Functional Anatomy of the Omasum in High Arctic Svalbard Reindeer (*Rangifer tarandus platyrhynchus*) and Norwegian Reindeer (*Rangifer tarandus tarandus*)

By *S.D. Mathiesen*[1,2,], *M.A. Vader*[1], *V.B. Rædergård*[1], *W. Sørmo*[2], *Ø.E. Haga*[2], *N.J.C. Tyler*[3] and *R.R. Hofmann*[4]

[1]Department of Arctic Veterinary Medicine, The Norwegian School of Veterinary Science, [2]Department of Arctic Biology and Institute of Medical Biology, and [3]Department of Biology, University of Tromsø, Tromsø, Norway, and [4]Institute for Zoo Biology and Wildlife Research, Berlin, Germany.

Mathiesen SD, Vader MA, Rædergård VB, Sørmo W, Haga ØE, Tyler NJC, Hofmann RR: Functional anatomy of the omasum in high Arctic Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and Norwegian reindeer (*Rangifer tarandus tarandus*). Acta vet. scand. 2000, 41, 25-40. – The structure and fill of the omasum was investigated in summer and in winter in adult female reindeer living on the polar desert and tundra of the high Arctic archipelago of Svalbard and in sub-Arctic mountain habitats in northern Norway. The mean total mass of the omasum in non-lactating adult female Svalbard reindeer was 467 g (0.65 g per 100 g live body mass (BM)) in September and 477 g (1.03 g per 100 g BM) in April. By contrast, the mean mass of the omasum in non-lactating adult reindeer in northern Norway was 534 g (0.83 g per 100 g BM) in September but only 205 g (0.35 g per 100 g BM p<0.05) in late March, owing to a decrease in both tissue mass and the wet mass of the contents of the organ. The mean absorptive surface of the omasum in Svalbard reindeer was 2300 cm^2 in September and 2023 cm^2 in April. In Norwegian reindeer, by contrast, the absorptive surface area decreased from 2201 cm^2 in September to 1181 cm^2 (p<0.05) in late March. The marked seasonal decline of omasal tissue and contents in Norwegian reindeer probably results from intake of highly digestible forage plants, including lichens, in winter. Svalbard reindeer, a non-migratory sub-species, survive eating poor quality fibrous vascular plants in winter. The absence of any marked seasonal change in the mass, total absorptive surface area or filling of the omasum in Svalbard reindeer in winter despite a substantial decline in body mass presumably reflects their need to maintain maximum absorption of nutrients, including volatile fatty acids, when feeding on such poorly fermentable forage.

Cervid; gastrointestinal tract; Rangifer; ruminant.

Introduction

Reindeer and caribou (*Rangifer tarandus*) live throughout the Arctic and sub-Arctic where they are subjected to extreme seasonal variation in the abundance, nutritional quality and availability of forage. The general strategies which the animals have evolved to cope with poor nutritional conditions in winter include a pronounced seasonal fluctuation in appetite. Voluntary dry matter intake is high in summer, reaching a peak in July and August, and falls to its annual nadir in January and February in a cycle corresponding to the seasonal changes in the quality and availability of natural forage (e.g. *Larsen et al.* 1985, *Tyler et al.* 1999). Re-

cently, much attention has been given to the seasonal plasticity of the gross anatomy of the gastrointestinal tract (GIT) of these northern ruminants, particularly the reticulo-rumen (RR), the intestines and the large distal fermentation chamber (caecum and proximal colon, DFC). The data have improved the understanding of anatomical and physiological adaptations to alternating periods of abundance and acute shortage of food and placed reindeer within the general classification of ruminant feeding types proposed by *Hofmann* (1985) (e.g. *Aagnes & Mathiesen* 1996, *Mathiesen et al.* 1999a,b, *Sørmo et al.* 1999). To date, however, the omasum has received little attention (*Hofmann* 2000). The omasum is thought to be the site of absorption of a variety of nutrients including volatile fatty acids (VFA), water from forage and from salivary secretion, minerals, water soluble vitamins and salivary bicarbonates. The relative size of this organ varies considerably between different species of ruminants. It is generally small and perhaps less functional in concentrate selectors (CS) like roe deer (*Capreolus capreolus*) and moose (*Alces alces*) (*Hofmann & Stewart* 1972, *Werner* 1990, *Hofmann & Nygren* 1992, *Holand* 1992). In grazers (GR) like African buffalo (*Syncerus caffer*) and grass-eating intermediates (IM) such as red deer (*Cervus elaphus*) (*Hofmann* 1973, 1985, 1989) the omasum is large and, therefore, perhaps more important for the processing of forage rich in dietary fibre.

We examined the structure and filling of the omasum in summer and in winter in adult female reindeer living on the polar desert and tundra of Svalbard and in sub-Arctic mountain habitats in northern Norway. The 2 sub-species, Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and Norwegian reindeer (*Rangifer tarandus tarandus*), feed on a variety of vascular plants of high nutrient quality in summer but select different diets in winter. Svalbard rein-

deer feed on poor quality, fibrous plants including dry grasses, dwarf shrubs and mosses in winter (*Staaland et al.* 1983, *White & Staaland* 1983, *Staaland* 1984, *Sørmo et al.* 1999) while reindeer on the mainland of northern Norway, by contrast, include a substantial proportion of highly digestible lichens in their winter diet (*Jacobsen & Skjenneberg* 1975, *Mathiesen et al.* 1999b, 2000a).

The ruminal production of volatile fatty acids is much reduced in Svalbard reindeer in winter compared with summer but no such seasonal decline is seen in Norwegian reindeer reflecting the difference in diet between the 2 sub-species (*White & Staaland* 1983, *Sørmo et al.* 1997, *Mathiesen et al.* 2000a). The difference in winter diet also has an important influence on the gross anatomy of the GIT. In Svalbard reindeer, for example, the reticulo-rumen represented 20% of live body mass (BM) and the organic dry matter (OM) of the contents of the RR contained as much as 25% plant lignin in winter (-*Sørmo et al.* 1999). In Norwegian reindeer the contents of the RR comprised only 14% of BM and its OM contained only 15% lignin, again reflecting the inclusion of lichen in the diet (*Mathiesen et al.* 1999b, 2000b). Svalbard reindeer have shorter intestines and a larger DFC than Norwegian reindeer and thus seem more similar to ruminants of the CS type than Norwegian reindeer. Nevertheless, several characteristics of the digestive system of reindeer and caribou are intermediate between ruminants of the CS and GR type (*Hofmann* 1985, *Aagnes & Mathiesen* 1996, *Mathiesen et al.* 1999b).

Using this knowledge of the effect of the composition of the diet in winter on fill and structure of the GIT, we predicted that the omasum of Svalbard reindeer would have a relatively small absorptive surface area typical of the CS ruminant-types compared to the omasum of Norwegian reindeer, at least in summer when Svalbard reindeer in particular feed on very

high quality forage. Furthermore, we predicted that the difference in the absorptive surface area of the omasum between the 2 sub-species would be small in winter when food quality and availability is much reduced both in Svalbard and in northern Norway.

Materials and methods

Study area

Svalbard reindeer were collected from Nord-austlandet (NA, 80°N) and Nordenskiöld Land (NL, 78°N; Fig. 1) in Svalbard. NA is an island dominated by ice caps which cover about 80% of the total surface area and is classified as an Arctic desert. The mean annual precipitation is approximately 250 mm and vegetation is species poor and mostly very scarce (cover < 5%). Snow lies on the ice-free ground for 9-10 months annually (*Glen* 1937). Approximately 300 reindeer live here (*Hindrum et al.* 1995) feeding on mainly *Saxifraga oppositifolia, Salix* spp. and a few graminoids (*Staaland & Punsvik* 1980, *Sørmo et al.* 1999).

Vegetated ground in NL is an Arctic tundra. Approximately 4000 reindeer live here (*Hindrum et al.* 1995) feeding on a variety of vascular plants including grasses and sedges (*Carex* spp., *Poa* spp, *Luzula* spp.), dwarf shrubs (*Dryas octapetala, Salix* spp.) and mosses, the latter especially in winter (*Sørmo et al.* 1999). Snow covers the ground for 8-9 months annually. Unlike NA, the climate is unstable with temperatures occasionally rising above freezing even in winter, resulting in alternating periods of thawing and freezing which can produce crusts of ice on the snow through which the reindeer have difficulty in digging to reach the plants beneath. Svalbard reindeer are sedentary, not migratory animals (*Tyler & Øritsland* 1989) and, consequently, all important dietary lichens (such as *Cladina* and *Cetraria*) have long ago been removed by grazing and trampling from those parts of Svalbard including NA and NL
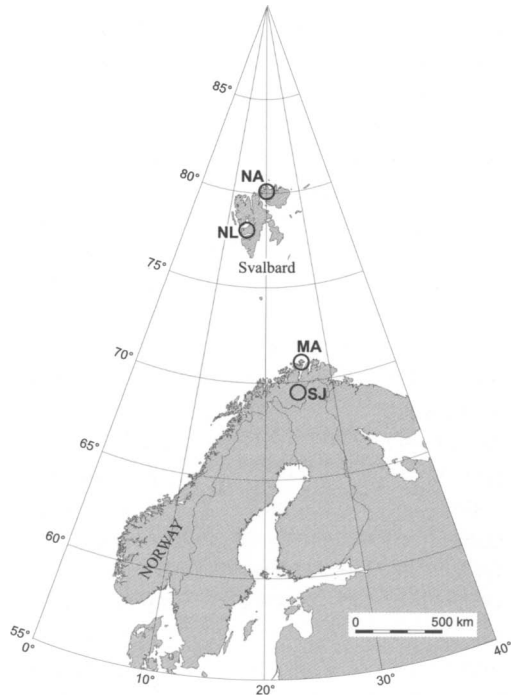

Figure 1. Svalbard reindeer were collected at Nordaustlandet NA (August and April) and Nordenskiöld Land NL (September, October and April) in the high Arctic archipelago of Svalbard and Norwegian reindeer at Magerøya MA (September) and Soussjavre SJ (November-March) in northern Norway.

where there are established populations of reindeer.

Reindeer on the mainland of northern Norway were collected from a herd of semi-domesticated animals in Finnmark (69°N). This herd migrates about 250 km between geographically distinct winter pastures inland and a coastal summer pasture (Fig. 1). They eat a wide variety of vascular plants in summer including dwarf shrubs (e.g. *Empetrum* spp. and *Loiseleuria procumbens*), birch (*Betula nana*), willows (*Salix* spp.), sedges (e.g. *Carex* spp.) and grasses (e.g. *Deschampsia* spp., *Poa* spp.); the

species composition of their winter diet is sim-
ilar to their late summer diet except for the in-
clusion of a significant proportion of lichens
(e.g. *Cladina* spp., *Cetraria nivalis, Stereocau-
lon* spp. (*Mathiesen et al.* 1999b, 2000b).

Animals
Adult (aged ≥2 years) female Svalbard rein-
deer, selected at random from groups grazing
undisturbed, were killed by a single shot in the
chest in April 1994 ($n = 2$), October 1994 ($n =
7$), April 1995 ($n = 4$), August 1995 ($n = 6$) and
in September 1996 ($n = 12$). Adult female Nor-
wegian reindeer were selected by hand after the
entire herd had been gathered in a paddock,
skinned by the traditional saami method of sev-
ering the spinal cord with a knife through the
foramen magnum and killed by bleeding after
cutting the major vessels at the heart in Septem-
ber 1995 ($n = 6$), November 1995 ($n = 6$), Jan-
uary 1996 ($n = 6$) and in March 1996 ($n = 6$).
Post-mortem examination of all animals was
carried out in field laboratories starting within
15 min of death. The animals used in this inves-
tigation included those described in *Sørmo et
al.* (1999), *Mathiesen* et al. (1999a,b, 2000b)
and *Tyler et al.* (1999). All animals were classi-
fied as lactating or non-lactating based on pal-
pation of the udder.

Body mass
BM was recorded to 1 kg using a Salter me-
chanical scale (1-100 kg). Hot carcass mass
(CM) was measured within 1 h of death by
weighing the dressed carcass to 0.1 kg on a 150
kg x 50g steel yard immediately after the ani-
mal was skinned. The dressed carcass is the
whole animal less the entire GIT and its con-
tents, the head, the pelt, the lower legs, the
uterus and its contents, the udder and all the vis-
ceral organs including the kidneys. The head
was removed by cutting between the cranium
and the first vertebra; the feet were removed by

cutting between the distal carpus and the meta-
carpus and between the distal tarsus and the
metatarsus.

Omasum
The omasum of each animal was separated
from the RR and abomasum by cutting at the re-
ticulo-omasal orifice (ROO) and at the omaso-
abomasal opening, allowed to cool to ambient
temperature (0-5 °C) and then weighed to 1 g on
an electronic balance. The length, height and
curvature of each omasum were then measured
to 1 cm with a flexible tape according to *Hof-
mann* (1973) after which the omasa were care-
fully opened by cutting along the dorsal curva-
ture. A sample of contents (approximately 10 g
wet mass) was collected from each organ after
which omasa were emptied completely, care-
fully washed out with fresh water, drained and
weighed to 1 g before being fixed in 10% buf-
fered formalin (pH 7.0). The wet mass of the
contents of each omasum was calculated by
subtraction. A sample of contents was then
dried in an oven (115 °C) to constant weight,
cooled in a dessicator, weighed to 1 g and the
dry matter content of each omasum was then
determined by difference. All first, second and
third order omasal leaves (Figs. 2, 3) were dis-
sected out according to *Werner* (1990) and the
surface area of each leaf and of the omasal wall
was recorded by tracing their outlines onto
transparent plastic and determining the area of
the tracings using a computerised digital board.
The diameter of the ROO was calculated after
opening the organ and measuring the inner cir-
cumference of the orifice to 1 mm with the tis-
sue laid out flat.

Gastroinstestinal tract
The wet weight of contents and of the tissue of
each section of the GIT was measured accord-
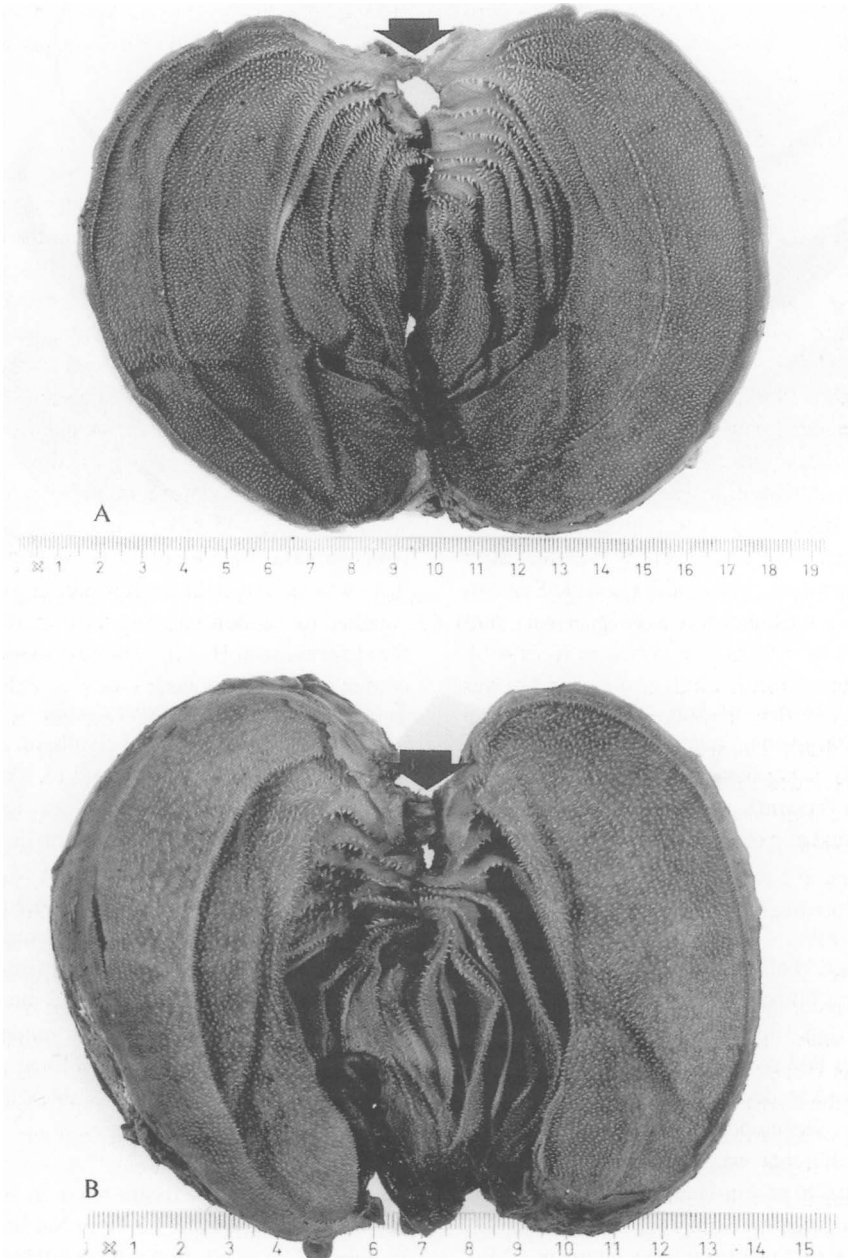ing to *Sørmo et al.* (1999) and *Mathiesen et al.*
(1999a,b).

Figure 2. Opened omasa from adult female Svalbard reindeer (A) and adult female Norwegian reindeer (B) in September illustrating the sizes of two different orders of leaves. Arrow: reticulo-omasal orifices. Bar: scale in cm.
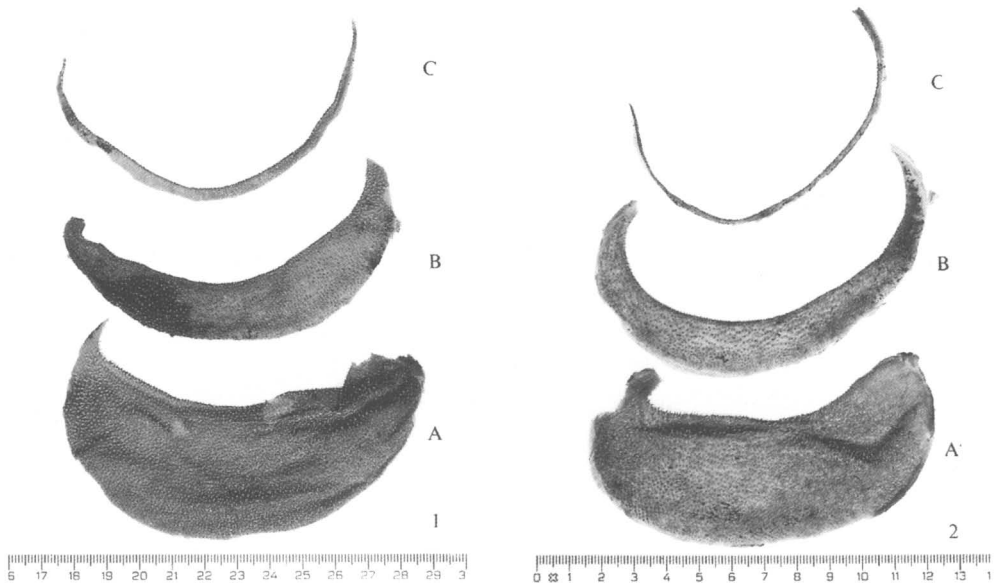
Figure 3. The 1st.-, 2nd.- and 3rd.- order (A, B, C) omasal leaves from the omasa of adult female Svalbard reindeer (1) and adult female Norwegian reindeer (2) in September. Bar: scale in cm.

Statistical analysis of data

Results are given as mean and standard deviation (SD) from the mean. Significance was tested by Student's *t*-test. The null hypothesis was rejected at $p < 0.05$ in all tests.

Results

Body mass

The mean BM of non-lactating female Svalbard reindeer in NL declined from 72.1 kg in September to 46.4 kg in April ($p < 0.05$, Table 1). The mean BM of Norwegian reindeer showed only a modest decline in winter falling from 65.9 kg in September to 59.8 kg in late March, and the difference was not significant (Table 1). The mean CM of non-lactating female Svalbard reindeer decreased from 36.0 kg in September to 19.9 kg in April ($p < 0.05$); the mean CM of Norwegian reindeer was 30.2 kg in September and 29.1 kg in March and the difference was not significant (Table 1).

Total GIT mass (content and tissue)

The mean mass of GIT in Svalbard reindeer was 16.3 kg in NA in August and 15.1 kg in NL in April and the difference was not significant (Table 1). In Norwegian reindeer the mean total GIT was 17.1 kg in September and 11.9 kg in March ($p < 0.05$). Likewise mean total mass of the omasum in non-lacating adult female Svalbard reindeer was 466.8 g in September and 477.0 g in March. By contrast, the mean mass of the omasum in Norwegian reindeer was 533.7 g in September and declined to only 205.2 g in late March ($p < 0.05$, Table 1).

Tissue mass

The mean total GIT tissue mass in Svalbard reindeer declined from 3.3 kg in NA in August to only 1.7 kg in NL in April ($p < 0.05$) while in Norwegian reindeer mean total GIT tissue declined from 3.6 kg in September to 2.7 in March but the difference was not significant (Table 1).

Table 1. Mean (SD) body mass (kg), carcass mass (CM), total mass (g), tissue mass (g), wet mass of contents (wm g) and dry matter (DM g) of the contents of the omasum in adult female Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and Norwegian reindeer (*Rangifer tarandus tarandus*).

| Season/ status | SVALBARD REINDEER | | | | | | NORWEGIAN REINDEER | | | |
| | Nord Austlandet | | Nordenskiöld Land | | | | Magerøya | Suossjarve | | |
	August non-lactating*	April*	September lactating	September non-lactating	October* non-lactating	April*	September non-lactating	November non-lactating	January	March
n	6	2	6	6	7	4	6	6	6	6
BM (kg)	54.2 4.5	44.0-59.5	68.9 5.5	72.1 5.3	64.1 5.3	46.4 7.1	65.9 8.3	63.2 9.7	60.1 6.9	59.8 10.3
CM (kg)	23.1 1.7	19-27	31.1 3.2	36.0 2.7	34.6 3.7	19.9 2.7	30.2 3.3	30.0 4.0	28.7 3.5	29.1 5.0
GIT (kg)	16.3 1.8	10.3-14.8	ND	ND	15.1 1.9	13.8 2.4	17.1 3.0	15.1 3.2	13.5 1.5	11.9 0.9
GIT contents wm (kg)	13.1	8.7-13.0	ND	ND	12.8 1.9	12.2 2.4	13.6 2.1	10.9 2.4	9.9 1.3	9.3 0.9
GIT wall (kg)	3.3 0.3	1.5-1.8	ND	ND	2.4 0.3	1.7 0.1	3.6 0.7	3.3 1.1	3.1 0.3	2.7 0.3
RR contents wm (kg)	9.9 1.3	6.5-10.2	11.2 1.1	9.3 1.2	9.6 1.7	9.3 1.9	11.3 2.7	8.8 2.0	8.1 1.2	7.7 0.8
RR wall (kg)	2.3 0.3	0.9-1.1	2.6 0.1	2.2 0.3	1.5 0.2	1.0 0.1	2.9 0.7	2.9 0.7	2.3 0.3	1.9 0.2
Omasum total mass (g)	495.0 135.0	375-475	537.3 32.2	466.8 184.9	543.6 132.1	477.0 106.0	533.7 102.4	300.8 59.1	234 44.7	205.2 48.6
Omasum wall (g)	133.0 28.0	99.0-125.0	160.3 48.2	167.5 48.6	131.7 21.6	107.0 12.0	225.3 40.1	ND	111.9 26.9	ND
Omasum contents wm (g)	363.0 108.0	276-350	347.9 47.9	314.3 132.9	517.5 54.6	370.0 98.0	383.7 92.8	ND	117.8 21.4	ND
Abomasum content wm (g)	251.0 82.0	175.0-259.0	ND	ND	203.0 53.0	172.0 50.0	315.2 121.2	287.1 148.0	275.9 109.6	241.0 83.2
Omasum contents DM (g/100g wet content)	19.5 1.4	25.4-27.8	17.7 2.1	16.3 2.8	19.0 3.01	23.0 0.76	17.5 5.5	23.1 0.2	21.5 1.3	23.3 1.3

* Modified data from *Sørmo et al. 1999.* ND: not determined.

Table 2. Mean proportion (%) of omasum total mass, tissue and content wet weight related to the total GIT (gastro-intestinal tract) mass, rumen wet weight content in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and Norwegian reindeer (*Rangifer tarandus tarandus*).

Season/ status	SVALBARD REINDEER						NORWEGIAN REINDEER			
	Nord Austlandet		Nordenskiöld Land				Magerøya	Suossjarve		
	August non- lactating*	April*	September lactating	September non- lactating	October* non- lactating	April*	September non- lactating	November non- lactating	January	March
Omasum total mass/GIT total mass (%)	3.0	3.4	ND	ND	3.4	3.5	3.1	2.0	1.7	1.7
Omasum contents wm/RR contents wm (%)	3.7	3.8	3.1	3.4	5.4	4.0	3.4	ND	1.5	ND
Omasum contents wm/GIT contents wm (%)	2.7	2.9	ND	ND	3.3	3.0	2.8	ND	1.2	ND
Omasum tissue GIT wall (%)	4.0	6.7	ND	ND	5.5	6.3	6.3	ND	3.6	ND

* Data modified from *Sørmo et al.* 1999; wm: weight mass.

The mean mass of the tissue of the RR in Svalbard reindeer in NL declined from 2.2 kg (3.0% of BM) in September to 1.0 kg in April (2.1% of BM) ($p<0.05$) and the mean mass of the tissue of the omasum declined from 167.5 g (0.23% of BM) in September to 107.0 g (0.23% of BM) in April, although the difference was not significant. The mean mass of the tissue of the RR in Norwegian reindeer decreased from 2.9 kg (4.4% of BM) in September to 1.9 kg in March (3.3% of BM) ($p<0.05$) and the mean mass of the tissue of the omasum declined from 225.3 g (0.34 % of BM) in September to 111.9 g (0.18% of BM) in January (Table 1; $p<0.05$).

Mass of contents
The mean mass of the contents of the GIT content was 13.1 kg in Svalbard reindeer in NA in August and 12.2 kg in NL in April ($p>0.05$). In Norwegian reindeer total mass of GIT contents declined from 13.6 kg in September to 9.3 kg in March ($p<0.05$; Table 1). The mean wet weight of the contents of the rumen of Svalbard reindeer was 9.3 kg both in September and April in NL but in Norwegian reindeer it declined from 11.3 kg in September to 7.7 kg in March ($p<0.05$). The mean wet mass of the contents of the omasum of non-lactating female Svalbard reindeer in NL increased from 314.3 g in September to 370.0 g in April but the difference

Table 3. Mean wet mass of the contents of the GIT (gastrointestinal tract) and RR (reticulo-rumen) as a proportion (%) of live body mass; mean wet mass of the contents of the omasum as a proportion (%) of the mean wet mass of the contents of the GIT; and ratio of the mean wet mass of the contents of the DFC (distal fermentation chamber) and the RR in different ruminant feeding types and in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and Norwegian reindeer (*Rangifer tarandus tarandus*). All data are from adult females.

	Concentrate selector		Intermediate type				Grazer
	Roe deer*		Norwegian reindeer		Svalbard reindeer		African buffalo ****
	Summer	Winter	Summer	Winter	Summer	Winter	Summer
GIT contents wm % BM	9.3	11.9	20.6	15.5	25.6***	26.3	ND
RR contents wm % BM	5.8	8.9	17.1	12.9	12.8	20.0	24
RR contents wm % CM	ND	ND	37.4	26.5	25.8	46.7	ND
Omasum contents wm % CM	ND	ND	1.3	0.4	0.9	1.8	ND
DFC:RR	1:7	1:7	1:14**	1:14**	1:10***	1:7***	1:30

* data from Holand & Staaland 1985, ** data from Mathiesen et al. 1999b, *** data from Sørmo et al. 1999, **** data from Hofmann, 1989, wm: wet mass, bm: bodymass, cm: carcass mass.

was not significant (Table 1). In Norwegian reindeer, by contrast, the mean wet mass of the contents of the omasum decreased from 383.7 g in September to 117.8 g in January (p<0.05; Table 1).

Relative mass
The total mass of the omasum (tissue and contents) in Svalbard reindeer increased from 0.65% of BM in September to 1.03% of BM in April. By contrast, the mean total mass of the omasum in Norwegian reindeer decreased by 61.6% from September (0.83% of BM) to March (0.35% of BM, p<0.05; Table 1). Furthermore, the total mass of the omasum (tissue and contents) in Svalbard reindeer in NA represented 3.0% of the total mass (tissue and contents) of the GIT in August and 3.4% in NL in April. In Norwegian reindeer the total mass of the omasum represented 3.1% of the total mass of the GIT in September but only 1.7% of GIT mass in March (p<0.05; Table 2).

The omasal tissue in Svalbard reindeer represented 4.0% of the total mass of the GIT tissue in August in NA and as much as 6.3% in NL in April. In Norwegian reindeer omasal tissue represented 6.3% of total GIT in September but only 3.6% in January (p<0.05; Table 2).
The mean wet weight mass of the contents of the GIT comprised 25.6% of BM in Svalbard reindeer on NA in August and 26.3% of BM in NL in April but the difference was not significant. In contrast, in Norwegian reindeer the mean mass of the contents of the GIT declined from 20.6% of BM in September to 15.5% of BM in March (p<0.05; Table 3). The wet mass of the contents of the RR in non-lactating female Svalbard reindeer in NL increased from 12.8% of BM and 25.8% of CM in September to 20.0% of BM and 46.7% of CM in April (Table 3; p<0.05). In Norwegian reindeer, by contrast, the wet mass of the contents of the RR decreased from 17.1% of BM and 37.4% of CM in September to 12.9% of BM and 26.5% of

Table 4. Mean (SD) in selected parameters describing the gross anatomy of the omasum in adult female Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and adult female Norwegian reindeer (*Rangifer tarandus tarandus*) by location and season.

| | SVALBARD REINDEER | | | | | NORWEGIAN REINDEER | | |
| | Nord Austlandet | | Nordenskiöld Land | | | Magerøya | Soussjavre | |
Season/status	August	September lactating	September non-lactating	October non-lactating	April	September non-lactating	November non-lactating	March
n	6	6	6	7	4	6	6	6
Length:height ratio	1.7	1.9	1.9	1.8	1.9	1.8	1.7	1.9
	0.1	0.1	0.1	0.2	0.1	0.2	0.1	0.1
Curvature	24.9	26.0	24.5	26.7	24.8	26.5	20.1	17.8
(cm)	1.5	1.1	3.2	2.0	2.9	2.3	1.2	1.9
Total absorptive area	2514.4	2007.7	2300.5	1867.3	2022.8	2200.6	1430.4	1181.0
(cm^2)	516.7	505.9	179.0	312.8	146.0	237.4	219.5	170.5
1st. order leaves	50.0	57.7	58.2	54.0	56.9	50.7	47.9	49.4
% total area	3.6	3.7	2.9	4.2	2.8	2.2	5.0	4.0
2nd. order leaves	27.9	24.9	21.7	25.8	23.4	29.2	29.6	29.6
% total area	3.0	2.9	5.3	3.2	1.3	0.9	3.7	2.6
3rd order leaves	10.5	7.7	6.6	6.8	8.2	7.2	8.1	9.8
% total area	1.9	1.6	1.3	2.7	1.1	1.5	1.1	1.3
Wall area	11.2	11.4	11.9	13.3	12.4	13.1	14.2	10.3
% total area	1.9	0.5	1.4	1.3	0.9	0.6	0.9	1.2
1st. order leaves (n)	14.8	18.1	17.7	14.0	13.7	14.5	14.2	14.8
	1.1	2.2	2.0	1.4	0.4	1.5	0.7	0.7
2nd. order leaves (n)	14.6	17.6	16.0	14.0	14.7	15.5	14.0	14.0
	1.1	2.8	3.3	1.1	0.7	0.9	0.8	0.8
3rd. order leaves (n)	26.0	25.7	24.2	23.7	23.7	25.3	24.7	24.5
	1.5	1.2	2.7	2.8	1.5	1.9	2.1	1.3
Max. leaf height (cm)	5.0	5.3	4.9	4.9	4.5	5.0	4.0	3.9
	0.6	0.4	0.6	0.3	0.6	0.3	0.6	0.4

CM in March (Table 3; p<0.05) .
The wet mass of the contents of the omasum in Svalbard reindeer increased from 0.5% of BM and 0.9% of CM in September to 0.8% of BM and 1.8% of CM in April (Tables 3&5; p<0.05).

In Norwegian reindeer the wet mass of the contents of the omasum represented 0.6% of BM and 1.3% of CM in September and 0.2% of BM and 0.4% of CM in March (Tables 3&5; p<0.05).

Table 5. Relative mean mass and surface area index of omasa in three feeding types of ruminants and in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and Norwegian reindeer (*Rangifer tarandus tarandus*). All data are from adult females.

	Concentrate selector* Roe deer		Intermediate type Reindeer				Grazer Cattle*** Bison**	
			Norway		Svalbard			
	Summer	Winter	Summer	Winter	Summer	Winter		
BM (kg)	26	25	66	60	69	46	250	400
Surface area index	25**	–	95	55	92	113	549**	212**
Omasum total wet mass % BM	0.1	0.2	0.6	0.2	0.5	0.8	1.1	2.8
Omasum contents dry mass % BM	0.02	0.04	0.1	0.04	0.06	0.08	0.2	0.5
Omasum:abomasum total weight mass ratio	0.15	–	1.2	0.4	1.4	1.5	–	13.8
Omasum contents wet mass RR contents wet mass (%)	1.7	2.2	3.4	1.5	3.4	4.0	–	12.9

* data from Holand & Staaland (1985); ** Surface area index is calculated from Werner (1990) and *** Reed (1983), BM: bodymass.

The wet mass of the contents of the omasum in non-lactating female Svalbard reindeer in NL represented 3.4% of the mass of the contents of the RR in September and 4.0% in April. In Norwegian reindeer the wet mass of the contents of the omasum represented 3.4% of the wet mass of the contents of the RR in September but only 1.5% in January (p<0.05) (Tables 1 & 3).

The ratio of total wet mass of the contents of the omasum and the abomasum was 1.4 in non-lactating female Svalbard reindeer in August but 1.5 in April. In Norwegian reindeer the omasum:abomasum ratio was 1.5 in September but only 0.4 in January (Table 5; p<0.05).

Omasum surface area and other linear measurements

The largest mean absorptive surface area of any of the omasa measured was 2514.4 cm2 in Svalbard reindeer from NA in August (Table 4); however, there were no significant differences within seasons in the mass or any of the linear measurements of the omasa in animals from the 2 locations investigated on Svalbard (Tables 1 & 4).

The mean absorptive surface area of the omasum in non-lactating female Svalbard reindeer showed only a small, non-significant decrease in winter, falling from 2300 cm^2 in September to 2023 cm^2 in April (Tables 4 & 5). In contrast, the mean absorptive surface area of the omasum of Norwegian reindeer decreased almost 50% over the same period from 2201 cm^2 in September to 1181 cm^2 in March (p<0.05, Tables 4 & 5).

There were no significant differences in the absorptive surface area, length:height ratio, curvature or the number of first, second and third order leaves and low crests along the omasal curvature of omasa in Svalbard and Norwegian reindeer in September (Table 4). By contrast, the mean length along the curvature of the oma-

sum in late winter was substantially greater in Svalbard reindeer (24.8 cm, 2.9 SD) than in Norwegian reindeer (17.8 cm, 1.9 SD; p<0.05; Table 4).

Reticulo-omasal orifice
The mean ROO diameter was significantly larger (p<0.05) in Svalbard reindeer compared to Norwegian reindeer in all seasons. The mean diameter of ROO was 74 mm (SD 10.5) in Svalbard reindeer in NL in September and 65.8 mm (SD 17.0) in April. The mean ROO diameter in Norwegian mainland animals varied from 40.0 mm (SD 3.5) in September to 47.7 mm (SD 3.2) in March.

Effect of reproductive status
There were no significant differences in any of the omasal parameters between lactating and non-lactating female Svalbard reindeer in September (Table 1,4).

Discussion
This study demonstrated a pronounced difference in the seasonal dynamics of the gross anatomy and the filling of the omasum in 2 sub-species of reindeer. These differences seem to reflect a major difference in the winter diet of the 2 sub-species, i.e. the inclusion of energy-rich lichen in the diet of Norwegian reindeer and the virtual absence of lichens, and an almost total reliance on fibrous vascular plants and mosses, in Svalbard reindeer (*Sørmo et al.* 1999, *Mathiesen et al.* 1999b, 2000b). In winter the omasum of Norwegian reindeer declined in the mass of its contents and tissue, and in its absorptive surface area. The omasum of Svalbard reindeer, by contrast, showed no major seasonal reduction either in filling, expressed as the wet mass of the contents of the organ, or in its absorptive surface area.

These differences reflect differences in the nutrition of these 2 sub-species of reindeer in win-

ter. Norwegian reindeer show high rates of ruminal production of volatile fatty acids and have relatively small rumens in winter, probably as a consequence of their eating a large proportion of lichens (*Mathiesen S.D. et al.* 2000a). Lichens, which are composed of fungi and algae, are chemically quite different from vascular plants. *Cladina stellaris,* a lichen commonly eaten by reindeer in winter, contains as much as 75% hemi-cellulose and lichen carbohydrates such as lichenin, no cellulose and very little protein (<3% of DM, *Person et al.* 1980). In contrast to most vascular plants, lichens of the genera *Cladina* and *Cetraria* remain highly digestible in reindeer in winter (*Jacobsen & Skjenneberg* 1975). Lichens are therefore a good source of metabolisable energy for reindeer and in Norwegian reindeer the ruminal absorptive surface area remained high in winter (*Mathiesen et al.* 2000b) probably owing to the stimulation of rumen microbial fermentation by the carbohydrates in the lichens. Perhaps not surprisingly, therefore, the mainland animals examined in the present study suffered no net decline in CM in winter (Table 1). The situation was quite different in Svalbard reindeer. In these, ruminal production of VFAs is low and their GIT fill and rumen fill are relatively large (Tables 1 & 4) reflecting a high intake of poorly digestible fibrous grasses and mosses (*Mathiesen et al.* 1984, *Sørmo et al.* 1997). Many of these animals mobilise a large proportion of their energy and protein reserves in winter (*Reimers et al.* 1982, *Tyler* 1987), resulting in a substantial decline in CM (Table 1).
The absorptive surface of the omasum remains large throughout winter in Svalbard reindeer, and the ratio of the mass of the omasal tissue to the total GIT tissue mass increased from summer to winter from 4.0% to 6.9%, reflecting the need to maintain absorptive function when the animals eat fibrous food. In contrast, in Norwegian reindeer the mass of omasal tissue de-

creased from 6.3% to 3.6% of total GIT tissue mass, respectively. The relatively large omasum in Svalbard reindeer presumably enhances the uptake of nutrients including the small quantity of VFAs produced in their rumens in winter (*Sørmo et al.* 1997). GR ruminants have large omasa. The organ is believed to have an important role in the processing of fibrous food, CS by contrast, have small omasa and rumens (Table 3; *Hofmann* 1985). In the muskoxen (*Ovibos moschatus*), an Arctic ruminant which lives in similar habitats as reindeer and is classified as GR (*Hofmann* 2000), the mass of omasal tissue was also relatively large in winter (12.2% of total GIT tissue; *Staaland & Thing* 1991) but was not as large as in domestic cattle (GR;16% of total GIT tissue; Tulloh 1966). In this respect reindeer are intermediate between ruminants of the GR and CS types, although in winter Svalbard reindeer tend to be more GR like than Norwegian reindeer. GR ruminants have large rumens (Table 3), long ruminal retention of plant particles, low rates of ruminal production of VFA and low ruminal VFA absorption as a result of reduced ruminal papillation. In such animals, the utilisation of plant fibre is enhanced by large omasal absorptive surface area which appears to be important for absorption of VFAs (*Hofmann* 1973, 1985, 1989).

We found no evidence of omasal hypertrophy in lactating females on Svalbard. The daily maintenance energy requirement of lactating reindeer in Alaska in summer was 457 $kJ/BM^{0.75}$ which was almost twice the value of 232 $kJ/BM^{0.75}$ in non-lactating females (*Chan-McLeod et al.* 1994). Lactating animals must therefore consume more digestible energy than non-lactating animals either by eating more or by selecting a more digestible diet. *Sørmo et al.* (1999) found that lactating females had a larger RR in autumn compared to non-lactating females. The absence of any omasal hypertrophy in lactating Svalbard reindeer in autumn indi-

cates that the omasum cannot be a specifically important site for the absorption of energy rich metabolites in these animals in summer.

Our value for the wet weight of the fill of the omasum of Svalbard reindeer in summer and winter (5.0 and 8.0 g/kg BM), though slightly larger than the value reported by *Staaland et al.* (1979) and *Staaland & White* (1991), is similar to the value from Norwegian reindeer in summer (5.8 g/kg BM). However, the omasal fill in Norwegian reindeer in winter was much less than in Svalbard reindeer in winter (Table 5). Both subspecies are intermediate in this respect between CS type ruminants (omasal fill = 0.9-1.8 g/kg BM) and GR type ruminants (omasal fill = 11-28 g/kg BM; Table 5), although the value in Norwegian reindeer in winter is close to the value for roe deer (Table 5; *Holand & Staaland* 1985). The omasal fill of reindeer was small compared to muskoxen in which omasal wet weight fill as large as 15.2 g/kg BM has been recorded in winter (*Staaland & Thing* 1991).

However, if the omasum functions primarily as an organ of absorption, the key parameter must be its tissue surface area rather than its mass. The mucosa of the omasum has a very large surface area owing to the presence of a large number of leaves attached to the dorsal wall. In late summer and early winter the total absorptive surface area of the omasum of reindeer ranged from 1867 to 2514 cm^2 (Table 5) which is larger than that found in moose, a large CS, in which the total absorptive surface area of the omasum was approximately 1820 cm^2 (*Hofmann & Nygren* 1992, *Werner* 1990). These values are small compared to cattle, a typical GR (absorptive area 42010 cm^2) but when converted into the surface area index (SAI), the values for both sub-species of reindeer (range 55-113 $cm^2/BM^{0.75}$, Table 5) are intermediate between the value for CS like the moose (SAI 26.6 $cm^2/BM^{0.75}$, *Werner* 1990) and the roe

deer (SAI 25.4 $cm^2/BM^{0.75}$, Table 5) and GR like cattle and bison (SAI 549 and 212 $cm^2/BM^{0.75}$, respectively; Table 5). The absorptive surface of the omasum is, therefore, relatively small in reindeer which is consistent with their classification as IM ruminants (*Hofmann* 1985).

Another possible function of the omasum is the enhancement of the transport of ingesta from the reticulum to the abomasum by aspiration or muscular pumping (*Sellers & Stevens* 1966). The larger size of the omasum and the larger diameter of the reticulo-omasal orifice of Svalbard reindeer compared to Norwegian reindeer in winter might, therefore, promote more rapid passage of digesta out of the RR. Small particles do seem to be more efficiently released from the rumen in Svalbard reindeer both in summer and in winter. The RR of Norwegian reindeer contained a very high (>90%) proportion of plant particles <1 mm in greatest length while in Svalbard reindeer the value was approximately only 70% (*Mathiesen et al.* 1999b, *Sørmo et al.* 1999). The flow of digesta from the rumen into the omasum, however, is mainly regulated by the relative density of the plant particles (*Lechner-Doll et al.* 1995) and we do not yet know the relationship between the size and density of particles from different species of plants in the RR of reindeer. The large DFC (10%-17% RR content) in Svalbard reindeer is similar in size to roe deer (Table 3) but larger than in Norwegian reindeer (8% of RR content) perhaps indicating more rapid escape of ingesta from the rumen and omasum to the abomasum in the former (*Sørmo et al.* 1999, *Mathiesen et al.* 1999b).

It is also conceivable that the omasum of IM ruminants like reindeer enhances the bypass of nutrients along the *canalis omasi* to the abomasum. *Meyer et al.* (1998) and *Rowell et al.* (1997) have provided strong evidence for the functional significance of the purported bypass of soluble metabolites. *Hofmann* (1985) suggested that some adult ruminants maintain the *sulcus ventriculi*, which is well developed for the bypass of nutrients directly into the abomasum throughout life but it remains to be shown whether the reticular groove functions in this manner in adult reindeer. Irrespective of this, our results show that the omasum is not conservative but is a seasonally dynamic and adaptable organ in the gastrointestinal tract of reindeer.

References
Aagnes TH, Mathiesen SD: Gross anatomy of the gastrointestinal tract in reindeer, free-living and fed baled timothy silage in summer and winter. Rangifer. 1996, *16*, 31-39.

Chan-McLeod ACA, White RG, Holleman D: Effect of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. Can. J. Zool, 1994, *72*, 938-947.

Glen AR: Under the Pole Star. Methuen, London 1937. 365 pp.

Hindrum R, Jordhøy P, Strand O, Tyler NJC: Svalbardrein: Et nøysomt liv på tundraen. (Svalbard reindeer: a thrifty life on the tundra). Villreinen 1995, 105-112.

Hofmann RR, Stewart DRM: Grazer or browser: A classification based on stomach structure and feeding habits of East African ruminants. Mammalia, Paris 1972, *36*, 226-240.

Hofmann RR: The ruminant stomach: Stomach structure and feeding habits of East African Game Ruminants. East African Monograph in Biology. Vol 2. Nairobi: East African Literature Bureau. 1973. 354 pp.

Hofmann RR: Digestive physiology of deer - Their morphophysiological specialization and adaptation. In: Fennessy, P. Drew, K. (eds): Biology of Deer Production. The Royal Society of New Zealand Bulletin 1985, *22*, 393-407.

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

Hofmann RR: Functional and comparative digestive system anatomy of Arctic ruminants. 2000. Rangifer. In press.

Hofmann RR, Nygren K: Morphophysiological specialization and adaptation of moose digestive system. Alces. 1992. Suppl. 1 pp 91-100.

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

Holand Ø, Staaland H: Nutritional Strategies and winter survival of European roe deer in Norway. In: Fennessy, P., Drew, K. (eds.): Biology of Deer Production. The Royal Society of New Zealand Bulletin 1985, *22*, 423-428.

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

Larsen TS, Nilsson NØ, Blix AS: Seasonal changes in lipogenesis and lipolysis in isolated adipocytes from Svalbard and Norwegian reindeer. Acta Physiologica Scandinavia 1985, *123*, 97-104.

Lechner-Doll M, Hume ID, Hofmann RR: Comparison of herbivory forage selection and digestion. In: M. Journet, Grenet, E., Farce, M-H., Theriez, M., Demarquilly, C. (eds): Recent developments in the Nutrition of herbivores. Proceeding of the 4th Intern. Symp. on the Nutrition of Herbivores, 1995, 231-248, INRA Editions, Paris.

Mathiesen SD, Orpin, CG, Blix AS: Rumen microbial adaptation to fibre digestion in Svalbard reindeer. Can. J. Anim. Sci. 1984, *64*, 261-262.

Mathiesen, SD, Rædergård, VB, Vader, MA, Haga, ØE, Norberg, HJ, Sørmo, W, & Tyler, NJC: Salivary glands in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and in Norwegian reindeer (*Rangifer t. tarandus*). Rangifer 1999a, *19*, 25-32.

Mathiesen SD, Sørmo W, Aagnes TH: Forage chemistry and the digestive system in reindeer (*Rangifer tarandus tarandus*) in northern Norway and on South Georgia. Rangifer.1999b, *19*, 91-101.

Mathiesen, SD, Sørmo, W, & Aagnes Utsi TH: Com-

parative aspects of volatile fatty acid production in reindeer (*Rangifer tarandus tarandus*) in northern Norway and on South Georgia. 2000a. Rangifer. In press.

Mathiesen SD, Haga, Ø.E., Kaino, T, & Tyler, NJC: Diet composition, rumen papillation and maintenance of carcass mass in Norwegian reindeer in winter. J. Zool. London 2000b, 250. In press.

Meyer HHD, Rowell A, Streich WJ, Stoffel B, Hofmann, RR: Accumulation of polyunsaturated fatty acids by concentrate selecting ruminants. Comp. Biochem. Physiol. A 1998, *120*, 263-268.

Person SJ, White RG, Luick JR: Determination of nutritive value of reindeer caribou range. *In:* Reimers E, Gaare E, Skjenneberg S (eds.): Proc. of the 2nd Inter. Reinder and Caribou Symposium. Direktoratet for vilt og ferskvannsfisk. Trondheim 1980, 224-239.

Reed JD: The nutritional ecology of game and cattle on a Kenyan ranch 1983. PhD thesis Cornell Univ. Ithaca, N.Y.

Reimers E, Ringberg T, Sørumgaard R: Body composition of Svalbard reindeer. Can. J. Zool. 1982, *60*, 1812-1821.

Rowell A, Dye J, Hofmann RR, Lechner-Doll M, Meyer HHD, Shirazi-Beechey SP, Wood IS: The expression of intestinal sodium-glucose cotransporter in cervids. Zschr. Saeugetierkunde 1997. Suppl. 2, *62*, 204-208.

Sellers AF, Stevens CE: Motor functions of the ruminant forestomach. Physiol. Rev. 1966, *46*, 634-661.

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

Staaland H, Punsvik, T: Reindeer grazing on Nord Austlandet, Svalbard.- In: E. Reimers, E. Gaare and S. Skjenneberg (eds.): Proc. 2nd. Int. Reindeer and Caribou Symposium. Direktoratet for vilt og ferskvansfiske, Trondheim 1980, 142-150.

Staaland H, Brattbakk I, Ekern H, Kildemo K: Chemical composition of forage plants in Svalbard and Norway. Holarctic Ecology. 1983, *6*, 109-122.

Staaland H: On the quality of Svalbard reindeer pasture in the summer and autumn. 1984. Rangifer. *4* (1) 16-23.

Staaland H, Thing H: Distribution of nutrients and minerals in the alimentary tract of muskoxen, *Ovibos moschatus*. Comp. Biochem. Physiol. 1991, *98A*, 543-549.

Staaland H, White RG: Influence of foraging ecology

on alimentary tract size and function of the Svalbard reindeer. Can.J. Zool. 1991, *69*,1326-1334.

Sørmo W, Haga ØE, White RG, Mathiesen SD: Comparative aspects of volatile fatty acids in the fermention chambers in Svalbard reindeer. Rangifer. 1997, *17*, 81-95.

Sørmo W, Haga ØE, Gaare. E, Langvatn R, Mathiesen SD: 1999. Plant dietary effect on the fermentation chambers in Svalbard reindeer. J. Zool., London. 1999, *247*, 247-256.

Tulloh NM: Physical studies on the alimentary tract of grazing cattle. New Zeal. J. Agric. Res. 1996, *9*, 999-1008.

Tyler NJC: Body composition and energy balance of pregnant and non-pregnant Svalbard reindeer during winter. Zool. Soc. London Symp. 1987, *57*, 203-229.

Tyler NJC, Fauchald P, Johansen O, Christiansen HR: Seasonal inappetence and weight loss in female reindeer in winter. Ecological Bull 1999, *14*, 105-116.

Tyler NJC, Øritsland NA: Why don't Svalbard reindeer migrate? Holarctic Ecology 1989, *12*, 369-376.

Werner A: Vergleichende morphometrische Untersuchungen am Blattermagen von Wiederkauern (RUMINANTIA) unterschiedlicher Ernahrungstypen. (Investigation of omasum from different ruminant feeding types). Vet Doctorate thesis, Justus-Liebig Universitat, Giessen, Germany, 1990.

White RG, Staaland H: Ruminal volatile fatty acid production as an indicator of forage quality in Svalbard reindeer.- Acta Zool. Fennic. 1983, *175*, 61-63.

Sammendrag

Bladmagens funksjonelle anatomi i Svalbardrein (Rangifer tarandus platyrhynchus) og fastlandsrein i Nord-Norge (Rangifer tarandus tarandus).

Bladmagens struktur og fyllingsgrad ble undersøkt i Svalbardrein som lever på den høy arktiske øygruppen Svalbard og i fastlandsrein fra Nord-Norge fra både sommer- og vinterbeite. Bladmagens gjennomsnittlig størrelse (mean) i ikke lakterende simler var 467 g (0.65 g pr 100g levende vekt) i september og 477g (1.03 g pr 100 g levende vekt) i april på Svalbard. I ikke lakterende simler på fastlandet veide bladmagen 534g (0.83 g pr 100 g levende vekt) i september, men bare 205 g (0.35 g pr 100 g levende vekt, p< 0.05) i mars. Både vevsmasse og innholdet i bladmagen var redusert i fastlandsreinen om vinteren. Gjennomsnittlig (mean) overflateareal av Svalbardreinens bladmager var 2300 cm^2 i september og 2023 cm^2 i april. I fastlandsreinen var overflatearealet av bladmagene 2201 cm^2 i september, men redusert til bare 1181 cm^2 i mars (p<0.05). Den reduserte bladmagen i fastlandsreinen skyldes antagelig inntak av høyt fordøyelige beiteplanter som reinlav på vinteren. Svalbardreinen trekker ikke mellom sesongbeiter, men overlever ved å spise fiberrike beiteplanter om vinteren. At Svalbardreinen opprettholder sine store bladmager om vinteren, kan reflektere disse dyrenes behov for å opprettholde en effektiv absorpsjon av næringsstoffer, som flyktige fettsyrer, når beiteplantene er av dårlig kvalitet.