Mineral absorption in relation to nutritional ecology of reindeer

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Abstract: This paper addresses the way which absorption of minerals relate to nutritional ecology and mineral conservation processes. A latin square designed experiment was used to assess the effects of diet on mineral (Ca, Mg, K, Na) absorption processes in reindeer (*Rangifer tarandus* L.). Three male calves were fed 3 different diets: concentrate with 25% grass meal (RF-71), lichens, and a mixed diet of lichens and RF-71. Two other male calves were fed the lichen or mixed diet, supplemented with 4 g Ca/day. Ca supplementation significantly increased fecal Ca excretion, reduced the excretion of K and Mg, but had no significant effect on Na excretion. Rates of intake and fecal exretion of Ca, Mg and K were highly correlated ($P<0.001$), while no correlations were found for Na. Negative digestibilities of Ca, Mg and K, and a positive Na digestibility were noted for the lichen diet. For the other diets, all minerals were in positive digestibility, and Ca supplements increased the digestibility of all minerals. Digesta from different sections of the alimentary tract were collected after termination of the experiment. Alimentary pools of Ca and K were equal for animals fed lichen or RF-71, whereas the Na pool was largest on the lichen diet and the Mg pool largest on the RF-71 diet. Rumen turnover time (rumen mineral pool size/daily mineral intake) was consistently less than 3 days for Ca and Mg, but was 22 and 82 days for Na on the RF-71 and lichen diets respectively. Estimates of mineral exchange in various parts of the tract showed that the intestines play and important role in scavanging endogenously secreted minerals. Results are discussed with respect to mineral binding by lichens and the possible role of natural mineral supplements in the nutritional ecology of reindeer.

Key words: reindeer, *Rangifer*, mineral absorption, digestion, calcium, Ca

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Introduction

In northern reindeer and caribou habitats the availability of minerals may vary by season and location. It is generally believed that the staple winter diet of reindeer (lichens, shrubs, etc.) are deficient in nutrients, resulting in the gradual depletion of body energy, protein and Na reserves (McEwan and Whitehead, 1970; White *et al.*, 1981; Staaland *et al.*, 1982). Also, the apparent Na deficiencies experienced by some northern herbivores in spring and summer, may be exacerbated by high dietary K levels which stimulate Na excretion (Weeks and Kirkpatrick, 1976, 1978; Staaland and Jacobsen, 1983). for moose on Isle Royale in Lake Superior, Na balance is maintained on a year-round by eating aquatic vegetation which accumulates Na (Belovsky and Jordan, 1981). Likewise, reindeer and caribou supplement their diets with mineral-rich sources such as aquatic and coastal vegetation, salt licks, soil, and sea water. In fact, these mineral-rich resources may be central to the location of home ranges of moose (Tankersley and Gasaway, 1983) and Dall sheep (Heimer, 1974). The occurrence of such resources within reindeer and caribou ranges could be important factors in establishing routes of seasonal migrations.

The physiological regulation of mineral metabolism in reindeer is poorly understood (White, 1979). However, studies on domestic species indicate that mineral absorption sets the pace for mineral turnover which shows adaption to dietary source (ARC, 1980). In this report, we describe some of the characteristics of mineral absorption in reindeer, and relate these findings to the nutritional ecology of the species.

Material and methods

Five male reindeer calves (9 months old), mean body weight 45±3 kg (±SE), were used in the feeding trials. The animals were brought from semidomestic herds in southern Norway to the Animal Science Laboratory at the Agricultural University of Norway, Ås, in early December 1983. The animals were given a commercial, pelleted feed, RF-71 (Jacobsen *et al.*, 1977), supplemented with lichens (200 g/d) until january 1984 when they were equipped with rumen and abomasal cannulae. During February and March they were kept in large stalls at room temperature (+20°C) and used in a multipurpose experiment (see also Hove *et al.*, 1986). We designed a 3x3 latin square experiment in which 3 animals were subjected sequentially to three dietary treatments: concentrate with 25% grass meal (RF-71), lichens, and a mixture of RF-71 and lichens (Table 1). The other two reindeer were fed lichens or the mixed diet and given a continous intraruminal infusion of calcium acetate equivalent to 4 g Ca/day. Ca absorption potential was estimated using an intravenous injection of absorption stimulant, 1,24 dihydroxy vitamin D_3 (20 μg) (see Hove *et al.*, 1986). All animals received a continous intraruminal infusion of the non-digestible marker Co-EDTA at a rate of 183±7 mg/day.

The reindeer were offered ca. 1 kg dry food/day and water *ad libitum*. At least 8 days conditioning to new diets was allowed before each Ca trial. Food and food remains were weighed daily throughout the experimental period. Total feces was collected and weighed over 5 consecutive days starting at 10:00 h. Fresh food and fecal samples were collected each day and dried overnight at 105°C; subsamples were dried to a constant weight, ashed and analyzed for Co, Ca, Mg, Na and K by conventional Atomic Absorption methods. Acid insoluble ash (AIA) content was determined by dissolving the ash twice in boiling 4N hydrochloric acid, filtering through as-free filter paper, and ashing again at 625°C.

Dry matter digestibility (DMD) was determined by conventional means and was also estimated based on the concentration of none-digestible marker in feces. The two markers used were AIA in the diet and Co-EDTA which was infused into the rumen. These markers were also used to assess cumulative absorption of dry matter, water and minerals down the intestinal tracts of animals fed the lichen and RF-71 diets.

After termination of the feeding trials two animals fed the RF-71 and three fed the lichens were slaughtered. The gastrointestinal tract was removed and divided into 11 sections: rumen, reticulum, omasum, abomasum, small intestine (3 sections), cecum, spiral colon (2 sub-sections) and rectum. For each section, total content was weighed and representative subsamples taken for chemical analysis were analyzed as described above.

Statistical analyzes included the t-test for comparisons of means and Duncans test for a general linear model using ANOVA (Helwig and Council, 1982).

Table 1. Chemical composition of food used in feeding trials (x̄±S.E.)

Diet		Lichens (n=3)	RF-71 (n=3)	Mixed diet[1]
Crude protein	(g/kg DM)	40.6±2	120.0±2.7	77.8
Ca	(mM/kg DM)	29±1	82±3	54
Mg	(mM/kg DM)	12±1	74±1	41
K	(mM/kg DM)	37±1	242±5	133
Na	(mM/kg DM)	6.4±0.3	15.5±1.1	10.7

[1] The composition of the mixed diet was calculated from the concentrations given for lichens and RF-71, contributing 53.2 and 46.8%, respectively.

Table 2. Feeding regimen, dry matter consumption and comparison of methods for estimating dry matter digestibility ($\bar{x} \pm$S.E.)

Diet		Lichens	RF-71	Mixed diet[1]
Food offered	(g DM/day)	1026 (20)	902 (13)	964 (23)
Intake	(g/day)	591±54	823±42	849±20
Food eaten	(g/kg$^{0.75}$day)	34±3	45±2	49±1
Dry matter digestibility (%)				
Total collection		68.0±4.4	70.9±2.2	66.4±1.2
Co-EDTA as marker		63.3±6.5	59.7±7.4	69.9±1.8
AIA as marker		72.3±2.0	70.7±2.5	71.4±2.2

( ) number of observations.

Results

The concentration of protein (Nx6.25) and minerals were lowest in the lichen diet, intermediate in the mixed diet and highest in the RF-71 diet (Table 1). Mean dry matter intake was lowest for the lichen diet, but differences in consumption of the other feed were not significant. Mean apparent DMD was not significantly different between diets, irrespective of the methods used to estimate DMD ($P > 0.05$) (Table 2). Intraruminal infusion of Ca had no significant effect on DMD; therefore, Table 2 includes all data for each diet.

Although previous studies indicate that vitamin D_3 supplementation may increase Ca absorption (Hove *et al.*, 1986) we detected no significant effect of this treatment on fecal Ca content or apparent Ca digestibility.

Highest concentrations of fecal Na were noted for reindeer fed lichens. Fecal concentrations of Ca, Mg and K were highest on the RF-71 diet. The addition of 4 g Ca/day to the RF-71 diet increased Ca and decreased fecal K and Mg concentrations but had no significant effect on fecal Na (Table 3). Fecal excretion of Na was independent of intake, whereas the intake and excretion of Ca, Mg and K were correlated with intake:

Eq. I: $Ca_{feces} = 0.37 \cdot Ca_{food} + 20.68$; $r^2 = 0.47$, $n = 54$, $P < 0.001$

Eq. II: $Mg_{feces} = 0.62 \cdot Mg_{food} + 2.46$; $r^2 = 0.86$, $n = 54$, $P < 0.001$

Eq. III: $K_{feces} = 0.15 \cdot K_{food} + 19.23$; $r^2 = 0.25$, $n = 54$, $P < 0.01$

A negative apparent digestibility of all minerals, except Na, was noted for reindeer fed the lichen diet (Table 4). Ca supplementation of the lichen diet had a positive effect on Ca, Mg and K digestibility, but had no significant effect on mineral digestibility of the mixed diets or RF-71.

Concentrations of AIA increased from the rumen-reticulum to the abomasum and then decreased to low levels in the duodenum (Fig. 1). AIA concentration increased steadily between the duodenum and the distal colon. Alimentary concentrations of AIA were consistently higher in the lichen fed animals in all sites except the

Table 3. The effects of dietary Ca supplementation of fecal mineral concentration (mM/kg DM) and water content (g/100 g wet weight) ($\bar{x} \pm$S.E.).

Diet	Ca	Mg	K	Na	Water
Lichen (n=13)	151±8 ab[1]	45±3a	164±11a	14.3±1.0a	60.1±1.4a
Lichen + Ca (n=9)	443±37c	35±2a	47±7 b	12.2±2.2ab	63.5±2.7ab
Mixed diet (n=13)	142±9 a	96±4b	183±11a	10.2±1.0bc	66.3±1.0b
Mixed diet + Ca (n=10)	254±25d	73±4c	83±13b	12.2±1.6ab	63.6±3.0ab
RF-71 (n=13)	199±15b	181±5d	198±23a	7.4±0.7c	71.7±0.8c

[1] Values in the same column followed by the same letter(s) are not significantly different.

Table 4. Mineral digestibility in reindeer fed different diets ($\bar{x}$% ±S.E.).

Diet	Ca	Mg	K	Na
Lichen (n=10)	—79±32a[1]	—33±27a	—57±22a	16±15a
Lichen + Ca (n=10)	42± 9b	9±24b	52±18b	40±17ab
Mixed diet (n=13)	16± 7b	28± 4b	57± 3b	69± 4bc
Mixed diet + Ca (n=10)	51± 4b	35± 5b	77± 4b	58± 7bc
RF-71 (n=13)	29± 7b	29± 6b	75± 4b	85± 3c

[1] Values in the same column followed by the same letter(s) are not significantly different.

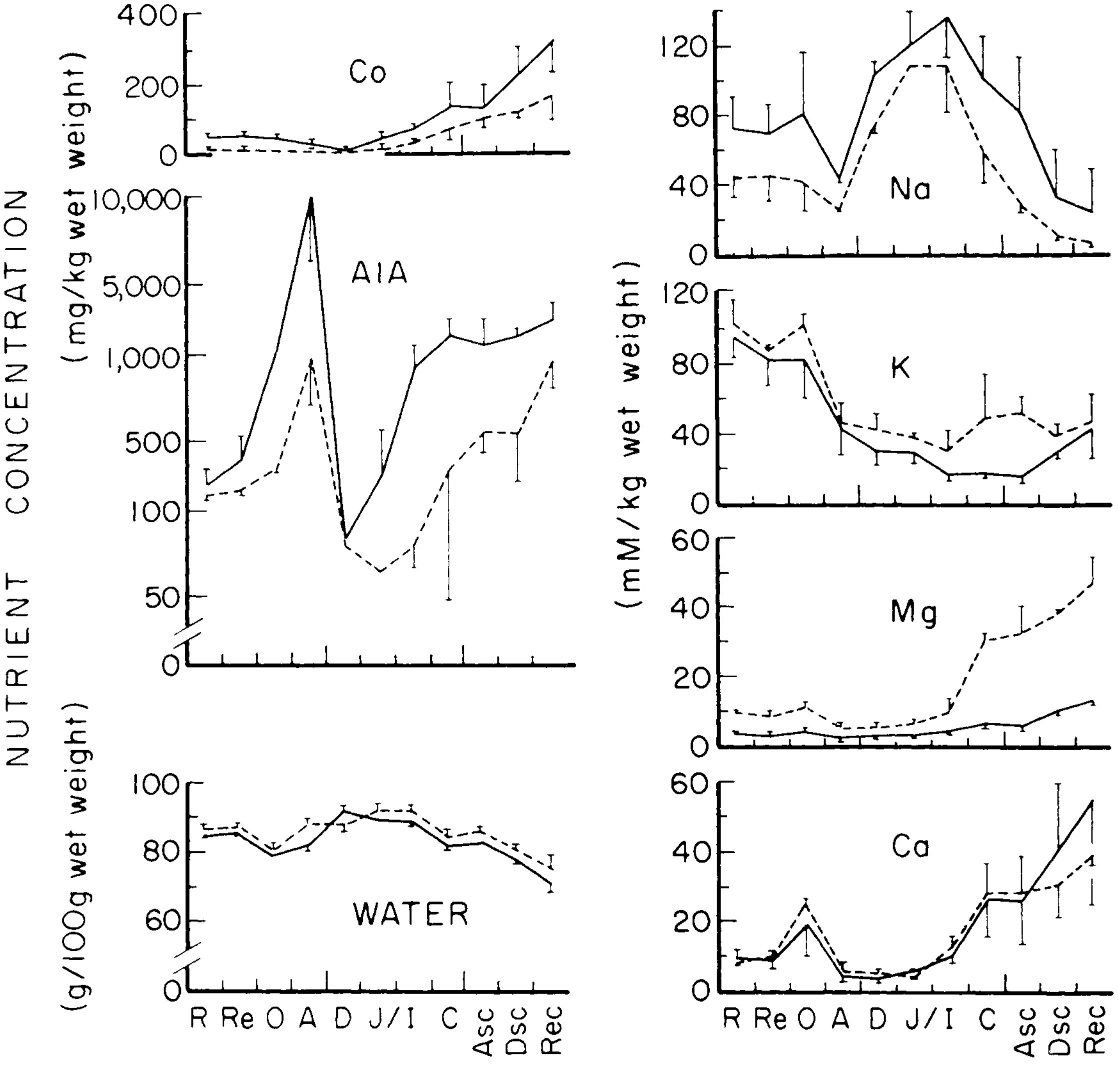

Fig. 1. Mean concentrations of markers, water and minerals in the alimentary tract of reindeer fed two different diets; ———————— Lichens (n=3) and --------------RF-71 (n=2). Vertical bar represents the SD. R, rumen; Re, reticulum; O, omasum; A, abomasum; D, duodenum; J/I, jejunum/ileum; C, cecum; Asc and Dsc, ascending and descending spiral colon; Rec, rectum.

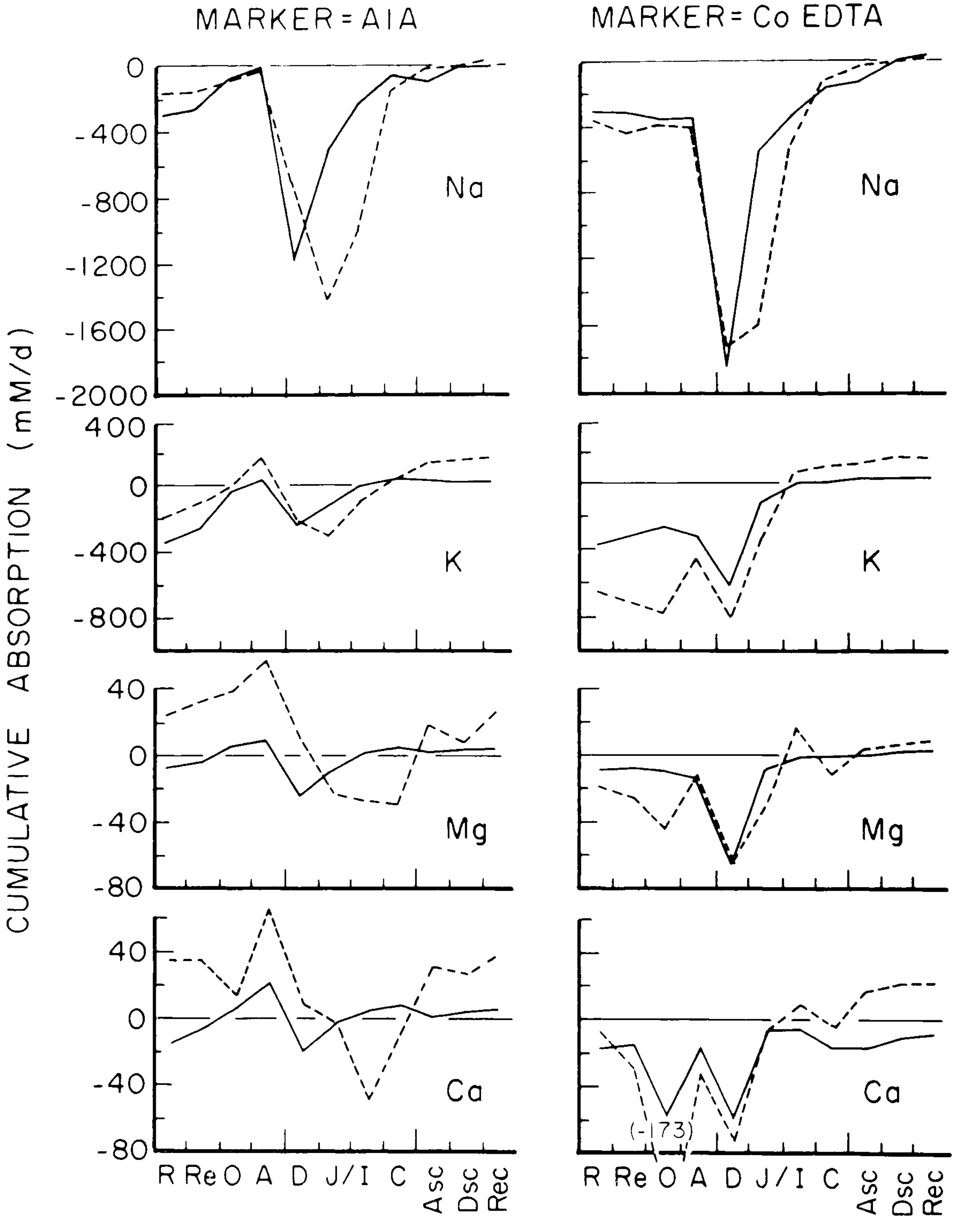

Fig. 2. Cumulative absorption of minerals in the alimentary tract of reindeer fed two different diets: ——————— Lichens; - - - - - - - - - - - RF-71. Acid insoluble ash (AIA) left, and Co-EDTA right, were used as reference markers. For reasons described in the text, calculations of mineral exchange within the omasum are assumed to be less reliable than those for the rest of the alimentary tract. Negative changes indicate secretion and positive changes indicate absorption. Calculations for each cation are made in relation to the respective dietary intakes. Abreviations are given in Fig. 1.

duodenum. High AIA concentrations in the abomasum can be attributed in part to an accumulation of sand and stones.

Co was derived mainly from the external marker Co-EDTA. The concentration of Co was remarkably constant in the forestomachs, but increased progressively through the intestines (Fig. 1). Co concentrations were higher in the alimentary contents from reindeer fed lichens than from those fed RF-71.

Concentration gradients of Ca and Mg in the alimentary tract were similar to that of Co. In contrast, K concentrations were highest in the forestomachs and remained relatively low in the intestines (Fig. 1). Na concentration decreased markedly in the abomasum, followed by an increase to a peak in the cecum and an abrupt decline in the large intestine. Na concentrations in the lichen-fed animals were consistently higher than those in animals on the RF-71 diet. Water content followed the same general pattern as Na concentration (Fig. 1).

The method of calculating absorption/secretion in the alimentary tract using non-absorbed markers has been described by White *et al.* (1984). Absorption calculations are based on the assumption that equal amounts of markers (i.e. AIA ingested in food or Co-EDTA infused) flow through each section of the alimentary tract per day. However, this method may not be applicable to the omasum, as liquids, separated from solids at the rumen-omasal orifice, are thought to move through the omasum more rapidly than solids. Some accumulation of sand or small stones in the abomasum may increase AIA concentration which would give a spuriously high apparent absorption of minerals using the AIA marker.

Irrespective of these limitations, there was generally good agreement on the calculated absorption/secretion patterns for Na and K between the two markers (Fig. 2). Calculations show a substantial secretion of Na into the proximal small intestine and an efficient absorption in the distal small intestine. K exchange in the forestomachs was small and was secreted in the duodenum, and reabsorbed in the distal small instestine and large intestine. The exchange of Mg and Ca across the wall of the alimentary tract follows a more irregular pattern, and the results differ with the marker used. The pattern of Ca and Mg secretion/absorption resembled that for K when Co-EDTA was used as marker: Co-EDTA is the preferred reference substance for minerals absorbed from the liquid phase. Net absorption of Ca from the small intestine is in agreement with *in vivo* results (Hove *et al.*, 1986), again suggesting that Co-EDTA may be the preferred marker for determining Ca absorption patterns. On a molar basis less endogenous Mg and Ca, compared to Na, was added to intestinal contents during exchange processes in the intestines (Fig. 2).

Standing pool sizes of minerals in the alimentary tract are shown in Table 5. The rumen contained 60 - 70% of the total alimentary pool of all 4 minerals. Turnover time of minerals, calculated as pool size/daily intake, was lower for Ca and Mg (0.6 - 2.4 days) than for Na (21.5 - 81.8 days), while K was intermediate. These results correspond to previous results obtained in earlier experiments (Staaland *et al.* 1984).

Table 5. Alimentary pool size (x̄±S.E.) and rumen mineral turnover time[1].

	Total alimentary pool[2]		Rumen pool		Turnover time (d)	
Diet	Lichens	RF-71	Lichens	RF-71	Lichens	RF-71
n	3	2	3	2	3	2
Total content	5.3±0.7	5.4±1.0	4.2±0.7	4.3±0.9	1.1[3]	0.7[3]
Ca	61±10	63±24	38±2	41±11	2.2	0.6
Mg	24±3	64±12	17±2	42±10	2.4	0.7
K	443±88	482±81	408±81	432±56	18.6	3.8
Na	411±82	275±89	311±63	196±70	81.8	21.5

[1] Food intake calculated from average daily food consumption and mineral concentrations in the diet (Tables 1 and 2).

[2] Total content in kg wet weight; mineral content in mM.

[3] DM turnover time = rumen pool x rumen DM/DM intake.

Table 6. Examples of natural sources of minerals (x̄ mM/kg DM ± S.E.).

Source	N	Ca	Mg	K	Na
Lichens[1]	17	19±2	10±1	42±11	12±1
Horsetail[1]	14	331±38	140±6	617±65	25±5
Grass[1]	55	49±2	36±3	330±20	10±1
Aquatic herbs (leaves)[1]	14	214±33	97±15	717±85	102±25
Aquatic herbs (roots)[1]	17	127±6	34±1	346±44	125±30
Sea water (34‰)[2]		10	52	10	459
Salt licks[3]		3	1.4	0.2	7
Salt licks[4]		0.15-2.15	0.07-1.15	0.01-0.19	1.8-37.0

[1] From Staaland and Sæbø (1985).

[2] In mM/1 sea water.

[3] From Fraser and Reardon, 1980; in mM/1 water.

[4] From Fraser *et al.* (1980), in mM/1 water.

Discussion

Adaptions in mineral ecology of herbivores can occur at the detection-acquisition, absorption and retention-recycling levels (White, 1979). This study addresses absorption function since the winter pasture of reindeer and caribou is generally low in minerals (Staaland *et al.*, 1983; Staaland and Sæbø, 1985). Furthermore, minerals are not evenly distributed within the food base or soil substrate, and reindeer appear to obtain extra minerals through the selective use of plants and inorganic material. Some terrestrial plants (buck-beans, *Menyanthes trifoliata* and horsetail, *Equisetum* spp.) and aquatic vegetation sought by reindeer are known to contain high levels of Na (Skjenneberg and Slagsvold, 1968; Staaland and Sæbø, 1985). Thus, it can be argued that a diverse flora provides for the best overall mineral balance.

Plants also change in chemical composition during the growing season; for example, K, P and N concentrations are high in rapidly growing vegetation but decrease substantially during senescence (Staaland and Sæbø, 1985). Habitats with some snowbeds and large altitudinal variations with plants in different phenological stages, should therefore also contribute to maintaining a high availability of most minerals, notably K and P (Klein, 1970; Skogland, 1980, 1984). The occurrence of certain types of bedrock and soil, as well as arctic seabird rookeries can also influence the effective quality of pasture and increase the overall value of some isolated areas to reindeer (Staaland *et al.*, 1983; Staaland 1985). Other potentially important sources of minerals are mineral licks and sea water (Table 6). Also it is well known that reindeer are attracted to urine on snow, may chew on shed antlers, or may even eat small mammals such as lemmings. Presumably these dietary novelties serve to supplement the minerals in forage, thereby improving mineral balance.

Lichens apparently have a special effect on mineral absorption. Fecal concentration of Na is frequently higher when anmimals are consuming lichens in winter than when grazing summer pasture (Staaland *et al.*, 1980). One might speculate that lichens bind some minerals, particularly Na and Ca, and lower their net absorption (White *et al.*, 1984). Indeed, it has been shown that the efficiency of Ca absorption is lower on lichen than high Ca diets (Hove *et al.*, 1986). Therefore mixing of lichens with vegetation higher in mineral resources, e.g. mosses and dead leaves, may serve to saturate these binding sites and maintain mineral balance in the wild.

It was reported previously that lactating reindeer on summer pastures in Interior Alaska depleted their body reserves of Na (Staaland *et al.*, 1982). Subsequent field studies in Norway showed that the rumen-reticulum can function as a reserve for Na; ruminal Na is gradually exchanged for extraruminal K to maintain osmotic balance. This may occur when intake of Na is too low to meet body requirement or when increased K intake in spring stimulates Na excretion in urine (Staaland and Jacobsen, 1983). It has also been shown that depleted body reserves of Na can be rapidly restored by the consumption of forages or other materials that are rich in Na (Staaland *et al.*, 1982). Na, and probably also K, may be replenished by different mechanisms than Mg and Ca. The slow ruminal turnover of Na (Table 5) indicates that most Na in the alimentary tract is of endogenous origin. Furthermore, considerable Na is involved in exchange between the alimentary tract and the body pools (Fig. 2). In fact, the daily addition of salivary Na may easily equal that in the entire total body pool (Bartley, 1976; White *et al.*, unpublished data) and serves to maintain rumen function even when animals become Na depleted.

In contrast to the Na and K pools, the ruminal Ca and Mg pools are turned over rapidly (Table 5), and there is a strong correlation between intake and fecal excretion (Eq. I and II). Although Ca supplementation increases fecal Ca content (Table 3), fractional Ca absorption from the small intestine increases (Hove *et al.*, 1986) giving an overall positive effect on Ca digestibility. The present study shows that increased dietary Ca also stimulates absorption from the spiral colon (Fig. 2). It is possible therefore that the consumption of Ca-rich soils or vegetation enhances short-term Ca absorption. The intake of highly soluble Ca has a stimulating effect on the absorption and digestibility of Mg and K (Tables 3 and 4), particularly when animals are eating lichens.

In conclusion, the results of this study show that the absorption of the major mineral elements Ca, Mg, Na and K can be stimulated by increasing the respective dietary intakes of each. This suggests that reindeer utilize mineral-rich licks and vegetation in relation to need. In addition, the present results indicate that supplementation with Ca in a highly soluble form can stimulate the absorption of other minerals. This observation highlights the complexity of events that occur when an animal feeds sporadically on mineral-rich substances.

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