Salivary glands in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and in Norwegian reindeer (*Rangifer tarandus tarandus*)

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Abstract: The aim of this investigation was to compare the size of salivary glands in Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and in Norwegian reindeer (*Rangifer t. tarandus*) in relation to feeding strategy, season and reproductive status. The mean body mass (BM, standard deviation s) in adult non-lactating female Svalbard reindeer was 72.0, s = 4.2, kg (n = 8) in September and 46.7, s = 7.1, kg (n = 4) in April. The mean BM of adult non-lactating Norwegian reindeer was 67.5, s = 7.7, kg (n = 8) in September and 59.2, s = 9.6, kg (n = 9) in March. In non-lactating female Svalbard reindeer the mean combined mass of parotid glands was 82.7, s = 4.5, g in September and 58.8, s = 8.7, g in April ($P < 0.05$). In the Norwegian reindeer the mean combined mass of the parotid glands was 95.2, s = 14.4, g in September and 68.1, s = 9.5, g in March ($P < 0.05$). We were not able to find any sub-species differences in the size of the salivary glands which could be related to phenotypic difference in feeding strategy. Both sub-species had parotid glands sizes similar to that of intermediate ruminant types, ranging from 0.11-0.14% of BM. The larger absolute size of salivary glands in summer compared to winter reflects the importance of high rates of production of saliva when the dry matter intake and microbial fermentation is high.

Key words: digestion, feeding strategy, seasonal variation.

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Introduction

The relative size of the salivary glands in different species of ruminants is closely associated with their feeding strategy and reflects a functional relationship between the mass of the glands and the composition of the diet (Kay *et al.,* 1980; Hofmann, 1985; 1989; Kay, 1987; 1989). Thus, the glands tend to be relatively small in grazers (GR), like sheep (*Ovis aries*), in which the parotid glands comprise only 0.07% of body mass (BM), and much larger in concentrate selectors (CS), like roe deer (*Capreolus capreolus*), in which the parotid glands comprise between 0.18 and 0.22% of BM (Kay, 1960; 1989; Hofmann, 1973; 1989). In addition to the importance for swallowing and rumination, ruminants produce saliva to supply alkali to buffer the ruminal microbial production of volatile fatty acids (VFA) and lactate and maintain the pH of the rumen close to 6.5. To achieve this, the four paired salivary glands (parotid, mandibular, sublingual and buccal glands) can produce as much as 16 litres of fluid per day in domestic sheep (Kay, 1958; 1960). The mandibular glands secrete mucus and hypotonic buffer (Kay, 1960; 1966). A secondary role of the parotid glands in concentrate selectors and intermediate feeders is to secrete tannin-binding proline rich protein in the saliva which makes these animals more tolerant to tannin in the diet compared to grazers like sheep (Robbins *et al.*, 1991). Concentrate selectors and some intermediate feeding types exhibit increased salivary secretion when offered tanniniferous feed, reflecting hypertrophy of the glands (Butler, 1989; van Soest, 1994). Several anatomical characteristics of the digestive system indicate that both Svalbard and Norwegian reindeer are intermediate ruminant feeding types (Aagnes & Mathiesen, 1996; Sørmo *et al.*, 1999) although the high arctic Svalbard reindeer bears some similarity to concentrate selectors, like high ruminal VFA production rates, short intestines and large distal fermentation chambers (White & Staaland, 1983; Staaland & White, 1991; Sørmo *et al.*, 1997; 1999; Mathiesen *et al.*, 1999a). We therefore predicted that Svalbard reindeer would have larger salivary glands than Norwegian reindeer at least in summer. According to Hofmann (1989) and Kay (1987; 1989) it is tempting to assume that parotid weight reflects daily saliva volume secreted and is influenced by food intake. We therefore predicted that the mass of these glands in reindeer would be influenced by the animals' reproductive status. Finally we predicted that the size of the salivary glands would fluctuate seasonally in both sub-species, reflecting changes in food intake and in the availability and quality of forage plants.

Material and methods

Study areas

Svalbard reindeer were collected in Sassendalen, a valley in Nordenskiöld Land (NL, 78°N), Svalbard (Fig. 1). Approximately 4000 reindeer live in NL (Tyler, 1987a) feeding on tundra vegetation dominated by different species of grasses, sedges, herbs and dwarf woody plants belonging to the genera *Poa, Deschampsia, Alopecurus, Luzula, Empetrum, Salix* and *Dryas*. Mosses make up a significant part of the plants found in the rumen of these animals in winter (Sørmo *et al.*, 1999). This part of Svalbard is cold and dry: the mean winter temperature at Longyearbyen is -14 °C, while mean temperature in July, the warmest month, is about 6 °C. The annual precipitation is 250 mm (climate data from the Norwegian Meteorological Office). Snow lies for up to ten months annually, but 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 in the snow through which the reindeer have difficulty in digging to reach the plants beneath. Consequently, in most years by late winter (March and April) the animals are restricted to feeding on exposed, windblown ridges where the aerial biomass of forage is low (Tyler, 1987a; b).

Norwegian reindeer were taken from a semi-domesticated herd in Finnmark, northern Norway (69°N). This herd, managed by Sami herders, migrates about 200 km between inland winter pastures and coastal summer pastures (Fig. 1). The animals feed on natural mountain pasture all year round, eating a wide variety of vascular plants, including sedges and grasses, e.g. *Carex* spp. and *Poa* spp, dwarf shrubs, e.g. *Loiseleuria procumbens* and *Empetrum* spp., birch and willows, *Betula nana* and *Salix* spp., and also including a significant amount of lichens in their diet in winter, e.g. *Cladina* spp., *Cetraria nivalis* and *Stereocaulon* spp. (Mathiesen *et al.*, 1999b). At the coast in summer, the weather is cool and wet, mean temperature for July being 10 °C, and precipitation exceeds 1000 mm annually. Inland winter range is cold and dry (mean temperature for February is -14 °C, while yearly precipitation is less than 400 mm (climate data from the Norwegian Meteorological Office). The cycles of thawing and re-freezing which create crusts of ice occur here much less frequently than at the coast.

Animals

Adult female Svalbard reindeer (age ≥ 2 years old based on the pattern of eruption of molariform teeth), were selected at random from groups grazing undisturbed, and killed by a single shot in the chest in October 1994 (n = 11), in April 1995 (n = 4) and in September 1996 (n = 13). Known age adult female Norwegian reindeer were killed in September 1995 (n = 8), November 1995 (n = 7), February 1996 (n = 6) and in March 1996 (n = 9). The animals were selected by hand after the entire herd had been gathered in a paddock, stunned in the traditional Sami manner, which involves the rapid insertion of a fine blade through the foramen magnum and into the cranium, and killed by bleeding by cutting the major vessels close to the heart. *Post mortem* examination of all reindeer was carried

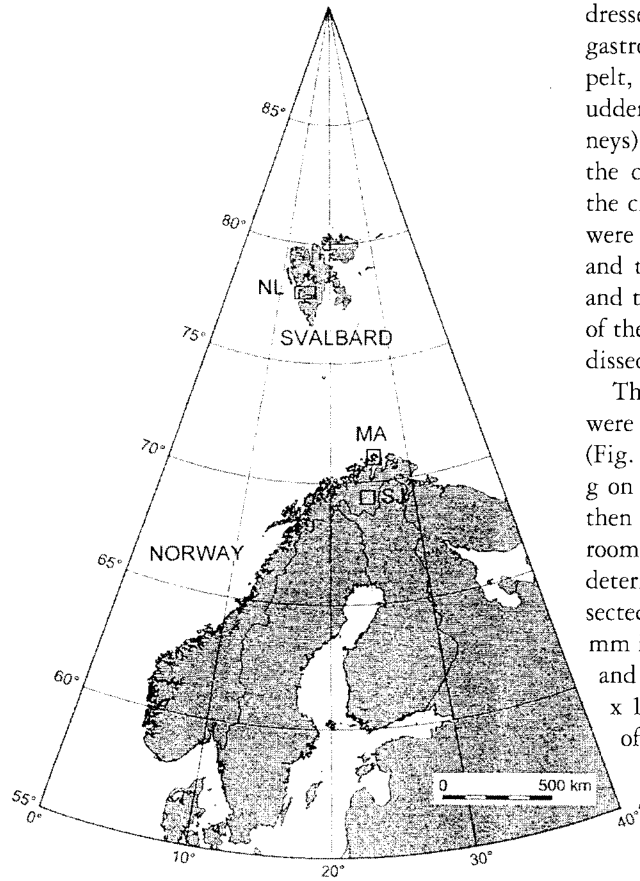


Fig. 1. The Svalbard reindeer were collected at Nordenskiöld Land (NL) in September, October and April. The Norwegian reindeer were collected at Magerøya (MA) in September and at Soussjavre (SJ) in November, January and March.

out in field laboratories starting within 45 minutes of death.

The total BM of Svalbard reindeer, less blood lost from the wound, was recorded to 1 kg using a Salter mechanical scale (1-100 kg). The live BM of the Norwegian reindeer was measured to 1 kg in a weighing crate equipped with an electronic digital scale. Once dead, the gastrointestinal tract was removed from each animal and the reticulo-rumen (RR) was weighed full to 1 g on an electronic balance after stripping off both the mesentery and the adhering adipose tissue. The wet mass of ingesta in the RR was calculated by subtraction after emptying the RR and re-weighing it, less contents, to 1 g. Hot carcass mass (CM) was measured by weighing the dressed carcass to 0.1 kg on a 150 kg steel yard immediately after the animal was skinned. (The dressed carcass is the whole animal less the entire gastrointestinal tract and its contents, the head, the pelt, the lower legs, the uterus and its contents, the udder and all the visceral organs including the kidneys). The head was removed by cutting between the cervical vertebrae approximately 20 cm from the cranium, to secure the salivary glands; the feet were removed by cutting between the distal carpus and the metacarpus and between the distal tarsus and the metatarsus. The weight of the short pieces of the neck was added to the slaughter weight after dissection of salivary glands.

The *Glandula parotis* and the *Gl. mandibularis* were carefully dissected out on right and left side (Fig. 2) and each pair of glands was weighed to 0.01 g on an electronic balance. The paired glands were then dried to constant weight at 115 °C, cooled to room temperature in a dessicator and re-weighed to determine dry mass (DM). The left femur was dissected out and its greatest length was measured to 1 mm in a bone box. Indices of the mass of *Gl. parotis* and *Gl. mandibularis* were calculated as $[(\text{g DM}/f^3) \times 10^6]$ where f^3 is the cube of the greatest length of the femur (cm) (Tyler, 1987a).

Statistical analyses

Results are given as mean and standard deviation (s) of the mean. Significance was tested by Students t-test. The null hypothesis was rejected at $P < 0.05$.

Results

Body mass

There was no significant difference in BM between non-lactating adult female Svalbard reindeer and Norwegian reindeer in September. In late winter, however, BM was significantly larger in Norwegian reindeer compared to the Svalbard reindeer ($P < 0.05$, Table 1). Non-lactating Svalbard reindeer (mean BM 72.0 kg) tended to be heavier in autumn than lactating animals (mean BM 66.6 kg) though the difference was not significant (Table 1). Both these groups, however, were heavier than Svalbard reindeer killed in late winter (April, mean BM 46.4 kg, $P < 0.05$, Table 1). Norwegian reindeer, likewise, tended to be heavier in September (mean BM 67.5 kg) than in March (mean BM 59.2 kg), but the difference was not significant (Table 1).

There was no significant difference in CM between Svalbard reindeer and Norwegian reindeer in September. In late winter, however, CM in the

Table 1. Mean (with standard deviation) body mass BM, carcass mass CM, reticulo-rumen RR wet mass in kg, femur length in cm and the absolute (g) and relative mass of salivary glands in adult female Svalbard reindeer (*Rangifer t. platyrhynchus*) and in Norwegian reindeer (*Rangifer t. tarandus*) in different seasons.

	SVALBARD					NORWEGIAN			
Months	SEPT		OCT		APR	SEPT	NOV	FEB	MAR
Status	NL	L	NL	L	NL	NL	NL	NL	NL
n	8	5	5	6	4	8	7	9	9
BM	72.0 (4.2)	66.6 (4.3)	68.3 (5.4)	62.5 (4.1)	46.4 (7.1)	67.5 (7.7)	61.5 (9.2)	60.5 (6.6)	59.2 (9.6)
CM	35.8 (2.8)	29.4 (1.8)	36.4 (1.1)	29.2 (3.2)	19.9 (2.7)	29.8 (3.9)	27.5 (1.2)	29.0 (3.4)	28.5 (5.0)
RR	8.9 (2.1)	11.2 (1.3)	9.8 (0.7)	12.0 (3.2)	9.3 (1.6)	10.9 (2.5)	11.4 (2.5)	8.08 (1.1)	8.4 (1.4)
Femur	21.8 (0.3)	21.6 (0.2)	22.1 (0.3)	21.6 (0.7)	21.9 (0.2)	25.5 (0.6)	26.0 (0.9)	25.7 (0.7)	25.0 (0.8)
Gl. parotis, g	82.7 (4.5)	94.5 (15.4)	62.7 (3.9)	70.5 (6.4)	58.8 (8.7)	95.2 (14.2)	80.2 (14.2)	74.9 (13.4)	68.1 (9.5)
index x10^{-6} g/cm^3	2.2 (0.2)	2.4 (0.2)	1.7 (0.1)	2.1 (0.3)	1.3 (0.1)	1.4 (0.7)	0.8 (0.4)	0.9 (0.1)	0.8 (0.1)
% BM	0.11 (0.01)	0.14 (0.02)	0.09 (0.01)	0.12 (0.01)	0.13 (0.02)	0.14 (0.02)	0.13 (0.01)	0.12 (0.01)	0.12 (0.05)
% CM	0.23 (0.02)	0.32 (0.02)	0.17 (0.01)	0.26 (0.03)	0.30 (0.06)	0.32 (0.04)	0.27 (0.02)	0.26 (0.03)	0.24 (0.03)
Gl. mandibularis g	34.5 (3.6)	42.3 (3.4)	28.8 (3.4)	29.7 (5.6)	26.3 (6.3)	48.0 (5.8)	35.5 (8.2)	32.3 (8.7)	30.3 (4.7)
index x10^{-6}g/cm^3	0.8 (0.1)	0.9 (0.1)	0.7 (0.1)	0.7 (0.1)	0.6. (0.1)	0.6 (0.1)	0.4 (0.1)	0.4 (0.1)	0.35 (0.1)
% BM	0.06 (0.01)	0.06 (0.01)	0.04 (0.01)	0.05 (0.01)	0.06 (0.02)	0.07 (0.01)	0.05 (0.01)	0.05 (0.01)	0.05 (0.01)
% CM	0.11 (0.01)	0.14 (0.05)	0.08 (0.01)	0.10 (0.02)	0.16 (0.03)	0.16 (0.02)	0.13 (0.03)	0.11 (0.02)	0.11 (0.02)

NL: non-lactating, L: lactating.

Norwegian reindeer was significantly greater compared to Svalbard reindeer ($P < 0.05$, Table 1). CM of non-lactating Svalbard reindeer (mean 35.8 kg) was significantly greater in autumn than in lactating animals (mean 29.4 kg, $P < 0.05$) and the CM of both groups was significantly greater compared to Svalbard reindeer collected in late winter (mean 19.9 kg, $P < 0.05$, Table 1). In the Norwegian reindeer, by contrast, there was no significant difference in CM between animals collected in September and in March (means 29.8 and 28.5 kg respectively, Table 1).

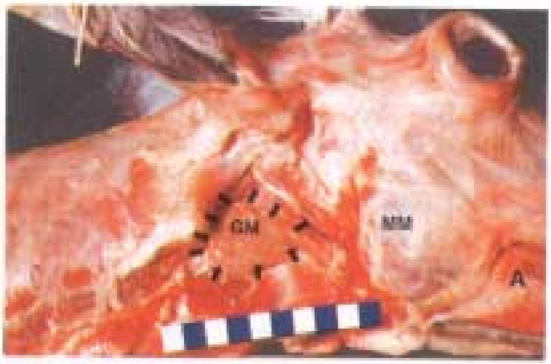
Reticulo-rumen content

Mean mass (wet weight) content of RR in Svalbard reindeer was 8.9 kg (12.3% of BM), compared to 10.9 kg (16.1% of BM) in Norwegian reindeer in September but the difference was not significant. In late winter, the mean mass (wet weight) of the contents of RR was 9.3 kg (20.0% of BM) in Svalbard reindeer compared to 8.4 kg (14.2% of BM) in the Norwegian reindeer (Table 1). The mass (wet weight) of the contents of the RR was not significantly greater in lactating Svalbard reindeer in September (mean 11.2 kg) compared to non-lactating Svalbard reindeer (mean 8.9 kg, Table 1). There was no significant difference in the absolute mass (wet weight) of RR contents between non-lactating Svalbard reindeer collected in September and in April (mean 9.3 kg, Table 1). In Norwegian reindeer the mean mass (wet weight) of rumen contents decreased from 10.9 kg in September to 8.4 kg in March but the difference was not significant (Table 1).

Table 2. The weight of right and left parotid glands (g) in relation to body mass (kg) or metabolic weight ($kg^{0.75}$) in roe deer (*Capreolus capreolus*), Svalbard reindeer (*R. t. platyrhynchus*), Norwegian reindeer (*R. t. tarandus*) and sheep (*Ovis aries*).

	CONCENTRATE SELECTOR	INTERMEDIATE FEEDERS				GRAZER
	Roe deer*	Svalbard reindeer		Norwegian reindeer		Sheep*
		Summer	Winter	Summer	Winter	
$g/kgBM^{0.75}$	4.7	4.1	3.3	4.1	3.2	1.3
g/kg BM	2.2	1.4	1.3	1.4	1.2	0.5

* Data from Kay (1987).



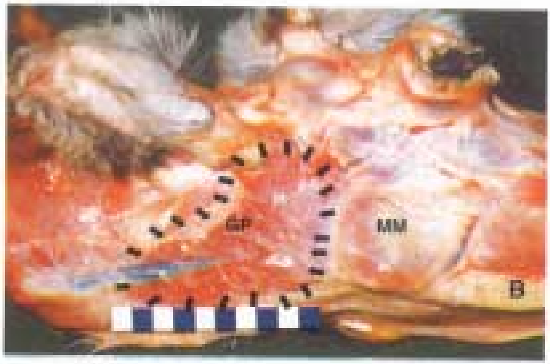


Fig. 2. The right side of the head of an adult female Svalbard reindeer shot in September showing the salivary glands, A: *Glandula mandibularis* (GM) and B: *Gl. parotis* (GP). Bar = 10 cm. The arrows indicate the borders of the two salivary glands. MM: *Musculus masseter*; J: *Vena jugularis externa.*

Salivary glands

Fig. 2. shows the position of the right salivary glands (*Gl. mandibularis* and *Gl. parotis*) in Svalbard reindeer in September. The parotid glands were heaviest, weighing 2.0 to 2.4 times more than the mandibular glands in Svalbard reindeer and 1.9 to 2.3 times more in the Norwegian reindeer (Table 1). The parotid glands were deeply embedded in the retromandibular fossa and were wrapped around the base of the ear. The mandibular glands were medial to the ventral part of the parotid. We found no significant difference between sub-species in the absolute or relative sizes of *Gl. parotis* in September or in late winter (April/March) (Table 1). The mean size of parotid glands ranged between 3.3-4.1 $g/BM^{0.75}$ in both sub-species. There was no significant difference in the absolute mass (wet weight) of *Gl. parotis* between lactating and non-lactating Svalbard reindeer in either September or in October although glands were heavier in September compared to October in both groups (Table 1). Mean mass of *Gl. parotis* relative to CM, however, was significantly ($P < 0.05$) larger in lactating compared non-lactating Svalbard reindeer in both September and October. In Svalbard reindeer both the mean mass ($P < 0.05$) and the DM index ($P < 0.05$) of glands were significantly greater in September (mean mass 82.7 g, mean index 2.2, $n = 8$) compared to April (mean mass 58.5 g, mean index 1.3, $n = 4$, Table 1). Likewise, in the Norwegian reindeer the mean absolute mass and the mean DM index of the parotid glands were significantly greater in September (mean mass 95.2 g, mean index 1.4) compared to March (mean mass 68.1 g, mean index 0.8; Table 1).

The mass (wet weight) of *Gl. mandibularis* was significantly greater in Norwegian reindeer compared to Svalbard reindeer in September ($P < 0.05$) but no sub-species difference was found in late winter (Table 2). There was no significant difference in the mass (wet weight) of *Gl. mandibularis* between lactating and non-lactating Svalbard reindeer in either September or in October although in both groups glands were larger in September compared to October ($P < 0.05$; Table 1). Likewise, the mean mass of *Gl. mandibularis* relative to CM was not significantly different between lactating and non-lactating Svalbard reindeer.

Both the mean mass ($P < 0.05$) and the DM index ($P < 0.05$) of glands were significantly greater in September (mean mass 34.5 g, mean index 0.8, $n = 8$) compared to April (mean mass 26.3 g, mean index 0.6, $n = 4$). In the Norwegian reindeer both the mass and the mean DM index of the mandibular glands were significantly heavier in September (mean mass 480 g, mean index 0.6, $n = 8$) compared to March (mean mass 30.3 g, mean index 0.3, $n = 9$) ($P < 0.05$).

Discussion.

Our hypothesis that Svalbard reindeer might have larger salivary glands than Norwegian reindeer, reflecting a more concentrate selector like feeding strategy in the former, was not supported. We found no difference in either the absolute or the relative mass of salivary glands between sub-species regardless of season (Table 1). The relative masses of the parotid glands and the mandibular glands of the two sub-species ranged between 0.09-0.14% and 0.04-0.07% of BM, respectively, indicating that both are intermediate feeding type ruminants according to Hofmann's (1985) classification (Tables 1 and 2). The classification of reindeer as an intermediate ruminant feeding type was also supported by data on the digestive anatomy and functions in the two sub-species investigated, including omasal structures and gastro- intestinal fill, although the Svalbard reindeer have several digestive adaptations found in ruminants of the concentrate selector type (Aagnes & Mathiesen, 1996; Sørmo *et al.,* 1999; Mathiesen *et al.*, 1999b).

The mass of the salivary glands and their secretion of buffer is not necessarily correlated with the mass or volume of the rumen, but rather with the quality of the diet eaten. In a cross-species comparison Kay (1987) predicted that the relative mass of the parotid gland might increase with the digestibility of the diet that is naturally consumed. Even so, the high ruminal need for buffer is not always a sufficient explanation of large salivary glands in concentrate selectors and intermediate feeders. These ruminant feeding types have a much more papillated rumen absorptive surface and, hence, very efficient absorption of VFAs across the rumen epithelium compared to grazers (Hofmann & Schnorr, 1982). In Norwegian reindeer calves the degree of rumen papillation was similar to that observed in concentrate selectors and decreased from summer to winter (Josefsen *et al.,* 1996). The rumen papillae in Svalbard reindeer remain to be investigated. Very rapid absorption of VFAs across the ruminal epithelium in Svalbard reindeer might explain why the salivary glands of this sub-species are no larger than in Norwegian reindeer despite the very high rate of production of VFAs in summer (White & Staaland, 1983). The use of salivary glands in the classification of feeding strategies in ruminants has therefore to be supplemented with other data.

Mean mass of salivary glands tended to be larger in lactating females than in non-lactating females (Table. 1). According to Hofmann (1989) and Kay (1958; 1960; 1989) it is tempting to assume that the weight of the parotid glands in domestic sheep reflects the rate of secretion of saliva and food intake. However, the rate of secretion has not been measured in wild ruminants. Presumably, however, the larger salivary glands of lactating Svalbard reindeer reflect higher food intake. Likewise, the mean mass of the RR contents tended to be greater in lactating Svalbard reindeer shot at the same time while foraging on the same vegetation, indicating greater food intake in these animals.

The fact that the mass of both the parotid and the mandibular glands was significantly greater in summer and autumn than in late winter in both sub-species lends further weight to our suggestion that the mass of the salivary glands is related to the level of food intake. Svalbard reindeer and Norwegian reindeer face a pronounced seasonal variation in appetite (Larsen *et al.,* 1985) and in seasonal changes in the availability of forage which influence both BM and body composition in these animals (Reimers *et al.,* 1982; Tyler, 1987a, b). We believe these factors also influence on the size and function of the salivary glands in reindeer.

The changes observed in the mass of the salivary glands may also reflect changes in the chemical composition in plants eaten in summer and winter. The quality changes of forage plants eaten are reflected in the chemical composition of RR contents in these animals. The crude protein concentration in the RR content was high in summer (34.4% DM), but very low in winter (15.1% DM) in Svalbard reindeer. Corresponding values for Norwegian reindeer are 28.0% in summer and 23% in winter (Staaland *et al.,* 1983, Sørmo *et al.,* 1999, Mathiesen *et al.*, 1999b). In moose, seasonal changes in the mass of salivary glands also reflect reduced forage quality and intake in winter. The parotid glands of moose atrophied from as much as 0.18% of BM in summer to 0.13% of BM in winter (Hofmann & Nygren, 1992). Further, specific chemical constituents in the diet of reindeer (Mathiesen *et al.*, 1998b; Sørmo *et al.*, 1999), like tannins, could also influence the mass of the salivary glands (Butler, 1989) but the tannin concentration in arctic plants eaten by reindeer remains to be investigated. Likewise, the forage fibre content is mainly responsible for reflex stimulation of the parotids from sensitive areas of the mouth, oesophagus and reticulorumen (Kay, 1989). According to Wilson (1963) the parotid glands in young lambs increased in response to the roughage content of their diet and not to the fermentability of the forage eaten. Recently, Chowdhury (1992) suggested a considerable regression of parotid glands of sheep after 7 weeks maintained on liquid gastric infusion without the mechanical stimulus of solid food consumption. In Svalbard reindeer ruminal lignin content increased from 18.2% organic dry matter (ODM) to 25.5% in winter, while the ruminal lignin content was about 15.0% ODM in Norwegian reindeer in both summer and winter (Sørmo *et al.*, 1999; Mathiesen *et al.*, 1999b). It is therefore unlikely that the plant fibre content but rather the level of food intake and forage digestibility are the reason for the seasonal changes in size of the salivary glands in the two subspecies observed.

Seasonally, therefore, the salivary glands in reindeer, vary in size, influenced by the quality and quantity of forage eaten. The large absolute size of salivary glands in summer compared to winter reflects their importance particularly in summer when rumen microbial fermentation is high.

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