REGIONAL VARIATION IN MINERAL CONTENTS OF PLANTS AND ITS SIGNIFICANCE FOR MIGRATION BY ARCTIC REINDEER AND CARIBOU

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ABSTRACT: Ten minerals, 6 macro (Na, K, Ca, P, Mg, Cl) and 4 trace elements (Co, Cu, Mo, Mn), were analysed in 13 forage plants of reindeer and caribou (*Rangifer tarandus*) to compare differences between coastal and interior areas. Samples were collected in northern Norway (coastal and interior regions), southern Norway (interior), and Alaska, USA (interior). We tested the hypothesis that the domestic herding practice of moving reindeer to spring-summer pasture on the coast is to allow reindeer to make up mineral balances that are negative during winter. This hypothesis was supported by data for Na and Cl, which were higher in 12 of 13 forage plants from the coastal region compared with inland areas. Analyses of the other minerals, however, indicated a higher variability among plants than between regions. Aquatic plants from the coast and inland were higher in Na and Cl than terrestrial species. A high concentration of Co in willows was independent of region. Graminoids were low in Na and Cl, independent of region. Lichens were low in all macro minerals but were high in trace minerals. This study supported hypotheses based on salt hunger; namely, that the primary reason to move in coastal regions was to compensate for Na deficiency in winter. We suggest this movement also would maximize milk synthesis, which would otherwise be limited because of high Na content of reindeer milk. Selective foraging within coastal vegetation allows animals to meet requirements for macrominerals. Selective use of willows not only supports the high protein requirements of lactation and growth, but an adequate Co intake is required for synthesis of vitamin B12, critical for animal growth and rapid development of rumen function in young reindeer and caribou.

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Reindeer and caribou (*Rangifer tarandus*) as well as other ungulates must have access to more than 24 mineral elements for growth and survival (McDowell 1992, Robbins 1993). Mineral contents in plants grazed by herbivores exhibit large regional variation because of soil substrate and transportation by wind, water, and animal actions (Låg 1963, Underwood 1977, Staaland et al. 1983, Nieminen et al. 1987, Robbins 1993, Staaland and Sæbø 1993). Availability of different plants, and access to grazing in different regions can affect growth rate and survival of herbivores (Underwood 1977). Overgrazing can eliminate plants containing essential mineral elements, but heavy grazing also can lead to animals foraging on plants (e.g., halophytes) with high concentrations of some elements, sometimes to the point where those plants become poisonous (Heady 1975).

Regional variation typified by the high levels of sodium in coastal regions compared with interior regions (Botkin et al. 1973, Staaland and Nedkvitne 1998) have been associated with seasonal migration between the interior and coast in the Saami culture of reindeer herding (Skjennebeg and Slagsvold 1968). Wild ungulates are attracted by mineral-rich sources (Fraser and Reardon 1980), be they plants, aquatic sources, or mineral licks. Seasonal variation in plant quality, typified by fiber and protein content, has been well studied (Nieminen and Heiskari 1989, Klein 1990, Robbins 1993), but seasonal variation in the mineral content of plants also may be considerable (Nieminen and Heiskari 1989, Staaland and Sæbø 1993). Nonetheless, possible effects on fitness and reproductive performance from variation in minerals are difficult to determine and, because the number of plant species involved is large, analysis of all species necessarily is incomplete.

Except for a study that reports on a restricted transect from the coast to the Brooks Range in Arctic Alaska, USA (Whitten and Cameron 1980), we know of no comparisons of coastal versus interior regions in mineral contents of forage plants for reindeer and caribou. The purpose of our study was to compare concentrations of 6 macro-elements (Na, K, Ca, P, Mg, and Cl) and 4 trace elements (Co, Mn, Cu, and Mo) in plants between the coastal and interior regions in northern Norway. Those analyses were compared with plants from interior regions in southern Norway, where reindeer graze year-round, and with a limited number plants sampled in interior Alaska, USA, where caribou graze year-round.

METHODS

Plants were collected in 1994, and 1997-99 from different regions in Norway: 9 from coastal regions (A1-A9); 7 from interior regions (B1-B7) in northern Norway; and 6 from interior regions in southern Norway (C1-C6) (Fig. 1). For comparison, a few plants also were collected in the interior regions of Alaska in 1997.

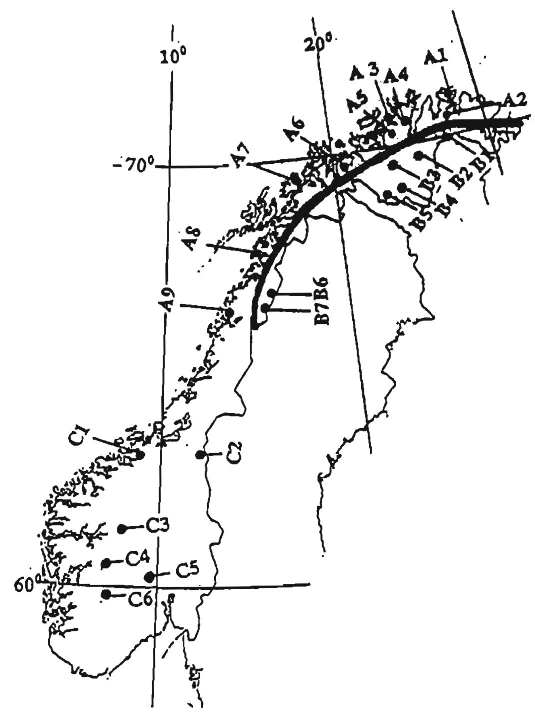

Fig. 1. Regions where plants were collected for chemical analyses in Norway (1994, 1997-99): A1-A9, coastal regions in northern Norway; B1-B7, interior regions in northern Norway; C1-C6, interior regions in southern Norway.

Areas and dates of collection in coastal regions of northern Norway included: A1, Nordkinnhalvøya (11 July 1998); A2, Ifjordfjellet (12 July 1998); A3, Kvaløya (16 August 1997); A4, Sennalandet (15 August 1997); A5, close to Olderfjord (6 July 1994); A6, Olderdalen (11 July 1997); A7, Senja (6 August 1999); A8, Steigen (5 August 1999); and A9, Melfjellet (15 July 1998). Interior regions in northern Norway sampled were: B1, Sáraskáidi (12 July 1998); B2, one-half way between Lakselv and Karasjok (5 July 1994); B3, one-half way between Alta and Láppoluoppal (17 August 1997); B4, Láppoluoppal (16 August 1997); B5, close to Kautokeino (6 July 1994, 16 August 1997, and 12 July 1998); B6, Junkerdalen (14 July 1998); and B7, Saltfjellet (14 July 1998). Interior regions sampled in southern Norway inlcuded: C1, Trollheimen (July 16 1998); C2, Tydalen (8 July 1998); C3, Valdresflyi (16 July 1998); C4, Hardangervidda (5 July 1998); C5, mountain regions Veggli-Nore (6 July and 27 August 1998); and C6, Edland, Setesdal (4 July 1998). Some plants were collected in interior Alaska, USA, close to Fairbanks on 26 June, and at Cantwell, Eagle Creek, and Summit Lodge on 27 June 1997.

Terrestrial species analysed were: lichens (*Cladonia arbuscula, C. stellaris,* and *C. stygiat*); mosses (*Polytrichum commune, Polytrichum* sp., *Sphagnum* sp., *Pleurozium schreberi,* and *Hylocomium splendens*); ferns (*Dryopteris linnaeána, D. dilatata, D. oreopteris, Athyrium alpéstre, A. filix-femina,* and *Cryptogramma crispa*); horsetails (*Equisetum silvaticum, E. pratense,* and *E. arvense*); leaves from dwarf birch (*Betula nana*); leaves from different species of willows (*Salix* spp.); leaves from bilberry (*Vaccínium myrtillus*); willow herb (*Chamaenerion angustifolium*); Lapland lousewort (*Pedicularis lapponica*); goldenrod (*Solidago virgaurea*); tufted hair-grass (*Deschampsia caespitosa*); three-leafed rush (*Juncus trífidus*); and stiff sedge (*Carex bigelowii*). Aquatic plants analysed were: buckbean (*Menyanthes trifoliáta*); water lilly (*Nymphaea alba*); water horsetail (*Equisetum fluviatile*); and bottle sedge (*Carex rostrata*).

Plants were dried to constant weight, ground in a Willey mill and analyzed for Na, K, Cl, Ca, P, Mg, Co, Cu, Mo, and Mn at the Chemical Analytical Laboratory, Agricultural University of Norway, Ås, by methods described by Staaland et al. (1984), AOAC (1990), and Selmer-Olsen (1993). For lichen, mosses, ferns, horsetail, and willows, mineral concentrations were estimated as mean values for all species within each group and each region. Macro-mineral concentrations are expressed as mmole/kg dry matter, and trace minerals, except for Mn (mmole/kg dry matter), as mg/kg dry matter.

Mineral nutrient requirements were expressed as dietary concentrations as proposed by the Agricultural Research Council (ARC 1980). This approach calculates requirements on a daily basis for animals at maintenance and adds requirements for pregnancy, lactation, and growth. The daily requirement for food is estimated to satisfy the energy requirement, and is divided into mineral requirements to give the dietary concentration that meets those needs. Values were estimated for domestic sheep producing milk at 2 L/d. This same approach has been used for some species of wildlife (Robbins 1993).

RESULTS

Sodium concentrations were highest in 12 of 13 plants from coastal regions (Table 1). Moreover, aquatic plants, such as water lilly, had extremely high concentrations of Na, with the exception of bottle sedge, which lacked those high concentrations (Table 2). Of the macro-elements, Cl was the most like Na, with a tendency to be higher in coastal than in interior regions, which occurred for 11 of 13 plants. Chloride concentrations were relatively low in lichens, mosses, dwarf birch, and willows. The highest levels of Cl occurred in the aquatic plants; water lilly and horsetail (Table 2). Except for aquatic plants, Na concentration generally was lower than that of other macro-elements (K, Ca, P, Mg, and Cl). Concentration of K was relatively low at approximately 30 mmol/kg in lichens, was higher in mosses (116-147 mmol/kg), and even higher in most other plants we analysed. In willow herb, K concentration exceeded 1,000 mmol/kg.

Calcium concentrations were low in lichens (18-27 mmol/kg; Table 3), and in

Table 1. Na, K, and Cl concentrations (mmol/kg) in plants collected in 1994 and 1997-99 from coastal and interior regions of northern and interior, southern Norway, and from interior Alaska. Data are means ± SE (n).

Plant Species	Na				K				Cl			
	Norway			Interior	Norway			Interior	Norway			Interior
	N. Coastal	N. Interior	S. Interior	Alaska	N. Coastal	N. Interior	S. Interior	Alaska	N. Coastal	N. Interior	S. Interior	Alaska
Lichens	7.8 ± 2.0 (4)	4.7 ± 1.6 (7)	5.8 ± 1.1 (7)	2.6 ± 0.7 (3)	34 ± 15 (4)	32 ± 9 (7)	26 ± 8 (7)	28 ± 8 (3)	24 ± 21 (4)	10 ± 5 (6)	10 ± 3 (4)	4 ± 1 (3)
Mosses	20.1 ± 3.1 (3)	13.0 ± 6.8 (4)	8.0 ± 5.1 (6)	—	147 ± 47 (3)	116 ± 48 (4)	119 ± 20 (6)	—	17 ± 8 (3)	38 ± 33 (3)	17 ± 22 (5)	—
Ferns	31.9 ± 36.3 (4)	3.8 ± 0.0 (2)	5.8 ± 2.2 (6)	—	770 ± 203 (4)	695 ± 107 (2)	717 ± 132 (6)	—	236 ± 132 (4)	185 ± 95 (2)	140 ± 42 (6)	—
Horsetails	21.3 ±12.0 (5)	5.5 ±1.7 (6)	6.2 ±2.3 (4)	7.4 ±3.3 (3)	760 ±238 (5)	795 ±272 (6)	803 ±32 (4)	947 ±136 (3)	615 ±175 (5)	422 ±172 (6)	264 ±131 (4)	148 ±96 (3)
Dwarf Birch	7.9 ±3.7 (6)	4.5 ±2.0 (8)	6.8 ±3.1 (7)	4.1 ±0.7 (3)	207 ±50 (6)	161 ±36 (8)	214 ±36 (7)	201 ±21 (3)	14 ±5 (4)	10 ±5 (6)	9 ±6 (3)	6 ±4 (3
Willows	15.4 ±4.8 (9)	5.7 ±2.7 (9)	6.9 ±2.8 (12)	4.4 ±0.3 (3)	366 ±55 (9)	370 ±134 (9)	372 ±45 (12)	297 ±30 (3)	32 ±18 (7)	16 ±11 (7)	12 ±5 (9)	28 ±14 (3)
Bilberry	8.0 ±3.7 (4)	4.9 ±0.9 (5)	5.3 ±1.9 (8)	—	286 ±165 (4)	402 ±188 (5)	547 ±413 (8)	—	133 ±161 (2)	148 ±81 (3)	145 ±82 (6)	—
Willow Herb	11.8 ±8.1 (5)	7.8 ±3.9 (3)	5.1 ±1.9 (3)	4.7 — (1)	919 ±357 (5)	1106 ±216 (3)	429 ±122 (3)	537 — (1)	239 ±108 (5)	216 ±73 (3)	89 ±74 (3)	77 — (1)
Lapland Louse-wort	11.0 ±2.6 (2)	9.5 ±3.5 (3)	8.3 ±1.3 (4)	—	537 ±129 (2)	567 ±70 (3)	574 ±31 (4)	—	50 ±12 (2)	31 ±5 (3)	25 ±6 (4)	—
Golden-rod	15.3 ±8.4 (4)	4.1 ±0.6 (3)	-	—	776 ±93 (4)	763 ±50 (3)	—	—	219 ±61 (4)	201 ±102 (3)	—	—
Tufted Hair-grass	3.3 — (1)	6.1 ±2.6 (3)	4.2 ±1.0 (6)	—	540 — (1)	397 ±42 (3)	479 ±65 (6)	—	200 — (1)	138 ±13 (3)	155 ±45 (6)	—
Three-leafed rush	20.7 ±15.4 (6)	5.3 ±2.0 (6)	6.2 ±1.3 (9)	—	374 ±48 (6)	310 ±57 (6)	404 ±92 (9)	—	208 ±52 (6)	141 ±32 (6)	135 ±52 (6)	—
Stiff sedge	12.0 ±4.9 (2)	5.3 ±0.7 (2)	7.9 ±1.9 (7)	—	502 ±20 (2)	350 ±26 (2)	469 ±25 (7)	—	141 ±38 (2)	68 ±2 (2)	52 ±31 (5)	—
[1]High	12	1	0	0	6	1	5	1	11	2	0	0
[2]Exceed	4	0	0	—	12	12	11/12	13	13	12/12	—	—

[1]Number of plant types with high concentrations observed in the study.
[2]Number of plants exceeding requirements for peak lactation (Na = 22 see text, Cl = 7, K = 82; ARC 1980).

Table 2. Mineral concentrations in aquatic plants. Macro-element (Na, K, Cl, Ca, P, and Mg) units, mmol/kg; microelement (Co, Mo, and Cu) units, mg/kg, and Mn units as mmole/kg. Data are means ± SE.

	Species				
Mineral	Buckbean	Water lilly	Water horsetail	Bottle sedge	Minimum[1]
	n = 3	*n* = 2	*n* = 3	*n* = 2	
Na	73.8±31	289±14	43±2	6.7±3.5	22
K	786±107	487±52	873±55	505±86	82
Cl	12±3	292±8	251±57	51±16	7
Ca	106±5	100±28	239±6	79±27	67
P	127±37	109±18	131±53	103±35	87
Mg	117±30	51±6	126±21	100±37	62
Co	0.30±0.10	0.40[2]	0.33±0.12	1.12±1.03	0.20
Mo	0.45±0.50[3]	0.30[2]	0.95±0.92	0.20[2]	nv[4]
Cu	7.91±1.68	5.00±1.41	3.33±0.58	11.29±4.06	5
Mn	0.13±0.05	0.10±0.07	0.10±0.02	0.37±0.10	0.40

[1]Minimum concentration to meet peak lactation (2 L/d; ARC 1980).
[2]Only one analysis.
[3]Two analyses. Plants collected in Southern Norway, except 1 Buckbean.
[4]nv = No value in ARC (1980).

horsetail, willow, blueberry, and willow herb. Comparatively high levels of Ca occurred in shrubs, except for dwarf birch. Graminoids, such as tufted hair-grass, were relatively low in Ca, as were aquatic plants. Concentrations of P and Mg were low in lichens. Herbaceous species were higher in P and Mg than graminoids and aquatic plants were lowest in P and Mg (Tables 2 and 3).

With respect to the 4 trace elements analysed (Co, Mo, Cu, and Mn), the most conspicuous observation was high concentrations of Co in willow. Otherwise, there was large variation among different species (Table 4), with high levels in horsetails, lousewort, and bottle sedge. Concentrations of Mo were low but variable in all plants analysed. Relative to the other trace elements, Cu was highest in all plants except lichens. Lapland lousewort was relatively high in Mn concentration. Mineral concentrations in the same plant species from interior Alaska and interior regions of Norway were about equal (Tables 1, 3-4).

DISCUSSION

Regional variation in concentrations of Na and Cl, with higher concentrations in coastal than interior plants, confirm earlier reports (Låg 1963); this study, however, is the first to document regional trends in Na and other minerals of forage for reindeer from northern and southern Norway. Regional differences in forage were less clear for mineral elements other than Na and Cl; variations in mineral concentrations were higher among plant types than between coastal and interior regions. Most plants collected in our study are essential grazing plants for reindeer (Warenberg et al. 1997). When compared with the concentration needed to meet requirements of female sheep producing milk at 2 L/d (ARC 1980), equivalent to peak lactation in reindeer, only lichens were deficient in all macro-elements. All other plant groups contained adequate

Table 3. Ca, P, and Mg concentrations (mmol/kg) in plants collected in 1994 and 1997-99 from coastal and interior regions in northern and interior, southern Norway, and from interior Alaska. Data are means ± SE (n).

Plant Species	Ca				P				Mg			
	Norway			Interior	Norway			Interior	Norway			Interior
	N. Coastal	N. Interior	S. Interior	Alaska	N. Coastal	N. Interior	S. Interior	Alaska	N. Coastal	N. Interior	S. Interior	Alaska
Lichens	19 ±10 (4)	26 ±14 (7)	18 ±8 (7)	27 ±10 (3)	15 ±12 (4)	21 ±8 (7)	12 ±5 (7)	18 ±2 (3)	21 ±4 (4)	17 ±7 (7)	14 ±7 (7)	19 ±3 (3)
Mosses	58 ±23 (3)	73 ±40 (4)	90 ±123 (6)	—	39 ±5 (3)	24 ±9 (4)	29 ±7 (6)	—	70 ±19 (3)	67 ±23 (4)	39 ±12 (6)	—
Ferns	88 ±40 (4)	68 ±3 (2)	54 ±10 (6)	—	113 ±59 (4)	78 ±16 (2)	114 ±60 (6)	—	190 ±53 (4)	180 ±22 (2)	134±28 (6)	—
Horsetails	193 ±111 (5)	380 ±129 (6)	226 ±28 (4)	269 ±26 (3)	69 ±28 (5)	67 ±35 (6)	122 ±28 (4)	117 ±57 (3)	265 ±77 (5)	159 ±57 (6)	354 ±413 (4)	125 ±5 (3)
DwarfBirch	94 ±16 (6)	96 ±25 (8)	91 ±14 (7)	102 ±9 (3)	91 ±35 (6)	88 ±15 (8)	111 ±20 (7)	76 ±7 (3)	106 ±18 (6)	88 ±9 (8)	83 ±9 (7)	86 ±14 (3)
Willows	153 ±48 (9)	193 ±84 (9)	136 ±32 (12)	132 ±15 (3)	130 ±51 (9)	99 ±33 (9)	122 ±26 (12)	110 ±45 (3)	149 ±50 (9)	117 ±24 (9)	94 ±21 (12)	95 ±25 (3)
Bilberry	176 ±81 (4)	181 ±42 (5)	168 ±69 (8)	—	87 ±25 (4)	113 ±39 (5)	104 ±45 (8)	—	122 ±106 (4)	137 ±59 (5)	96 ±47 (8)	—
Willow Herb	226 ±74 (5)	176 ±55 (3)	206 ±116 (3)	196 — (1)	107 ±12 (5)	95 ±16 (3)	120 ±53 (3)	151 — (1)	204 ±82 (5)	129 ±24 (3)	131 ±77 (3)	184 — (1)
Lapland Louse -wort	120 ±1 (2)	166 ±60 (3)	181 ±15 (4)	—	137 ±19 (2)	120 ±21 (3)	141 ±26 (4)	—	148 ±14 (2)	137 ±26 (3)	145 ±33 (4)	—
Golden-rod	162 ±42 (4)	286 ±75 (3)	—	—	95 ±44 (4)	96 ±48 (3)	—	—	206 ±64 (4)	133 ±178 (3)	—	—
Tufted Hair-grass	29 — (1)	40 ±11 (3)	35 ±10 (6)	—	58 — (1)	59 ±9 (3)	63 ±15 (6)	—	35 — (1)	35 ±2 (3)	36 ±5 (6)	—
Three-leafed rush	32 ±6 (6)	40 ±11 (6)	33 ±7 (9)	—	51 ±10 (6)	50 ±7 (6)	64 ±11 (9)	—	49 ±7 (6)	46 ±7 (6)	42 ±6 (6)	
Stiff sedge	44 ±4 (2)	42 ±1 (2)	64 ±18 (7)	—	71 ±16 (2)	59 ±4 (2)	73 ±12 (7)	—	66 ±8 (2)	42 ±6 (2)	47 ±11 (7)	—
[1]High	2	6	3	2	2	3	7	1	10	1	2	0
[2]Exceed	8	9	6/12	—	7	6	7/12	—	10	9	7/12	—

[1]Number of plant types with highest concentrations observed in this study.
[2]Number of plants exceeding requirements for peak lactation (Ca = 67, P=87, Mg = 62; ARC 1980).

Table 4. Co, Mo, and Cu concentrations (mg/kg) and Mn (mmole/kg), in plants collected in 1994 and 1997-99 from coastal and interior regions in northern and interior, southern Norway, and from interior Alaska. Data are means ± SE (n).

Plant	Mineral and region															
	Co				Mo				Cu				Mn			
	Norway			Interior	Norway			Interior	Norway			Interior	Norway			Interior
Species	N. Coastal	N. Interior	S. Interior	Alaska	N. Coastal	N. Interior	S. Interior	Alaska	N. Coastal	N. Interior	S. Interior	Alaska	N. Coastal	N. Interior	S. Interior	Alaska
Lichens	0.18 ±0.03 (3)	0.20 ±0.08 (6)	0.35 ±0.21 (3)	0.70 ±0.37 (3)	0.11 ±0.00 (2)	0.11 ±0.07 (4)	0.21 — (1)	<0.04 —	2.76 ±0.85 (4)	2.80 ±0.78 (6)	2.25 ±0.71 (6)	4.16 ±1.04 (3)	0.04 ±0.02 (4)	0.11 ±0.09 (6)	0.21 ±0.37 (6)	0.23 ±0.09 (3)
Mosses	0.25 ±0.10 (3)	0.60 ±0.46 (4)	2.78 ±5.23 (5)	—	0.17 ±0.04 (3)	0.72 ±1.02 (3)	0.20 ±0.07 (6)	—	6.36 ±1.85 (3)	4.93 ±2.32 (4)	6.79 ±2.15 (6)	—	0.16 ±0.14 (3)	0.33 ±0.01 (4)	0.30 ±0.22 (6)	—
Ferns	0.53 ±0.74 (4)	0.18 — (1)	0.18 ±0.05 (3)	—	0.17 ±0.04 (2)	0.36 — (1)	0.14 ±0.06 (4)	—	8.88 ±3.55 (4)	6.10 ±1.27 (2)	9.61 ±4.89 (6)	—	0.44 ±0.47 (4)	0.15 ±0.03 (2)	0.19 ±0.05 (6)	— —
Horsetails	3.39 ±1.77 (5)	2.50 ±2.77 (5)	0.61 ±0.39 (4)	0.22 ±0.12 (3)	0.24 ±0.11 (5)	0.27 ±0.24 (3)	0.33 ±0.13 (4)	0.17 ±0.12 (2)	8.20 ±4.51 (5)	6.65 ±3.73 (6)	9.05 ±2.20 (4)	10.66 ±4.15 (3)	0.07 ±0.03 (5)	0.23 ±0.37 (6)	0.09 ±0.03 (4)	0.10 ±0.07 (3)
Dwarf Birch	0.76 ±0.13 (4)	0.37 ±0.27 (6)	0.50 ±0.34 (4)	0.43 ±0.23 (3)	<0.10 —	1.05 — (1)	<0.10 —	<0.04 —	6.24 ±1.32 (4)	6.03 ±2.31 (6)	8.63 ±1.30 (4)	5.95 ±0.62 (3)	0.30 ±0.19 (4)	0.48 ±0.20 (6)	0.45 ±0.24 (4)	1.33 ±0.54 (3)
Willows	3.55 ±3.82 (7)	3.73 ±3.56 (7)	1.16 ±0.73 (9)	4.78 ±2.33 (3)	0.12 ±0.6 (3)	0.20 — (1)	0.30 ±0.19 (4)	0.05 — (1)	11.80 ±2.06 (7)	9.47 ±2.77 (7)	10.61 ±1.29 (9)	5.76 ±0.83 (3)	0.33 ±0.24 (7)	0.36 ±0.29 (7)	0.76 ±0.44 (9)	0.83 ±0.43 (3)
Bilberry	0.13 ±0.02 (2)	<0.10	0.20 ±0.11 (2)	—	0.11 ±0.05 (2)	0.77 ±1.04 (3)	0.32 ±0.19 (3)	—	9.35 ±1.35 (2)	8.69 ±2.38 (3)	13.03 ±3.40 (6)	—	0.85 ±0.98 (2)	0.19 ±0.15 (3)	0.37 ±0.20 (6)	—
Willow Herb	0.20 ±0.12 (5)	0.21 — (1)	0.17 ±0.10 (2)	0.10 —(1)	0.31 ±0.14 (5)	0.90 ±1.21 (3)	0.82 ±0.66 (3)	0.11 — (1)	12.46 ±3.83 (5)	13.30 ±1.02 (3)	8.06 ±3.36 (3)	9.60 — (1)	0.25 ±0.15 (5)	0.41 ±0.12 (3)	0.16 ±0.07 (3)	0.12 — (1)
Lapland Louse -wort	1.13 ±1.13 (2)	0.41 ±0.11 (3)	0.85 ±0.51 (4)	—	<0.10 —	2.59 — (1)	<0.10 —	—	13.52 ±1.77 (2)	14.98 ±0.68 (3)	14.62 ±7.01 (4)	—	0.72 ±0.29 (2)	1.35 ±1.05 (3)	1.91 ±0.36 (4)	—
Golden-rod	0.22 ±0.11 (4)	0.52 ±0.46 (2)	—	—	0.34 ±0.29 (2)	0.08 ±0.02 (2)	—	—	11.51 ±3.10 (4)	10.94 ±5.10 (3)	—	—	0.22 ±0.05 (4)	0.17 ±0.12 (3)	—	—
Tufted Hair-grass	<0.08 — (1)	0.30 —	0.13 ±0.08 (3)	—	0.28 — (1)	0.60 — (1)	0.31 ±0.11 (5)	—	3.40 — (1)	5.33 ±1.62 (3)	4.34 ±1.89 (6)	—	0.25 — (1)	0.37 ±0.19 (3)	0.40 ±0.22 (6)	—
Three-leafed rush	0.25 ±0.18 (3)	0.16 ±0.12 (3)	0.15 — (1)	—	0.72 ±1.00 (3)	0.43 ±0.47 (3)	0.12 ±0.01 (2)	—	6.06 ±1.62 (6)	6.63 ±1.85 (6)	8.39 ±1.39 (6)	—	0.20 ±0.07 (6)	0.28 ±0.08 (6)	0.24 ±0.13 (6)	—
Stiff sedge	<0.10 —	0.15 — (1)	0.12 — (1)	—	<0.10 —	0.11 — (1)	0.13 — (1)	—	10.29 ±1.57 (2)	9.16 ±1.48 (2)	11.92 ±3.61 (5)	—	0.32 ±0.09 (2)	0.38 ±0.03 (2)	0.34 ±0.07 (5)	—
High[1]	5	4	2	2	2	7	4	0	2	3	6	2	3	5	2	3
Exceed[2]	9	9	7/12	—	nv[3]	nv[3]	nv[3]	—	11	11	11/12	—	3	3	4/12	—

[1]Number of plant types with highest concentrations observed in the study.
[2]Number of plants exceeding minimum requirements for peak lactation (Co=0.2, Cu=
[3]nv = No value in ARC (1980).

concentrations of K. For Ca, P, and Mg, only 3 plant species (tufted hair-grass, three-leafed rush, and stiff sedge) contained all 3 elements below concentrations necessary for peak lactation. Na concentrations did not meet demands of peak lactation in any plant group. Although lichens were deficient in macro-minerals, they possessed sufficiently high concentrations of Co, Mo, and Mn for maintenance of reindeer in winter. Lichens and tufted hair-grass were deficient in Cu. Other plant groups likely were sufficiently high in Cu concentrations to meet requirements, but this conclusion should be assessed critically because of the generally low assimilation coefficient of Cu, and the strong negative synergistic effects of S and Mo on Cu assimilation (ARC 1980).

Because 24 elements likely are essential for growth, health, and survival of animals, mechanisms by which animals balance their requirements for each may be complex. Use of a variable mix of plant types should result in an intake of minerals that would more closely meet requirements for these many macro and micro minerals than would specialization on a single group of plants (Nieminen and Heiskari 1989). Factors such as harassment by insects, poor herding practices, and a lack of free access to vegetation may prevent animals from meeting their mineral requirements. Chronic overgrazing, likewise, has implications for meeting mineral requirements. On overgrazed ranges, preferred plants are the first to disappear from the vegetation assemblage (Heady 1975). Thus, mineral deficiency can be a problem for domestic reindeer in many regions (Hyvärinen et al. 1977, Åhman et al. 1986). For reindeer and caribou given free access to lichen-dominated ranges, botanical analyses of rumen samples show a lichen dominance (~ 60-70%), with the balance of forage composed of leaves of shrubs and forbs, mushrooms, and mosses (< 5%) (Gaare and Skogland 1975, Skogan 1984, Thomas and Hervieux 1986). Disappearance of preferred lichens from winter range can result in a shift to a diet high in moss or woody browse (Gaare and Skogland 1975, Skogan 1984, Thomas and Hervieux 1986, Russell et al. 1993). Although mosses are more mineral rich than lichens (Tables 1 and 3), their low digestibility (< 15%; White and Trudell 1980, Staaland et al. 1983) and low nitrogen content overwhelm positive effects of those minerals. Nevertheless, higher mineral levels in mosses than lichens raises the possibility that mosses may be actively consumed specifically to compensate for extremely low macro mineral levels of lichens (Jacobsen et al. 1978), as proposed by White (1983). On summer range, overgrazing removes many preferred forbs and willows. Willows are a preferred species for several weeks in summer, and those shrubs support high protein and energy requirements of lactation and of growing animals (Russell et al. 1993). We suggest that high concentrations of both Co and Cu, essential for Vitamin B12 synthesis and rumen function (ARC 1980, McDowell 1992), may be equally important to summer productivity in *Rangifer*. A deficiency in either of those 2 micro-minerals has serious implications for growing animals and for lactation. One or both of those elements have been associated with ill thrift in weaning domestic sheep in Australia and New Zealand, and Cu deficiency has been implicated in reproducing reindeer (Hyvärinen et al. 1977), Alaskan ruminants (Barboza and Blake 2001), and a moose (*Alces alces*) die-off in Alaska (O'Hara et al. 2001). In contrast, Co levels in plants were in excess of forage levels (< 0.08 mg/kg) associated with deficiencies (ARC 1980); we maintain that an assessment of Co requirements for rapidly growing and lactating reindeer is necessary to solve this discrepancy.

Traditionally, the Saami have moved reindeer herds to the coast for calving and summer grazing after wintering in interior regions of Norway, Sweden, and Finland (Skjenneberg and Slagsvold 1968). Those herders reported strong directionality and apparent desire of reindeer to reach the coast in spring, and attribute that drive to a "hunger" for salt (Skjenneberg and Slagsvold 1968), as well as the maternal drive for calving. Likewise, herds of Circumarctic wild reindeer and caribou migrate to coastal areas for calving and foraging in summer. Late in summer, those herds slowly move south, often following a pattern of mushroom availability, to eventually settle on a wintering area within the boreal forest. Although there is well-supported evidence that the spring migration to coastal calving grounds minimizes risks of predation (Fancy and Whitten 1991) and may reduce parasite burdens (Batzli et al. 1980), the nutritional advantages of maximizing energy balance on lichen-dominated ranges in winter, and making up a protein deficit on vegetation undergoing a rapid green-up at the coast, is equally compelling (Russell et al. 1993). Based on mineral analyses herein, and using data from a series of studies on seasonal dynamics of Na metabolism (Staaland et al. 1980, 1982, 1983; Staaland and Jacobsen 1983; Staaland 1984; White and Luick 1984; White et al. 1984; Staaland and Hove 2000), we hypothesize that the dependence on lichens in the interior presents a serious challenge to meeting Na requirements for lactation, and for growth of immature reindeer and caribou. The low Na concentration in winter forages in the interior (Table 1) results in a Na insufficiency (Staaland and Sæbø 1987), which also is evident from behavioral observations for caribou and other ruminants such as moose (Tankersley and Gasaway 1983) and Dall's sheep (*Ovis dalli*). Migration to coastal ranges allows repletion of Na because coastal forages are more Na rich (Table 1), salt is available as a supplement in seawater, and reindeer can replenish a Na deficiency rapidly (Staaland et al. 1980, 1982; Staaland and Sæbø 1987). Robbins (1993) reported a Na concentration of 0.05% (21 mmole/kg) in the diet is required for domestic mammals, and an intake requirement for Na balance of 9 mg (0.39 mmole).$kg^{-1}.d^{-1}$ for wildlife. That requirement is equal to our estimates of Na output in reindeer milk at maximum production. Our calculations indicate that the Na content of summer forage must exceed 11 mmole/kg to meet a milk output of 2 L/d (White and Luick 1984), assuming milk contains 16 mmole Na/L (Luick et al. 1974) and assuming a daily feed intake of about 100 $g/kg^{0.75}$ (3 kg/d; McEwan et al. 1976, White 1983). In addition, loss of Na in urine and feces must be considered, which probably is equal to the Na balance of 0.39 mmole.$kg^{-1}.d^{-1}$ of nonproductive animals (Pletscher 1987, Robbins 1993). If the Na requirement of maternal balance is added to the lactation requirement, however, then the minimum concentration of Na in plants becomes 22 mmole/kg. No plants from interior regions of Norway or Alaska, USA, approached 11 mmole/kg, but 9 of 13 coastal plants exceeded that value. Only 4 of the coastal plants (mosses, ferns, horsetails, and three-leafed rush) were sufficiently high in Na to meet the concentration for peak lactation (Table 1). A clear role for a Na supplement is indicated, even in coastal regions. The Na requirement of growing animals is likewise high. For example, a yearling reindeer weighing 50 kg and growing at 100 g/d requires about 54 mmole Na/d (ARC 1980), which translates to a dietary concentration of 31 mmole/kg. Again, access to a Na supplement is indicated. In support of this ecological constraint, Staaland and Sæbø (1987) reported that young reindeer can have low Na and high K concentrations in the rumen during summer when access to Na is inadequate. Under many ecological conditions, a low level of Na in food is associated with visits to mineral licks or seawater (Weir 1972, Botkin et al. 1973, Calef and Lortie 1975, Weeks and Kirkpatrick 1976, Tankersley and Gasaway 1983). Although field reports of effects of low Na on growth and reproductive performance in reindeer and caribou are lacking, Na insufficiency is thought to be important elsewhere (Belovsky and Jordan 1981, Batzli 1986), and is known to restrict growth and milk production in livestock (Smith and Aines 1959, Kemp 1964). Such effects likely occur regionally and ephemerally in domestic reindeer and caribou (Staaland and Hove 2000). Physiological and behavioral adjustments made by animals to low-salt environments are well documented (Blair-West et al. 1968, Denton and Nelson 1971, Botkin et al. 1973, Denton 1982, Robbins 1993). Where access to more Na-rich coastal ecosystems is not possible, continental populations of reindeer and caribou must make Na adjustments through use of Na-rich aquatic plants, consumption of ash from forest fires, and visits to mineral licks (Calef and Lortie 1975). Although mobility and migration can be behavioral compensating mechanisms that prevent destruction of food resources (Klein 1967, 1990), we suggest that the directionality and drive to reach coastal ranges may be facilitated by the ability of Na-deficient animals to detect Na gradients in the atmosphere (Robbins 1993); we hypothesize that this phenomena is an integral component of migration in the Arctic. Whatever the mechanism, Na concentrations and their role in the nutrition and movements of *Rangifer* deserves further study.

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