Forage chemistry and the digestive system in reindeer (*Rangifer tarandus tarandus*) in northern Norway and on South Georgia

Svein D. Mathiesen[1,2], Tove H. Aagnes Utsi[1] & Wenche Sørmo[1]

[1] Department of Arctic Biology and Department of Medical Biology, University of Tromsø, N-9037 Tromsø, Norway.
[2] Department of Arctic Veterinary Medicine, The Norwegian School of Veterinary Science, N-9292 Tromsø, Norway (Svein.D.Mathiesen@veths.no).

Abstract: Comparative chemical and botanical analyses of the reticulo-rumen content (RR) and the fill of the digestive system were carried out in free-living Norwegian reindeer (*Rangifer t. tarandus*) on South Georgia (SG) in summer (mean body mass (BM) = 74 kg, n = 10), and in northern Norway in late summer (NS) (mean BM = 77 kg, n = 6) and winter (NW) (mean BM = 60 kg, n = 11). The RR of SG reindeer contained mainly grasses, while grasses dominated in NS reindeer and woody plants and lichens in NW reindeer. Mean ruminal plant cell-wall contents (CWC) comprised 37% of organic dry matter (OM) in SG reindeer and 50 and 69% in NS and NW reindeer, respectively. The high CWC in NW reindeer was due to high intake of lichens containing as much as 45% hemi-cellulose. Mean ruminal content of lignin was as low as 5% of OM in SG reindeer, which was different (P < 0.05) from NS (14%) and NW reindeer (15%), respectively. The mean total gastro-inresrinal tract (GIT) (fill and tissue) weight was 27% of BM in SG reindeer, different (P < 0.05) from NS (18% of BM) and NW reindeer (22% of BM), respectively. Wet weight RR content was 14.5% of BM in SG reindeer, not different from NS (12.2% of BM) and NW reindeer (14.2% of BM). The ratio between the wet weight content of the distal fermentation chamber (DFC) and the RR wet weight content was 1:10 in SG reindeer, different (P < 0.05) from NS (1:14) and NW reindeer (1:14). We did not find any significant differences between the intestinal lengths of the groups investigated. It was concluded that the degree of fill of the different parts of GIT in reindeet seems to be related to the lignin content of plants eaten and not only of seasonal changes in appetite and availability of plants. Our data stress the fact that reindeer are highly adaptable to a wide range of different dietary plants, even in the southern hemisphere.

Key words: fermentation, plant cell-wall, rumen, *Rangifer*

Rangifer, 19 (2): 91–101

Introduction

In ruminants the anatomy of the gastro-intestinal tract (GIT, abbreviations see Appendix p. 100) has evolved in relationship to the physical structure and the plant cell wall composition of the diet eaten. Hofmann & Stewart (1972) classified wild ruminants into three general feeding strategies according to the anatomy and function of their digestive tracts. Of all ruminants species 25% are grazers (GR) like cattle and sheep, eating food with high concentrations of cellulose, hemi-cellulose and lignin. They have large reticulo-rumens (RR) and omasa, long intestines, but small distal fermentation chambers (DFC). Concentrate selectors (CS) such as roe-deer (*Capreolus capreolus*) comprise about 40% of all species. They select diets with low fibre

content, have relatively small RR and omasa, short intestines and latge DFC's. In both sheep and toe-deer, however, the RR fill inctease with increasing plant cell wall content in the diet as a short-term adaptation to fibrous forage (Weyreter *et al.*, 1987; Lechner-Doll *et al.*, 1990; Holand, 1992). Intermediate mixed feeders (IM) have qualities which lie between GR and CS. Hofmann (1985; 1989) classified *Rangifer* and Sørmo *et al.* (1999) classified Svalbard reindeer (*Rangifer t. platyrhychus*) as IM. Captive Norwegian reindeer calves (*Rangifer t. tarandus*) are severely limitated in their ability to utilise fibrous grasses (Aagnes *et al.*, 1996). Reindeer have a cyclic pattern in appetite, with high voluntary food intake in summer and low intake in winter (Larsen *et al.*, 1985). Appetite and availability of plants in the winter season seem therefore to influence the fill of digesta in these highly seasonal ruminants (Staaland *et al.*, 1979; Tyler, 1999). Most reindeer herds in northern Norway migrate as far 250 km between coastal summer pastures and inland winter pastures. In winter, they eat a diet dominated by lichens and woody plants, low in protein but rich in energy, while in summer the diet is dominated by gtasses and herbs, high in both protein and energy. Norwegian reindeer (n = 22) were successfully introduced from Norway to South Georgia (54-55°S), early this century (Leader-Williams, 1988). These animals do not migrate between seasonal pastures, but forage on the vegetation which is different from reindeer and caribou pastures in the north. Few plant species grow on the island, which is dominated by grasses and lacks true woody plants (Leader-Williams *et al.*, 1981). Reindeer on South Georgia represent an interesting comparative model, since, the animals have survived for almost one hundred years independent of lichens and woody plants, eating mainly graminoids throughout the year (Leader-Williams, 1988). Given these major differences in diet between South Geotgia and northern Norway we predicted that the gastto-intestinal tract (GIT) of reindeer on South Georgia would have evolved in direction of a digestive strategy similar to that employed by ruminants of the grazing type. Secondly, we predicted that reindeer in northern Norway contain less digesta in winter than in summer due to reduced appetite, availability of plants, and intake of highly digestible lichens. The aim of this study was to determine whethet the degree of fill in the digestive system of reindeer in South Georgia in summer differed from that of reindeer from northern Norway in late summer and in winter, and whether ruminal plant species and the composition of plant cell wall material in the rumen content affected GIT fill.

Materials and methods

Study area

One part of this investigation was carried out in Husvik Harbour, South Georgia (54-55°S, 33-38°W), in January and February 1990 (austral summer). Permanent ice and snow cover 60% of the island's surface area and the snow covers the ground for five or six months of the year. The flora of South Georgia is dominated by *Paridiochola flabellata,* a winter green tussock grass, with high biomass and productivity. Swards of the grasses *Deschampsia antarctica, Phleum alpinum* and *Poa annua* also occur locally on wet areas. The deciduous nurnet *Aceana magellanica* is the only dwarf shrub with rhizomes on the island (Walton, 1975; Kightley & Lewis Smith, 1976; Leader-Williams, 1988).

The second part was carried out 15 September (late summer) in 1994 on the island of Reinøy in Troms county (69°N, 21°E). This island is used as summer pasture from May to October by semi-domestic reindeer from the inland of Finnmark county. The vegetation is dominated by graminoids, herbs, willows and birch.

The third part of the investigation was carried out on inland winter pasture at Kautokeino, Finnmark county (69°N, 23°E) in February and March 1991. During winter the climate is cold continental with low precipitation. Snow covers the ground for about eight months of the year. The vegetation is dominated by birch forest, mainly poor oligotrophent deciduous forest types on gneiss and granite bedrocks, with lichen and heather. The boggy areas in the study area are characterised by dwarf shrubs, heather and sedges (Johansen & Tømmervik, 1990).

Animals

On South Georgia, ten adult female Norwegian reindeer (SG) were shot, under a licence given by the Governor of the Dependencies of Falkland Islands and South Georgia. The gross GI-tract analyses were carried out in the field in a laboratory established in a former whaling station. Samples from the GI-tracts were stored frozen for further investigations in Norway. In Norway in summer six adult female reindeer (NS) were rounded up in a paddock, selected by hand and killed by a bolt pis-

tol immediately after arrival in the corral. The *post mortem* examinations, including gross-analysis of GIT was subsequently carried out in the field and samples were frozen and furthet investigated in the laboratory. In winter, eleven adult female reindeer (NW) were captured by lasso while grazing and stunned, by a rapid insertion of a fine blade through the *foramen magnum* and into the cranium, and then killed by bleeding. After death the animals were transported to a field laboratory (20 min). The GIT was then removed, gross analyses were carried out and samples of rumen content were collected and frozen for further analysis in the laboratory. All animals investigated were adults (more than two years old as determined by the annulation of the cementum of the first incisor teeth). Live body mass (BM), less blood lost from the wound, was measured to an accuracy of 0.5 kg using a Salter model 235 balance. The GIT was removed from the dead animals and the reticulo-rumen (RR) contents and tissue were weighed on a Salter balance to 0.2 kg. The liver, kidney fat, GIT tissue and the contents of the other parts of the GIT were measured to 1 g using a calibrated electronic balance.

Plant species analyses

The ruminal content of each animal were stirred in a bucket and a one-litre sample from each animal was fixed with equal volumes of 70% ethanol. The botanical composition of the RR content was determined for each animal in two parallel samples by the method of Gaare *et al.* (1977) and Sørmo *et al.* (1999). Approximately 200 ml of fixed rumen contents were washed for 2-3 min over a 2 mm screen in a washing sieve shaker, after which a random sample was spread out in water in a transparent glass dish over a 1 cm grid. Two hundred fragments which touched intersections in the grid were collected in each parallel sample, examined either macroscopically or with a stereo microscope (30-100 X) and identified at species level or, where this was not possible, in one of five categories (grass, herb, lichen, moss and woody plant.

Chemical composition

Mixed RR contents (500 g) from each animal were frozen (-25 °C) immediately after death. In the laboratory a sub-sample of this material was later thawed, weighed and then dried at 115 °C for dry matter (DM) determination. Plant fibre analyses were carried out on pre-dried sub-samples (50 °C for 17 h) using the techniques of Van Soest (1963a; b; 1967) and Goering & Van Soest (1970). Neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) were determined directly. Hemi-cellulose was calculated as the difference between NDF and ADF and cellulose was calculated as the difference between ADF and ADL. Hemi-cellulose, cellulose and lignin (ADL) are termed plant cell wall contents (CWC). The ether extract was determined by the Soxhlet method using diethyl ether for extraction. Ash, minerals and ammonia were analysed as described by Olsen *et al.* (1994). Crude protein (N x 6.25) was determined in both mixed RR contents as with all other analyses, and in sieved rumen contents (2 mm mesh size) to minimise the influence of microbial protein (Horwitz, 1980). All data are expressed as a proportion (%) of organic dry matter (OM) in whole RR contents. Samples from other parts of the GIT (5-10 g) were frozen and used for DM determination.

Particle size distribution

The size distribution of plant fragments in frozen rumen content samples was determined by wet sieving in six reindeer from each group according to the method of Sørmo *et al.* (1999). Thawed ruminal contents were thoroughly mixed and sub-samples were washed with water into sieve trays (200 mm) with square pores of 5.6, 4.0, 2.0, 1.0, 0.5, 0.25, and 0.125 mm. Sub-samples were also taken for DM estimation. The sample was sieved using a Fritech GBR sieving machine for 10 min, shaken at 2 sec intervals, with an amplitude of 3 mm. All material left on each sieve was transferred to a previously dried and weighed filter paper (Whatman no 1, 9.0 cm in diameter) and dried at 105 °C to constant weight. The cumulative proportion of the total DM retained on each sieve was calculated as the dry-mass of material on all sieves with larger pore size divided by the total dry mass of material retained on all sieves in the shaker.

GIT-fill

The GIT was divided into eight sections: RR, omasum, abomasum, small intestine (from abomasum to the ileo-caecal junction), caecum, (the appendix from the junction with small intestine), proximal colon (from the ileo-caecal junction to the start of the coiled colon), coiled colon and distal colon. The distal fermentation chamber (DFC) is defined as the combined contents of the caecum and proximal colon. Each section was stripped of its fat, weighed and emptied by squeezing the contents out by hand.

Table 1. Mean proportional composition (%), distribution, and frequency (F) of plant species in the reticulo-rumen of reindeer on South Georgia (n = 10) in summer (SG) and in northern Norway in late summer (NS) (n = 6) and winter (NW) (n = 11).

SG			NS			NW		
Plants	Mean %	F	Plants	Mean %	F	Plants	Mean %	F
-	-	-	*Cladina* sp.	8.4	83	*Cladina* sp.	31.2	100
-	-	-	*Stereocaulon* sp.	2.4	83	*Stereocaulon* sp.	5.0	73
Woody plants (u)	1.5	50	Woody plants (u)	3.1	50	Woody plants (u)	28.4	100
-	-	-	*Empetrum* sp. (l)	4.6	100	*Empetrum* sp. (l)	2.8	81
-	-	-						
			Betula nana (l)	1.1	33	*B. nana* (l)	1.06	45
Vascular plants (u)	2.3	60	*Salix* sp.	5.2	66	*Calluna* sp.	0.08	18
Seeds (u)	2.4	50	*Vaccinium vitisidae* (l)	1.1	50	*V. vitisidae* (l)	0.88	36
Paridiochola flabellata	4.9	70	*V. myrtillus* (l)	2.5	66	*V. myrtillus* (s)	0.22	18
Poa annua	8.9	80	-	-	-	Woody plants (l)	2.57	54
Graminoids sp. (u)	41.4	100	Graminoids (u)	16.7	100	Graminoids (u)	12.7	100
Vascular bundles (u)	30.4	90	Vascular bundles (u)	48.5	100	Vascular bundles	8.41	91
Mosses	4.0	90	Mosses	4.2	83	Mosses	6.3	83
-	-	-	Mushroms	0.4	50	-	-	-
Others	4.2	90	Others	1.8	100	Others	0.40	36

u: unidentified; l: leaves; s: stem; others: include plant litter.

The tissue was thereafter weighed and the mass of the contents was determined by subtracting tissue weight from total weight. The lengths of the individual segments of the intestines were measured to 1 cm by laying the emptied tissue flat on a bench without stretching.

Statistics

Data are expressed as means and standard deviations (s). Student's t-test (Bhattacharyya & Johnsen, 1977) was used to determine differences ($P < 0.05$) among animal groups.

Results

Plant species analyses

The botanical composition of the RR contents from the different groups of animals is shown in Table 1. In SG reindeer, plant fragments in the rumen consisted mainly of grasses (90%), compared with NS reindeer, in which grasses (65%) and woody plants (17%) dominated. In NW reindeer, rumen contents included lichens (35%), grasses (21%) and woody plants (36%). We found no lichens in the rumen contents of SG reindeer. However, *P flabellata* and unidentified woody plants which we assume were *A. magellanica* were found among the rumen particles in SG reindeer.

Animals

The mean body mass of SG reindeer was not significantly different from that of NS reindeer, but both SG and NS reindeer were larger ($P < 0.05$) than NW reindeer (Table 2). Mean kidney fat weight was 123.0, s = 45.0, g in SG reindeer, 121.0, s = 45.8, g in NS reindeer and 91.0, s = 85.4, g in NW reindeer. Mean liver mass was 18.5, s = 2.6, g/ kg BM in SG reindeer and larger ($P < 0.05$) than in NW reindeer (12.1, s = 1.4, g/kg BM), but not different from NS reindeer (15.9, s = 0.7, g/kg BM).

Chemical composition

The DM of RR content was lower ($P < 0.05$) in SG reindeer than in NS and NW reindeer (Table 3). Ruminal OM was also lower in SG animals than in NS ($P < 0.05$) and NW reindeer (Table 4). The concentration of ash did not significantly differ in SG, NS, and NW reindeer (Table 5). Mean crude protein content in sieved rumen plant particles tended to be highet, although not significantly, in SG rein-

Table 2. Mean (standard deviation) body mass and wet weight (kg) of content and tissue in different parts of the gastro-intestinal tract (GIT), and dry weight content of reticulo-rumen and distal fermentation chamber (DFC) of reindeer on South Georgia in summer (SG) (n = 10) and northern Norway in late summet (NS) (n = 6) and winter (NW) (n = 11).

	SG	NS	NW
Body mass	73.8 (7.7)	76.8 (6.6)	59.4 (11.4)
Total GIT			
Total	19.9 (3.9)	14.0 (1.9)	14.2 (2.9)
Tissue	4.7 (0.9)	3.1 (0.3)	3.2 (0.6)
Content	15.2 (3.3)	10.9 (1.6)	11.0 (2.4)
Reticulo-rumen			
Total	13.6 (2.9)	10.6 (1.9)	9.4 (3.1)
Tissue	2.7 (0.5)	2.1 (0.3)	1.8 (0.4)
Content	10.9 (2.5)	8.5 (1.6)	8.2 (2.2)
Dry-matter	1.4 (0.3)	1.4 (0.3)	1.7 (0.5)
Omasum			
Total	0.3 (0.1)	0.4 (0.1)	0.2 (0.1)
Tissue	0.1 (0.1)	0.2 (0.0)	0.1 (0.0)
Content	0.2 (0.1)	0.3 (0.1)	0.1 (0.1)
Abomasum			
Total	0.7 (0.2)	0.3 (0.1)	0.4 (0.1)
Tissue	0.4 (0.1)	0.2 (0.1)	0.2 (0.04)
Content	0.4 (0.1)	0.2 (0.0)	0.3 (0.1)
Small intestine			
Total	2.9 (0.5)	1.4 (0.1)	1.1 (0.1)
Tissue	0.9 (0.2)	0.4 (0.1)	0.5 (0.1)
Content	1.9 (0.5)	1.0 (0.1)	0.6 (0.08)
Caecum			
Total	0.7 (0.2)	0.4 (0.1)	0.4 (0.1)
Tissue	0.1 (0.1)	0.1 (0.0)	0.1 (0.0)
Content	0.6 (0.2)	0.3 (0.0)	0.4 (0.1)
Colon			
Total	1.8 (0.3)	0.8 (0.1)	1.1 (1.1)
Tissue	0.5 (0.2)	0.2 (0.1)	0.3 (0.1)
Content	1.3 (0.2)	0.4 (0.1)	0.7 (0.2)
DFC			
Total	1.3 (0.3)	0.7 (0.2)	0.8 (0.2)
Tissue	0.2 (0.1)	0.1 (0.1)	0.1 (0.1)
Content	1.1 (0.3)	0.6 (0.1)	0.6 (0.1)
Dry-matter	0.14 (0.03)	0.1 (0.02)	0.1 (0.01)

deer than NS and NW reindeer. The concentration of ammonia in RR of NS reindeer was almost twice the levels measured in NW reindeer ($P < 0.05$) (Table 4). The concentration of plant cell walls, which include hemi-cellulose, cellulose and lignin, in the RR contents was lower ($P < 0.05$) in SG reindeer compared to NS reindeer. Likewise, in NW reindeer plant cell wall concentration (CWC) was larger ($P < 0.05$) than in NS and SG animals. The lignin concentration of RR contents was very low in SG reindeer, and was different ($P < 0.05$) from those of NS and NW reindeer (Table 4).

GIT-fill, gross anatomy

The mean relative mass of the wet contents of the whole GIT was higher ($P < 0.05$) in SG reindeer (20% of BM) than in NS reindeer (14% of BM). There were no significant differences in relative total GIT fill between SG and NW reindeer (18% of BM) (Table 6). The mean relative mass of the total GIT tissue was larger in SG reindeer than in NW reindeer, but the difference was not significant. In SG reindeer the relative mass of the GIT tissue was larger ($P < 0.05$) than in NS reindeer (Table 6).

Particle size distribution

The cumulative distributions of RR plant particle size from SG, NS and NW reindeer are shown in Table 7. There were no significant differences in the distributions between locations and seasons and more than 90% of the RR particles were less than 1 mm long.

Fermentation chambers

The absolute wet weight of the digesta in RR was 11 kg in SG reindeer, 8.5 kg in NS reindeer, and 8.2 kg in NW reindeer, these differences were not significant (Table 2). The RR wet weight content contributed 75% of total wet weight GIT fill in SG reindeer, 77% in NS reindeer and as much as 79% in NW reindeer, which was not significantly different among the groups. Reticulo-rumen wet weight content relative to BM did not differ significantly different among the groups (Table 6). The weight of RR tissue contributed to 60% of the total GIT tissue in SG reindeer which was not different from NW reindeer, but less ($P < 0.05$) than in NS reindeer. The relative weight of RR tissue to the BM in SG and NW reindeer was not significantly different, while both groups were larger than in NS reindeer ($P < 0.05$) (Table 6). The absolute wet weight content of DFC, and DFC wet weight content relative to RR wet weight content in SG reindeer, were larger ($P < 0.05$) than in NS and NW reindeer (Table 2; 6; 8). The DFC wet weight content relative to the RR wet weight content decreased ($P < 0.05$) with increasing concentration of lignin in the RR digesta (Fig. 1) in all groups investigated.

Table 3. Mean (standard deviation) dry matter content (%) in the gastro-intestinal tract of reindeer on South Georgia in summer (SG) (n = 10), and in northern Norway in late summer (NS) (n = 6) and winter (NW) (n = 11).

	Reticulo-rumen	Omasum	Abomasum	Small-intestine	Caecum	Proximal colon	Coiled colon	Distal colon
SG	13.2 (1.1)	-	-	-	12.3 (1.7)	-	-	-
NS	17.3 (2.2)	19.4 (0.8)	17.3 (1.4)	15.1 (0.6)	16.9 (0.8)	16.8 (0.9)	19.9 (1.1)	23.9 (2.2)
NW	19.9 (1.2)	20.2 (2.2)	16.9 (2.5)	14.2 (0.9)	15.7 (0.6)	15.3 (1.5)	18.7 (1.7)	27.1 (3.7)

- : not measured.

Table 4. Mean (standard deviation) chemical composition of reticulo-rumen organic dry matter content (% OM) in reindeer on South Georgia in summer (SG) (n = 10) and northern Norway in late summer (NS) (n = 6) and winter (NW) (n = 11).

	% OM	Total crude protein	Crude protein*	NH_4**	Ether extract	Hemi-cellulose	Cellulose	Lignin	Cell walls
SG	12.0 (1.2)	38.2 (2.7)	13.4 (2.6)	-	8.9 0.7	18.9 (2.7)	13.2 (1.5)	5.0 (0.5)	37.1 (3.9)
NS	16.1 (2.1)	31.2 (4.2)	12.0 (0.8)	500 (57)	6.1 (0.6)	22.7 (2.4)	12.3 (1.4)	14.4 (3.4)	50.5 (7.0)
NW	19.0 (1.4)	33.3 (5.9)	9.9 (1.1)	260 (64)	3.4 (0.6)	44.5 (4.7)	11.2 (2.3)	15.1 (3.5)	68.9 (2.9)

* sieved rumen plant material; ** mg / 1000 ml wet rumen content; - : not measured.

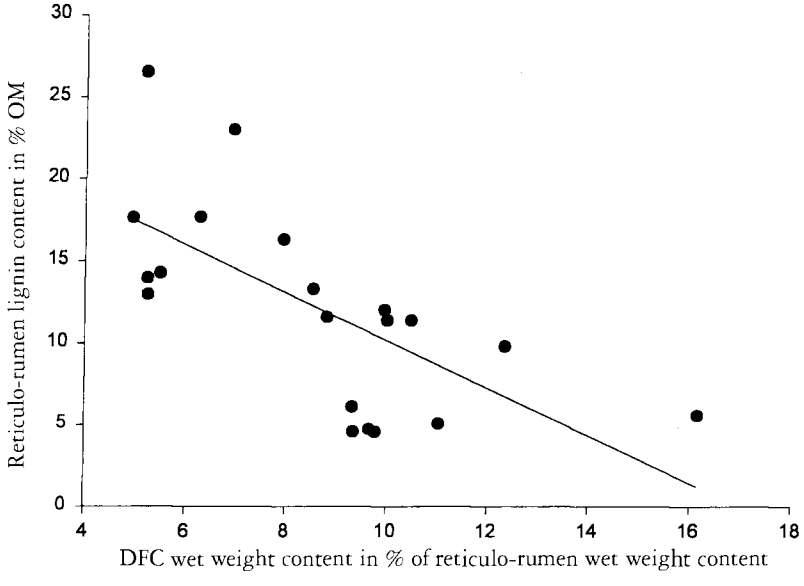

Fig. 1. The wet weigh of distal fermentation chamber (DFC) contents relative to reticulo-rumen wet weight contents related to lignin in % of reticulo-rumen organic dry matter content (OM) from reindeer on Sourh Georgia in summer and northern Norway in summer and winter ($y = -1.75x + 19.139$, $r^2 = 0.4245$).

Intestinal length

The ratio of the mean length of the total intestine (small intestine and latge intestine) to the body length of adult female reindeer on SG and in NS and NW are shown in Table 9. There were no significant differences between the groups in total intestinal length or in the ratio of large intestine to small intestine.

Discussion

Our results demonsttate that Norwegian reindeer eat a large variety of plants (Table 1). Likewise, the different plants eaten by SG, NS and NW teindeer strongly influenced the chemical composition of the RR content (Tables 3, 4, 5). The remarkable low concentrations of plant cell walls including lignin in RR contents in SG reindeer are explained by the fact that these animals eat almost only grasses. This result was supported by the low lignin content measured in forage plants collected on South Georgia in summer, when the SG reindeer were shot (Mathiesen & Utsi, 2000). In contrast, the high concentration of lignin in RR contents in reindeer in northern Norway, particular-

Table 5. Mean (standard deviation) ash content (% of dry matter) and mineral composition (g/kg wet weight) of reticulo-rumen conrent from reindeer on South Georgia (n = 10) in summer (SG) and northern Norway in late summer (NS) (n = 6) and winter (NW) (n = 11).

	Ash	P	Mg	Ca	K	Na
SG	10.6 (1.1)	1.3 (0.2)	0.2 (0.1)	0.7 (0.2)	1.7 (0.5)	2.5 (0.3)
NS	8.8 (0.9)	1.3 (0.1)	0.2 (0)	0.5 (0.1)	2.2 (0.3)	2.9 (0.4)
NW	6.6 (0.6)	1.3 (0.09)	0.14 (0.02)	0.36 (0.06)	2.7 (0.8)	-

- : not measured.

ly in winter, seem to be related to the intake of fibrous plants. In comparison with the Svalbard reindeer in winter (25% lignin of OM in RR) the lignin contents in RR of the NW reindeer in the present study was low (Table 4) (Sørmo *et al.*, 1999). Furthermore, it is likely that lichens eaten by the NW reindeer could explain the high proportion of hemi-cellulose observed in the RR content (Table 4). Lichens, like *Cladonia stellaris* contains as much as 75% hemi-cellulose, almost no cellulose and only small amounts of lignin (Person *et al*, 1980). With as much as 36% of RR plant fragments identified as lichen in NW reindeer, our results are comparable to those obtained

Table 6. Mean (standard deviation) relative weight (g/100g BM), (mean % of GIT*) of the gastro-inresrinal tract of reindeer on South Georgia in summer (SG) (n =10), in northern Norway in late summer (NS) (n = 6) and in winter (NW) (n = 11).

	SG		NS		NW	
	g/100g BM	*% of GIT*	*g/100g BM*	*% of GIT*	*g/100g BM*	*% of GIT*
GIT						
Total	26.8 (3.3)	100	17.8 (1.8)	100	22.2 (3.1)	100
Tissue	6.5 (1.2)	100	3.9 (0.1)	100	4.9 (0.5)	100
Content	20.3 (2.9)	100	14.2 (1.1)	100	18.3 (3.6)	100
Reticulo-rumen						
Total	18.6 (2.3)	72.2	13.7 (1.4)	75.5	16.8 (2.7)	76.3
Tissue	3.6 (0.5)	59.9	2.7 (0.2)	69.9	3.1 (0.3)	63.8
Content	14.5 (2.3)	74.8	12.2 (3.1)	77.3	14.2 (2.0)	79.3
Omasum						
Total	0.6 (0.2)	1.6	0.5 (0.1)	2.7	0.4 (0.1)	1.8
Tissue	0.4 (0.1)	2.9	0.2 (0.1)	4.7	0.2 (0.1)	3.6
Content	0.2 (0.1)	1.2	0.3 (0.1)	2.6	0.2 (0.9)	1.2
Abomasum						
Total	1.2 (0.2)	3.9	0.4 (0.1)	2.2	0.7 (0.1)	3.2
Tissue	0.4 (0.1)	5.7	0.2 (0.1)	5.6	0.3 (0.1)	5.3
Content	0.6 (0.2)	3.7	0.2 (0.1)	2.2	0.5 (0.1)	2.7
Small intestine						
Total	3.9 (0.5	10.3	1.8 (0.2)	9.9	1.8 (0.2)	7.8
Tissue	1.2 (0.3)	21.2	0.5 (0.1)	12.5	0.8 (0.2)	15.4
Content	2.7 (0.5)	7.1	1.3 (0.2)	9.4	1.7 (0.2)	5.9
Caecum						
Total	1.0 (0.3)	3.3	0.5 (0.1)	2.8	0.7. (0.2)	3.1
Tissue	0.1 (0.3)	1.5	0.1 (0.1)	1.8	0.1 (0.0)	1.9
Content	0.8 (0.3)	4.2	0.4 (0.1)	3.1	0.6 (0.2)	3.4
*DFC***						
Total	1.8 (0.3)	6.8	0.9 (0.2)	5.1	1.3 (0.4)	5.5
Tissue	0.2 (0.1)	3.4	0.1 (0.1)	3.3	0.2 (0.1)	4.1
Content	1.5 (0.3)	7.7	0.8 (0.2)	5.6	1.0 (0.2)	5.9

* GIT: gastro-intestinal tract; ** DFC: distal fermentation chamber.

Table 7. Mean (standard deviation) proportions of particle size (% of dry matter) in the reticulo-rumen of reindeer on South Georgia in summer (SG) (n = 6) and in northern Norway in late summer (NS) (n = 6) and winter (NW) (n = 6).

	Particle size			
	< 0.5 mm	0.5-1.0 mm	1.0-2.0 mm	> 2mm
SG	80.3 (2.9)	6.2 (1.1)	4.4 (1.7)	9.9 (2.8)
NS	76.2 (2.7)	11.1 (3.1)	5.0 (1.9)	7.8 (4.5)
NW	84.2 (1.0)	8.2 (2.0)	3.9 (1.5)	4.4 (1.7)

Table 8. Omasum/abomasum wet weight ratio and DFC/ reticulo-rumen wet content ratio in reindeer on South Georgia in summer (SG) (n = 10), and in northern Norway in late summer (NS) (n = 6) and winter (NW) (n = 11) compared with grazers and concentrate selectors.

	Omasum/abomasum	DFC/reticulo-rumen
Grazers	13.8*	1 :15-30**
NS	1.5	1 :14
NW	0.3	1 :14
SG	0.5	1 : 10
Concentrate selectors	0.15*	1 : 6-10**

* from Werner, 1990; ** from Hofmann, 1989.

from reindeer from southern Norway, which contained 34-56% lichens in RR (Gaare & Skogland, 1975), suggesting that the NW reindeer select a high proportion of lichen in winter. Nevertheless, the method used may underestimate plant species easily digested in the rumen and, thus, only partially reflect the composition of the diet (Gaare *et al*, 1977), however, this would not alter any of the conclusions of the present study. The daily intake of lichens in NW reindeer is regarded as high, since the digestibility of lichens like *C. stellaris* is as high as 75% DM (Jacobsen & Skjenneberg, 1975). Our investigation of the SG reindeer also confirm earlier studies that these animals have adapted to a diet free of lichens and woody plants (Leader-Williams, 1988).

Protein concentrations in RR contents were different between the groups, which reflects differences in the plant species eaten and their nutrient qualities (Table 4). Lichens contain less than 3% crude protein (Jacobsen & Skjenneberg, 1975) and this might explain the low nitrogen content measured in the RR contents in NW reindeer compared to the NS and SG reindeer. Woody plants and grasses in the RR of NW reindeer may, however, supply important nitrogen to rumen fermentation in winter when reindeer eat protein poor lichens. Captive Norwegian reindeer fed lichen, recycle nitrogen efficiently (Hove & Jacobsen, 1975), but even so a significant difference in ruminal ammonia concentration between the NS and NW reindeer was found (Table 4). Recently, Sørmo *et al.* (1999) found RR ammonia concentrations in Svalbard reindeer to be less than 100 mg/kg wet weight, and this could limit rumen microbial metabolism. In comparison with domestic animals, however, the ruminal ammonia levels measured in NS and NW reindeer do not seem to be a rate limiting factor for ruminal carbohydrate fermentation (Ørskov, 1992).

Our first prediction, that reindeer on South Georgia had evolved a GR-like digestive strategy (Hofmann, 1985), eating mainly grasses independent of season, failed. In SG reindeer, total GIT was larger than in NS and NW reindeer, almost as large as in Svalbard reindeer in winter (30% of BM) or in GR (Hofmann, 1985; Sørmo *et al*, 1999). The large GIT in SG reindeer can be explained by intake of

Table 9. Mean (standard deviation) length (m) of the intestines in reindeer on South Georgia in summer (SG) (n = 10), and in northern Norway in late summer (NS) (n = 6) and winter (NW) (n = 11) compared with ruminants of the grazer and concentrate selector types.

	INTESTINES				
	Total	Small	Large	Ratio total/ body length	Ratio large/small
Grazers*				30	0.23
SG	34.1 (5.1)	24.3 (4.6)	11.6 (1.4)	22	0.47
NS	30.3 (2.1)	20.5 (2.4)	9.8 (0.8)	20	0.47
NW	31.7 (3.2)	21.8 (1.8)	9.8 (1.4)	21	0.45
Concentrate selectors*				15	0.47

* from Hofmann, 1985.

low-lignified food in summer, when appetite is high (Larsen *et al.,* 1985; Mathiesen & Utsi, 1999). In Svalbard reindeer, which eat lignified forage in winter, RR contribute as much as 20% of BM (Sørmo *et al.,* 1999), but in SG, NS and NW reindeer relative RR volumes were much smaller (Table 6). The SG reindeer seem to be highly selective, eating plants and low lignin content and of high nutrient value, and have developed a digestive strategy with a large DFC relative to RR capacity (1:10) and a small omasum/abomasum content ratio (Table 6; 8). Ruminants of the CS type also have small rumens, and large distal fermentation chambers accounting for 10% of the rumen capacity and a low omasum/absomasum ratio (Hofmann, 1989; Holand, 1992) (Table 8). Hofmann (1983) reported that the DFC in CS changes its capacity concurrently with the RR in response to forage quality and intake. Similar adaptations were also found in Svalbard reindeer, with their short intestines and large DFC's. The DFC in the Svalbard reindeer seemed to increase with increasing concentration of hemi-cellulose in the diet (Sørmo *et al.,* 1999). No such correlation was found in NW reindeer in Norway which eat hemi-cellulose-rich lichens in winter (Table 2; 4 & 6). Lichens, which consist of fungi and algae, are chemically very different from vascular plants. The unusual physical and chemical nature of lichens could therefore be the reason that the DFC does not inctease in size relative to the rumen when reindeer eat them.

Another functional application of the digestive strategy in CS and related IM could be ruminal bypass of highly digestible nutrients. Strong evidence for the functional significance of a ruminal bypass of soluble plant nutrients has recently been published (Rowell *et al.,* 1997; Meyer *et al.,* 1998). Hofmann (1985) suggested that adult ruminants maintain their *sulcus ventriculi* throughout their lives, since it is well developed to bypass soluble nutrients directly into the omasum. The observation that DFC in reindeer on South Georgia increased in size relative to the rumen with decreasing plant lignin content might support this hypothesis (Fig. 1., Table 6). Furthermore, the relative length of the intestines in ruminants is closely related to feeding strategies (Hofmann, 1985). Svalbard reindeer have short intestines (Sørmo *et al.,* 1999), but no major anatomical differences in intestinal lengths between SG reindeer and NS and NW reindeer were found. In fact, the intestinal ratio of Norwegian reindeer also suggests that they ought to be classified as IM feeders and that the large DFC might be a consequence of the short-term adaptation to the low lignified forage eaten on South Georgia (Table 9).

Our second prediction, that reduced availability of food and depressed appetite in NW reindeer would reduce rumen fill, also failed. Northern ungulates are strongly influenced by seasonal changes in day-length, which increases food intake by three fold in summer over winter levels (Larsen *et al.,* 1985). In NW reindeer, however, the relative RR mass in winter was similar to the RR mass in SG reindeer and NS reindeer, when diet quality, availability and appetite were assumed to be different. The passage of ingested plants out of RR into the omasum thus seems to affect the degree of ruminal fill. The rate of passage is primarily limited by plant particle density and size and functional specific weight, which is influenced by the plant structure and chemistry, like lignification, reduction of particle size by chewing and by ruminal microbial activity (Lechner-Doll & Engelhardt, 1989; Lechner-Doll *et al.,* 1995). We assume that lichens, grasses and shrubs have different densities, but differences in RR particle density remains to be investigated in reindeer. Plant particles can not pass out the RR until they have been sufficiently reduced in size to pass through the reticulo-omasal orifice, which is two mm in cattle (Poppi *et al.,* 1980). RR particle size distribution, however, did not differ among the groups (Table 7), and since as much as 90% of rumen plant particles were smaller than one mm, we concluded that Norwegian reindeer were capable of efficient mastication regardless of what they ate. Thus, ruminal particle size distribution seems to have little effect on the GIT fill in the three groups investigated. In contrast, in the RR of Svalbard reindeer only 70% of the particles were smaller than one mm (Sørmo *et al.,* 1999) and in moose (*Alces alces*) a typical CS, only 30 and 60% of the RR particles in summer and winter, respectively, were smaller than 1 mm (Nygreen & Hofmann, 1990). This indicates that ruminants of the CS type could release small particles from the RR efficiently. Likewise, Renecker & Hudson (1990) and Hofmann & Nygreen (1992) reported that ruminants of CS type seem to use this strategy to escape lignified browse from the rumen more than GR which suggests a better adaptation to lignified plants in CS. This seems not to be the case in Norwegian reindeer, since plant cell wall contents, especially lignin, seems to influence the relative degree of fill

of GIT in these animals (Fig. 1). We believe that increased plant lignification decreases ruminal passage rate. Therefore rumen wet weight fill in Norwegian reindeer seems to increase relative to the size of the DFC, as observed in NW reindeer. Also in sheep and roe-deer RR fill increased when the plant cell wall content in the diet increased (Weyreter *et al.*, 1987; Lechner-Doll *et al.*, 1990; Holand, 1992). Interestingly, in captive reindeer fed lichens *ad lib.* with low lignin content, RR content comprised only 10.4% of BM, while in animals fed *ad lib.* highly fibrous timothy silage RR contents was as high as 33% of BM (Aagnes & Mathiesen, 1994; Aagnes *et al.*, 1996). Our data teflects the extreme plasticity of the GIT in Norwegian reindeer, a classical adaptable IM ruminant feeding type, which is able to utilise the large seasonal changes in availability of forage, with different dietary plant species and nutrient qualities, and even adapt to new plant species in the Southern hemisphere with low lignin content.

Appendix:

Abbreviations and symbols used in the text.

CS	Concentrate selector
GR	Grazer
IM	Intermediate feeders
NS	Northern Norway in late summer
NW	Northern Norway in winter
SG	South Georgia in summer
BM	Live body mass
CWC	Cell wall content
DFC	Distal fermentation chamber
GIT	Gastro-intestinal tract
RR	Reticulo-rumen
OM	Organic dry matter
DM	Dry mattet
NDF	Neutral detergent fibte
ADF	Acid detergent fibre
ADL	Acid detergent lignin
P	Probability
s	Standard deviation

Acknowledgement

This investigation was a part of the Norwegian Antarctic Research Expedition 89/90 and was supported by the Research Council of Norway and Norwegian Reindeer Husbandry Research Council. E. Gaare, Norwegian Institute for Nature Research, Trondheim, Norway is thanked for the botanical analysis. Chemical analysis were carried out at Holt Plant Research Centre, Tromsø, Norway. Kirsri Johnsen, Marit A. Vader and Vigdis B. Rædergård, The Norwegian School of Veterinary Science, are thanked for skilful technical support.

References

Aagnes, T. H. & Mathiesen, S. D. 1994. Food and snow intake, body mass and rumen function in reindeer fed lichen and subsequently starved for 4 days. – *Rangifer* 14: 33–37.

Aagnes, T. H., Blix, A. S. & Mathiesen, S. D. 1996. Food intake, digestibility and rumen fermentation in reindeer fed baled timothy silage in summer and winter. – *J. Agric. Sci. Camb.* 127: 517–523.

Bhattacharyya, G. K. & Johnsen, R. 1977. *Statistical concepts and methods.* John Wiley & Sons, Inc. Singapore.

Gaare, E. & Skogland, T. 1975. Wild reindeer food habits and range use at Hardangervidda. – *In:* F. E. Wiegolaski (ed.). *Fennoscandian Tundra Ecosystems.* Ecological Studies Vol. 17; Part 2, pp.195-205. Springer-Verlag, Berlin.

Gaare, E., Sørensen, A. & White, R. G. 1977. Are rumen samples representative of the diet? – *Oikos* 29: 390–395.

Goering, H. K. & van Soest, P. J. 1970. *Forage analysis. Agriculture Handbook 379.* Agr. Res. Service. U.S. Dept. Agr. Washington DC. 20 pp.

Hofmann, R. R & Stewart, D. R. M. 1972. Grazer or browser: A classification based on the stomach structure and feeding habits of East African ruminants. - *Mammalia* 36: 226–240.

Hofmann, R. R. 1985. Digesrive physiology of the deer- their morphophysiological specialisation and adaptation. – *In:* K. Drew, P. Fennessy (eds.). *Biology of Deer Production. – Royal Society of New Zealand Bulletin* 22: 393–407.

Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. – *Oecologia* 78: 443–457.

Hofmann, R. R. & Nygren, K. 1992. Morphophysiological specialisation and adaptation of the moose digestive system. – *Alces,* suppl. 1: 91–100.

Holand, Ø. 1992. Winter digestive strategy of a concentrate selector in Norway: the European roe deer. – *Can. J. Zool.* 70: 1331–1335.

Horwitz, W. 1980. *Official Methods of Analysis of the Association of Analytical Chemists.* 13th ed. Washington; AOAC.

Hove, K. & Jacobsen, E. 1975. Renal excretion of urea in reindeer: effect of nutrition. – *Acta Vet. Scand.* 16: 513–519.

Jacobsen, E. & Skjenneberg, S. 1975. Experiments with different diets to reindeer. Feeding value of reindeer feed (RF-71). – *Scientific Report, Agriculture College, Norway* 58: 1–11.

Johansen, B. & Tømmervik, H. 1990. Mapping winter grazing areas for reindeer in Finnmark County, northern Norway, using Landsat 5 (tm) data. – *In: Remote sensing science for the nineties. 10th intern. Geoscience & remote sensing symposium,* I: 613–616.

Kightley, J. P. & Lewis Smith, R. I. 1976. The influence of reindeer on the vegetation of South Georgia: I. Long-term effects of unrestricted grazing and the establishment of exclosure in various plant communities. – *British Antarctic Bulletin* 44: 57–76.

Larsen, T. S., Nilsson, N. Ø. & Blix, A. S. 1985. Seasonal changes in lipogenesis and lipolysis in isolated adipocytes from Svalbard and Norwegian reindeer. – *Acta Physiol. Scand.* 123: 97–104.

Leader-Williams, N., Scott, T. A. & Pratt, R. M. 1981. Forage selecrion by introduced reindeer on South Georgia and its consequence for rhe flora. – *J. Appl. Ecol.* 18: 83–106.

Leader-Williams, N. 1988. *Reindeer on South Georgia.* University Press, Cambridge, UK, 319 pp.

Lechner-Doll, M., Rutagwenda,T., Schwartz, H. J., Schultka, W. & Engelhardt, W. v. 1990. Seasonal changes of ingesta mean retention time and forestomach fluid volume in indigenous camels, cattle, sheep, and goars grazing in a thornbush savannah pasture in Kenya. – *J. Agric. Sci.* 115: 409–420.

Lechner-Doll, M., Hume, I. D. & Hofmann, R. R. 1995. Comparison of herbivore forage selection and digestion – *In: M.* Journet, E. Grenet, M.-H. Fatce, M. Theriez & C. Demarquilly (eds.). *Recent developments in the nutrition of herbivores. Proceeding of the IVth International Symposium on the Nutrition of Herbivores,* pp. 231–248. INRA Editions, Paris.

Lechner-Doll, M. & Engelhardt, W. v. 1989. Particle size and passage from the forestomach in camels compared to cattle and sheep fed similar diet. – *J. Anim. Physiol. Anim. Nutr.* 123: 97–104.

Mathiesen, S. D. & Utsi, T. H. Aagnes. 2000. Forage quality of Norwegian reindeer on South Geotgia in summer. – *Rangifer* 20 (1): (in press).

Meyer, H. H. D., Rowell, A., Streich, W. J., Stoffel, B. & Hofmann, R. R. 1998. Accumularion of polyunsaturated fatty acids by concentrate selecting ruminants. – *Comp. Biochem. Physiol. A* 120; 263–268.

Nygreen, K. & Hofmann, R. R. 1990. Seasonal variations of food particle size in moose. – *Alces* 26: 1–10.

Olsen, M. A., Aagnes, T. H. & Mathiesen, S. D. 1994. Digestion of herring by indigenous bacteria in minke whale forestomach. – *Appl. Environ. Microbiol.* 60: 445–455.

Person, S. J., White, R. G. & Luick, J. R. 1980. Determinarion of nutritive value of reindeer caribou range. – *In:* E. Reimers, E. Gaare & S. Skjenneberg (eds.). *Proceedings of the 2nd Int. Reindeer/Caribou Symposium, Røros.* Direkroratet for vilt og ferskvannsfisk, Trondheim, pp. 224–239.

Poppi, D. P., Norton, B. W., Minson, D. J. & Hendricksen, R. E. 1980. The validity of the critical size theory for parricles leaving the rumen. – *J. Agric. Sci. Cam.* 94: 275–280.

Renecker, L. A. & Hudson, R. J. 1990. Digestive kinetics of moose (*Alces alces*), wapiti (*Cervus elaphus*) and cattle. – *Anim. Prod.* 50: 51–61.

Rowell, A., Dyer, J., Hofmann, R. R., Lechner-Doll, M., Meyer, H. H., Shirazi-Beechey, D. & Wood, S. P. 1997. The expression of intestinal sodium-glucose co-transporter in cervides. – *Zschr. Saugetiere* Suppl. 262: 204–208.

van Soest, P. J. 1963a. Use of detergents in analysis of fibrous feeds. I. Preparation of fibre residues of low nitrogen content. – *J. Assoc. Off. Agric. Chem.* 46 (5): 825–829.

van Soest, P. J. 1963b. Use of detetgents in the analysis of fibrous feeds II. A rapid method for determination of fibre and lignin. – *J. Animal. Sci.* 23 (3): 838–845.

van Soest, P. J. 1967. Use of detergent in the analysis of fibrous feeds IV. Detetmination of plant cell wall constituents. – *J. Assoc. Off. Anal. Chem.* 50 (1): 40–55.

Staaland, H., Jacobsen, E & White, R. G. 1979. Comparison of the digestive tract in Svalbard and Norwegian reindeer. – *Arctic and Alpine Research* 11: 457–466.

Sørmo, W., Haga, Ø. E., Gaare, E., Langvatn, R. & Mathiesen, S. D. 1999. Forage chemistry and fermentation chambers in Svalbard reindeer. – *J. Zool.* Lond. 247: 247–256.

Tyler, N. J. C., Fauchald, P., Johansen, O. & Christiansen, H. R. 1999. Seasonal inappetance and weight loss in female reindeer in wintet. – *Ecological Bulletin* 47: In press.

Walton, D. W. H. 1975. European weeds and other alien species in the Sub-Antarcric. – *Weed Research* 15: 271–282.

Werner, A. 1990. *Vergleichende morphometrische Untersuchungen am Blattermagen von 17 Widerkauen (RUMINANTIA) untersuchungen Ernahrungstypen.* Vet. Doctorate thesis, Just-Liebig Universiat, Giessen, Germany.

Weyreter, H., Heller, R., Dellow, D., Lechner-Doll, M. & Engelhardt,W. v. 1987. Rumen fluid volume and retention time of digesta in an indigenous and a conventional breed of sheep fed a low quality fibrous diet. – *J. Anim. Physiol & Anim. Nutr.* 58: 89–90.

Ørskov, R. E. 1992. *Protein nutrition in ruminants.* Academic Press, London, UK, 175 pp .

Manuscript received 20 January, 1998
accepted 17 September, 1999