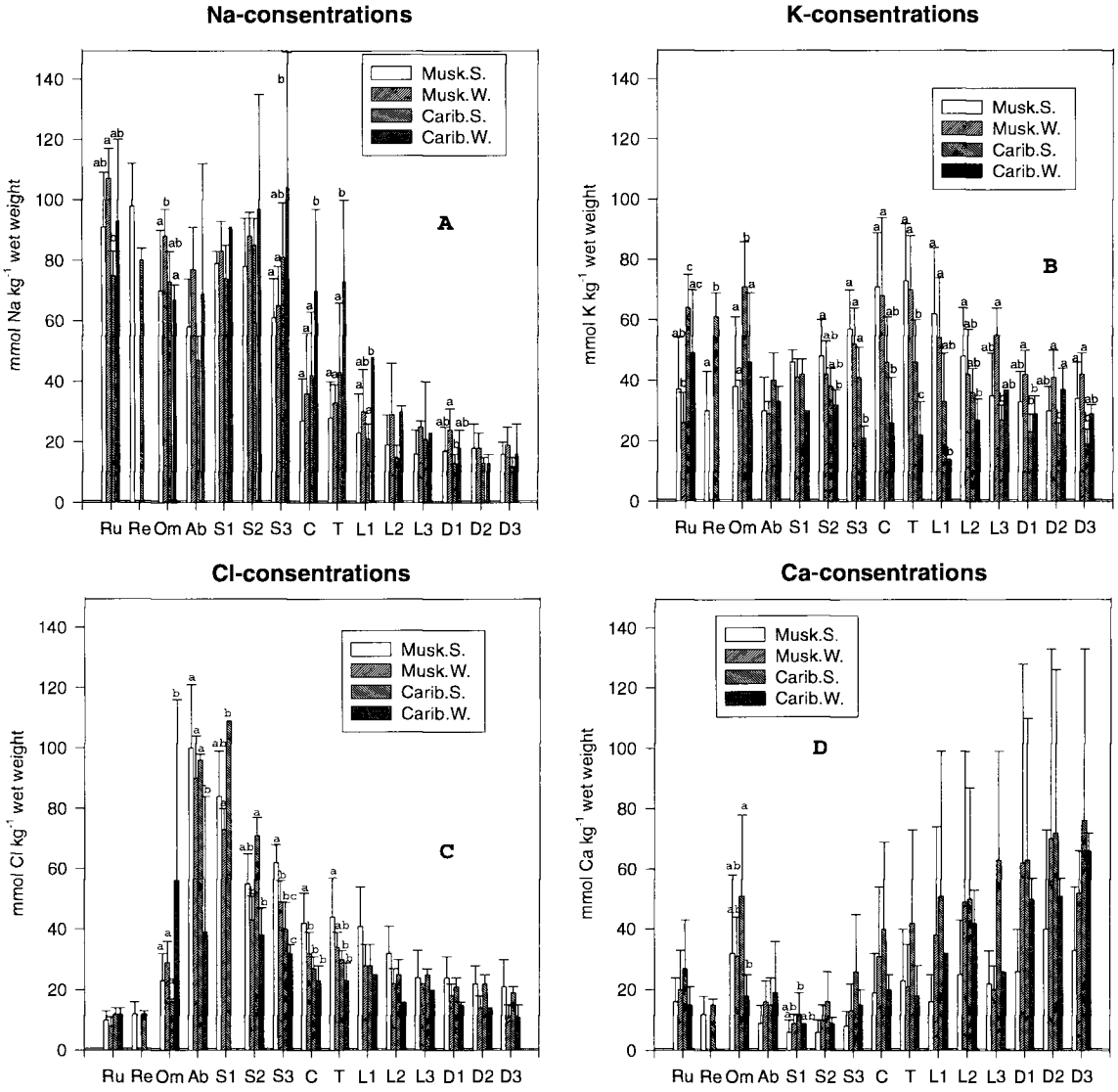
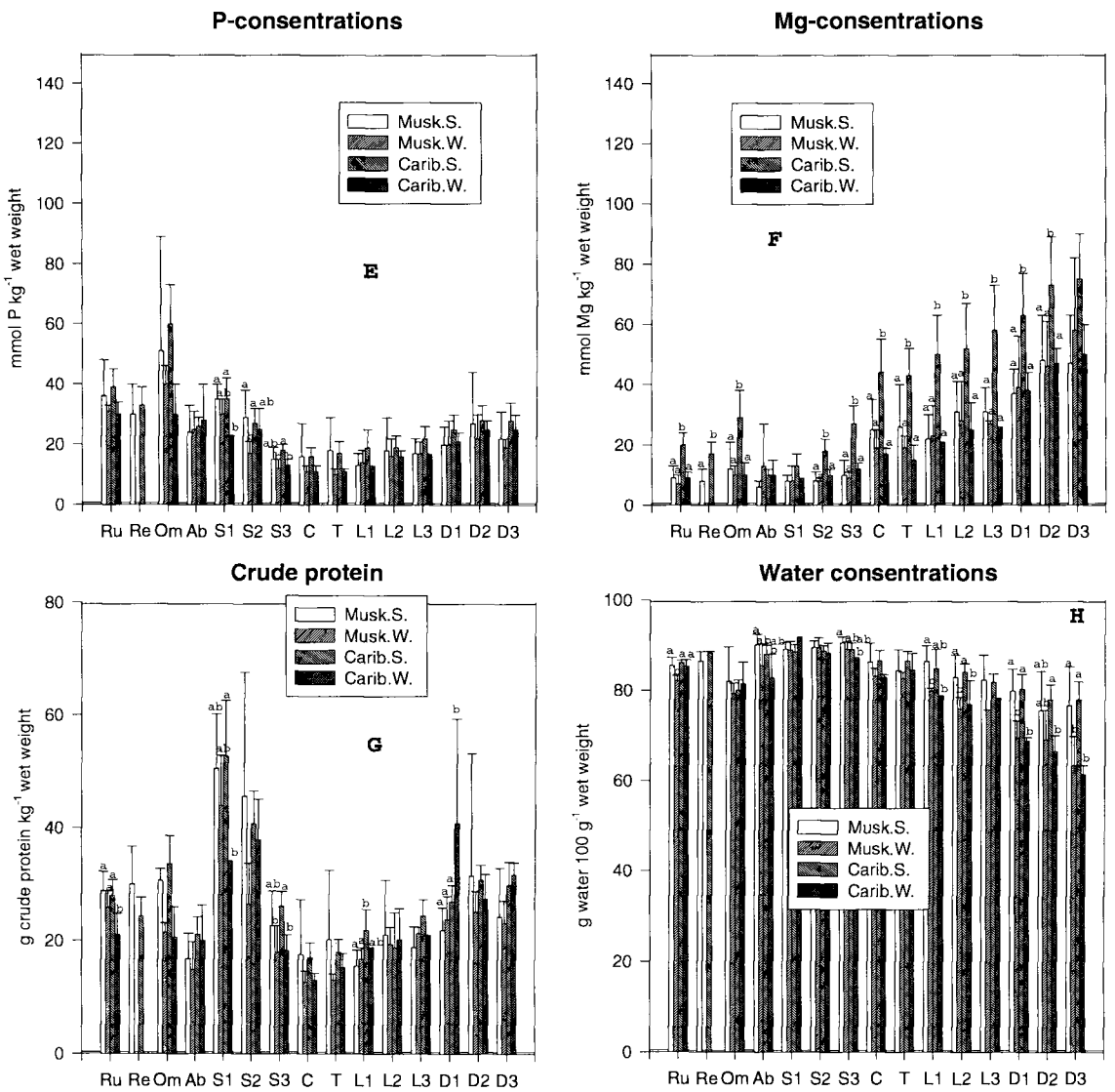


Fig. 1. A–H. Mineral, crude protein and water concenrrations with standard deviation (*s*) in different sections of the alimentary tract of muskoxen and caribou. Concentrations in each sections of the alimentary tract followed by different letters are significantly different (Duncan Mulriple range test $P < 0.05$). Ru:rumen, Re:reticulum, Om:omasum, Ab:abomasum, S1-S3:small intestine, C:caecum, T:proximal colon, L1-L3:coiled colon, D1-D3:

Nedkvitne, 1998). Lower Na concentrations in the vegetation than observed in the present study are also observed in other countries like Canada and Finland (Fraser *et al.*, 1984; Nieminen & Heiskari, 1989). The diversity of the vegetation in an area is also important for mineral intakes, e.g. herbs do generally have higher mineral concentrations than leaves from deciduous trees and grasses (Staaland & Sæbø, 1993). Lichens have usually low mineral concentrations and consequently caribou feeding on grasses and herbs may have higher mineral intakes than reindeer/caribou feeding more on lichens. In addition muskoxen and caribou in the study area can increase their mineral intakes by visiting mineral licks and feeding on some aquatic plants (Belowsky & Jordan, 1981; Table 1).

Potassium concentrations in the vegetation were highest in the summer which may reduce the Na concentrations in the alimentary tract (Staaland & Garmo, 1987; Staaland & Sæbø, 1987; Birke *et al.*, 1995). This correspond to the observations that caribou collected during the winter, when K con-



distal colon. BM (Body mass, kg (s) and (range): Muskoxen summer (4 adult males, 1 female* yearling, 2 male yearlings): 249(95)(149-347) and winter (8 adult males): 293(40)(227-346), Caribou summer (4 adult males, 1 yearling female):123(40)(54-146) and winter (3 adult males) 86(4)(81-89). *BM of one female yearling with assumed BM of 150 kg missing.

Table 2. Total alimentary content, and alimentary pools of minerals, crude protein and water in the alimentary system [mean (standard deviation)] of muskoxen and caribou collected on Greenland in August 1990 (Figures followed by different letters are significantly different, *t*-test $P < 0.05$). Total pools are measured in mmol for all minerals, g for protein and kg for water and total content. Data are from 5 muskoxen (4 adult males, 1 yearling female*) with BM in kg (*s*) 289 (80) (range 149-347) and 5 caribou (4 adult males, 1 yearling female) with BM in kg (*s*) 123 (40) (range 54-146).

		Total cont.	Ru+Re %	Om %	Abo %	S.int %	L.int.** %	Caecum %
Na	Muskoxen	3759 (1317)a	83.9 (2.0)	4.1 (1.1)a	1.5 (1.2)a	7.9 (2.5)	2.7 (1.2)	1.7 (0.7)a
	Caribou	1696 (472)b	81.4 (4.4)	1.8 (0.3)b	1.2 (0.3)b	10.4 (1.9)	5.3 (2.9)	4.2 (2.4)b
K	Muskoxen	1731 (825)	65.2 (5.0)a	4.0 (1.3)a	1.9 (0.4)a	13.0 (4.8)a	16.0 (4.2)a	9.5 (1.8)a
	Caribou	1444 (459)	82.7 (0.2)b	2.1 (0.2)b	1.2 (0.3)b	6.3 (2.2)b	7.8 (2.5)b	5.4 (1.9)b
Cl	Muskoxen	878 (258)a	33.5 (8.6)a	5.4 (1.6)a	11.2 (1.8)	31.1 (12.0)	18.9 (4.2)	11.4 (2.9)
	Caribou	472 (162)b	46.7 (5.7)b	1.4 (0.1)b	8.6 (2.2)	27.4 (5.0)	15.9 (2.6)	10.2 (1.6)
P	Muskoxen	1358 (439)a	80.6 (3.0)a	6.0 (1.9)a	1.8 (0.4)a	6.5 (1.3)	5.1 (1.6)	1.9 (0.5)a
	Caribou	849 (206)b	83.9 (0.9)b	2.9 (0.4)b	1.3 (0.4)b	6.1 (0.8)	5.9 (0.4)	3.0 (0.3)b
Mg	Muskoxen	477 (235)	59.6 (6.5)	5.6 (3.8)	1.5 (0.5)a	7.2 (3.7)	26.2 (6.8)	9.2 (1.2)a
	Caribou	546 (112)	64.5 (5.0)	2.1 (0.2)	0.8 (0.2)b	8.4 (1.7)	24.2 (3.4)	12.5 (1.5)b
Ca	Muskoxen	670 (295)	72.5 (5.5)	7.5 (2.4)a	1.4 (0.4)	4.3 (1.9)	14.3 (4.4)	5.1 (1.2)a
	Caribou	741 (448)	68.1 (10.1)	3.3 (1.1)b	1.2 (0.7)	8.6 (6.8)	18.8 (3.6)	10.6 (3.2)b
Cr.prot.	Muskoxen	1228 (380)a	77.6 (3.4)	3.9 (1.1)a	1.4 (0.3)	10.6 (2.5)	6.5 (1.6)	2.5 (0.5)a
	Caribou	666 (168)b	76.9 (1.6)	2.1 (0.2)b	1.3 (0.5)	11.5 (1.1)	8.2 (0.9)	4.2 (0.4)b
Water	Muskoxen	37.3 (11.2)a	73.7 (4.2)	4.7 (0.8)a	2.2 (0.4)	9.8 (3.6)	9.5 (2.4)	4.8 (1.2)a
	Caribou	20.9 (5.8)b	76.1 (2.6)	1.6 (0.2)b	1.8 (0.4)	9.3 (1.3)	11.2 (1.3)	6.8 (0.7)b
Total	Muskoxen	43.9 (13.1)a	74.0 (4.0)	4.8 (0.7)a	2.1 (0.3)	9.2 (3.3)	9.8 (1.3)	4.7 (1.1)
content	Caribou	24.3 (6.7)b	76.2 (2.4)	1.7 (0.2)b	1.7 (0.4)	9.1 (1.2)	11.3 (1.3)	6.8 (0.6)

* BM from rhe female yearling missing, but assumed ro be 150 kg.

** Large intestine include caecum+colon, in addition the content of caecum relative to total alimentary content is presented.

centrations in the food were lowest, had higher concentrations of Na and lower concentrations of K in the section from the caecum and into the large intestine than the other animals studied. In the muskoxen the K concentration in this section reached a high level both in summer and winter which then corresponded to the relatively low Na concentrations. It is commonly observed that high K concentrations in e.g. rumen of reindeer and moose (*Alces alces*) coincide with reduced Na concentrations during summer (Staaland & Sæbø, 1987; Staaland *et al.*, 1992). High levels of K in the caecum has also been observed in moose and in previous studies on muskoxen from Jameson land, Greenland (Staaland & Thing, 1991; Staaland *et al.*, 1992). In reindeer used in feeding experiments, K concentrations remained low and Na concentrations high in this section of the alimentary tract (Staaland *et al.*, 1984). Svalbard reindeer (*R. t. platyrhynchus*) had relatively higher Na and lower K concentrations in the alimentary tract in winter than in summer (Staaland & White, 1991). Sodium is probably therefore no limiting factors in these arctic regions.

With respect to Ca, P and CI concentrations few significant variations inter- and intraspecifically were observed. To be noted is the large individual variations (S.D.) in Ca concentrations in the alimentary tracts, which are typical observations also from other studies (Staaland & White, 1991). The concentrations of Mg in the alimentary tract of caribou collected during the summer were higher than in caribou collected during the winter and in muskoxen from summer and winter seasons. Relative to the metabolic BM (mmol $Mg*BM^{-0.75}$) the alimentary content of Mg in the caribou was 14.8 mmol and 6.8 mmol (estimated from the mean values Table 2) in the muskoxen collected during the summer. Similar observations were made for moose in south central Sweden (Staaland *et al.*, 1992) and for roe deer in southern Norway (Holand, 1994). This could reflect higher Mg intake in the caribou than in the muskoxen and also reflect some dietary differ-

ences, e.g. the muskoxen feeding more on grasses with lower Mg concentrations and the caribou more selective for herbs with higher concentrations (Table 1). The decrease in Na, K, Cl concentrations and water content through the distal alimentary tract indicate more or less efficient absorption, whereas the increase in Ca, P and Mg concentration indicate less or no absorption of these elements. This is in agreement with earlier findings (Perry *et al.,* 1967; Staaland *et al.*, 1984; Staaland & Thing, 1991; Staaland *et al.*, 1992; Holand & Staaland, 1995).

Alimentary pool sizes could only be compared for 5 muskoxen and 5 caribou collected in August 1990. A relative large omasum is assumed to be an adaptation to grass diets and the observation that muskoxen had relatively higher total content as well as relatively larger mineral pools in the omasum than the caribou, could therefore indicate that muskoxen is more adapted to grass diets than caribou and reindeer. The caribou with a relatively small omasum and larger caecum could then be more adapted to a diet of higher quality with e.g. more herbs and less grass, than the muskoxen (Staaland *et al.,* 1979; Klein & Staaland, 1984; Hofmann, 1989; Staaland & White 1991; Staaland & Olesen, 1992; Staaland *et al.,* 1997).

The caribou on the Angujaartorfiup Nunaa range has possibly in recent time been forced to feed more on graminoids and may have a diet more similar to the muskoxen. In other areas like Svalbard, South Georgia, Arctic Islands of Canada etc. grasses dominate reindeer diets. In these areas, however, reindeer are without competition from other large herbivores and/or has adapted to these diets through a long period of time. It has also been observed that the diet of the peary caribou (*R. t. pearyi*) is more diverse than the diet of the muskoxen on Banks Island (Larter & Nagy, 1997). Since muskoxen is more adapted to a grass diet it could have a competitive advantage over the caribou when introduced to West Greenland. In Svalbard reindeer which has developed a rather large caecum, data indicate a high fibre low sugar fermentation in the caecum which allows for high non-protein, water and mineral absorption as an adaptation to grazing (Staaland & White, 1991). Hofmann's theories on anatomical adaptations in the alimentary systems of ruminants to grazing-browsing etc. (Hofmann, 1989) has been challenged (Illius & Gordon, 1992; Gordon & Illius, 1994; Robbins *et al.,* 1995), nevertheless there are some differences in the structure of the alimentary systems of muskoxen and caribou which can have a function that indicate adaptations to different diets. Seasonal variations in the size of different functional segments of the gastrointestinal tract can also be an adaptation to different qualities of available food in e.g. winter and summer (Pehrson *et al.*, 1997). Minerals are essential elements in all sections of the alimentary tract and has effects on micro-organisms, enzymes, digestibility, osmotic balance, secretion and absorption of different elements from the alimentary tract etc. and they have different functions in different sections. (see. e.g. McDowell, 1992; Stevens & Hume, 1995). Further studies are therefore needed to explain all effects of different mineral concentrations in different sections of the alimentary tract of the animals studied. Such studies can give new information's on how e.g. muskoxen and reindeer/caribou are adapted to their grazing habitats.

Based on the chemical analyses of vegetation and alimentary contents it appears that macrominerals should be no limiting factor for muskoxen and caribou in the study area. It may also appear that the anatomical structure of the alimentary tract of the muskoxen is more adapted to a grass diet while the caribou has an alimentary system more like that of a concentrate selector. Comparison of the structure of the alimentary systems and its mineral contents of muskoxen and reindeer/caribou in different regions may give information's on how different subspecies and separate populations are adapted to different grazing systems.

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