Influence of diet on the morphology of the ruminal papillae in reindeer calves (*Rangifer tarandus tarandus* L.)

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Abstract: The influence of diet on the morphology of reindeer ruminal papillae was investigated in 4 groups of 3 free-ranging reindeer calves at different seasons, and in 11 groups of 3 reindeer calves fed experimental diets. Length, cross-sectional perimeter and density (number/cm^2) of the ruminal papillae were measured in 4 sample sites in the rumen wall, and the ruminal surface enlargement factor (SEF) was calculated at each sample site. The range of group means were 2.3 to 3.4 mm for overall papillary length (mean of the four sample sites), 2.2 to 3.5 mm for overall cross-sectional perimeter, 85 to 189 papillae/cm^2 for overall papillar density and 5.8 to 18.6 for overall SEF. Differences between sample sites wete observed, *atrium ruminis* having the highest and caudodorsal blind sac the lowest SEF (25% over and 24% below overall value, respectively). The differences between sample sites were considered to be small, indicating a homogenous ruminal content. The SEF of free-ranging animals showed a seasonal pattern, with high overall SEF (18.6) in September (late summer) and lower overall SEF (9.7) in April (late winter). Groups fed timothy silage with low content of cellulose (18.7% of dry matter) showed highest overall SEFs of the fed animals (17.8 and 13.9), while groups fed timothy silage with high content of cellulose (30.4% of dry matter) showed lowest overall SEFs (5.8 and 7.0), indicating low ability to ferment silage with high content of cellulose. The SEF in animals fed experimental diets seemed partly to be influenced by SEF at the beginning of the feeding period.

Key words: feeding, rumen, seasonal changes, surface enlargement factor.

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Introduction

The ruminal mucosa of all ruminant species is covered by papillae (Langer, 1973) that serve to enlarge the internal absorptive area of the organ. The size of the papillae is influenced by the diet (Hofmann & Schnorr, 1982), and the effect of diet is mediated through the concentrations of volatile fatty acids (VFA), especially butyrate, in rumen (Kauffold *et al.*, 1977; Sakata & Tamate, 1978; Sakata & Tamate, 1979; Gálfi *et al.*, 1991): High levels of VFA lead to larger papillae and increased absorptive surface area, low VFA concentrations lead to smaller papillae and reduced absorptive surface area. This simple relationship leaves the ruminal mucosa as an indirect measure of ruminal fermentation, and the size and density (number/cm^2) of the ruminal papillae have been used as an indicator of the quality and/or suitability of the diet, especially when comparing

artificial diets of zoo ruminants to free-living ruminants of the same species (Hofmann & Matern, 1988; Marholdt, 1991; Hofmann & Nygren, 1992), but also when evaluating the suitability of an habitat (Hofmann *et al* , 1988).

The size and density of ruminal papillae show variation between different regions in rumen, and this variation seems to reflect the extent of stratification of the ruminal content. Grass- and roughage eating ruminants have a stratified ruminal content, with the highest fermentative activity, and hence largest papillae in the mid layer (e.g. *atrium ruminis* and floor of the caudodorsal blind sac), and poor papillar development in ventral rumen (sedimentation layer) and dorsal rumen (gas dome) (Hofmann & Schnorr, 1982). Concentrate selecting ruminants have a homogenous ruminal content with only small differences in fermentation activity between regions, hence uniform papillae throughout the ruminal mucosa. Thus, the variation in papillar size and density between different regions of the ruminal mucosa serves as an indicator of the feeding strategy of the ruminant species (Hofmann & Stewart, 1972; Hofmann & Schnorr, 1982).

The two aspects of the ruminal mucosa: Within species an indicator of ruminal fermentation and hence diet, and between species, an indicator of feeding strategy, have been studied in a number of ruminant species (Hofmann, 1973; Hofmann *et al.*, 1976; Geiger *et al* , 1977; Hofmann, 1982; Hofmann, 1984; Stafford & Stafford, 1991; Agungpriyonon *et al.*, 1992; Hofmann & Nygren, 1992; Faurie & Perrin, 1995). The ruminal mucosa in reindeer has been investigated by Soveri & Nieminen (1995), who found that reindeer calves on a natural winter diet had an even and dense distribution of ruminal papillae, indicating a selective feeding strategy.

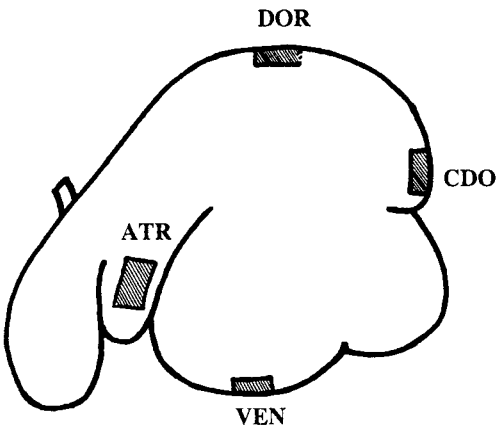

Fig. 1. Schematic drawing of the ruminoreticulum in reindeer, with sample sites indicated. ATR = *atrium ruminis,* VEN = ventral rumen, DOR = dorsal rumen, CDO = caudodorsal blind sac.

When a new series of feeding experiments with reindeer calves started in 1991 at Department of Arctic Biology, University of Tromsø, it was decided to include an investigation of the ruminal mucosa at the experimental diets. The idea was, besides providing general data on reindeer ruminal papillae, to see how specific diets influenced the papillar morphology. The present paper gives the results of this investigation.

Materials and methods

Animals and diets

The study included 15 groups of 3 reindeer calves each (Table 1), mean live weight 46 kg, SD = 4.6 kg (n = 42; Group 2 not weighed). The animals were provided by local reindeer herders around Tromsø (69°N,19°E). Groups 1-4 ("free-ranging animals") were slaughtered and sampled within short time after capturing, either in the field (Group 2) or after transport (3-4 hours) to laboratory facilities. The other 11 groups ("fed animals") were taken to the Department of Arctic Biology, University of Tromsø, and fed experimental diets as the only feed for 25-71 days (Table 1) before slaughtering. Calves within each group were given the same diet at the same time, the feeding period differing not more than 2 days (exceptions in Groups 7 and 15 as noted in Table 1). Groups fed experimental diets were taken from the same herd and at the same time as free-ranging animals, so that the free-ranging groups served as reference for the status of one or more groups of fed animals at the start of the feeding period (Table 1). Groups 13 and 15 lacked reference group. The fed animals (except Group 11) were kept indoors in metabolic cages. The ambient temperature was kept at 0-5°C, and the light was regulated to mimic natural photoperiod. Group 11 was kept in individual pens in a shed, exposed to natural temperature and light conditions. All groups were fed *ad libitum*, and received their diet once (Group 10 only) or twice a day. The chemical composition of the experimental diets is described by Aagnes & Mathiesen (1995), Olsen *et al.* (1995), Aagnes *et al.* (1996), Øksendal (1994) and Mathiesen, S. D. (unpubl. data), and is summarized in Table 2.

Table 1. Groups of reindeer calves used to study the influence of diet on the morphology of ruminal papillae. There were 3 calves in each group. All calves were males except 2 calves in Group 2. Age is calculated from the 20th of May (common birth time).

Group No.	Age (months)	Diet	Period of feeding (days)	Time of slaughter	Reference group (see text)
1	4	Free-ranging	-	Mid-September (late summer)	
2	5.5	Free-ranging	-	Beg. November (early winter)	
3	6	Free-ranging	-	End November (early winter)	
4	11	Free-ranging	-	Mid-April (late winter)	
5	8	Lichen (*Cladonia stellaris*)	47-49	Mid-January	3
6	5.5	Timothy silage (*Phleum pratense*), first cut	45-47	Beg. November	1
7	12.5 (12[2])	Timothy silage, first cut (same as Group 6)	45-46 (25[2])	Beg. June	4
8	5.5	Timothy silage, regrowth	45-47	Beg. November	1
9	12.5	Timothy silage, regrowth (same as Group 8)	45-47	Beg. June	4
10	12.5	Timothy silage, regrowth	48	Beg. June	4
11	8	Mixed grass silage[1], regrowth	47-48	Mid-January	2
12	8	Meadow fescue silage (*Festuca pratensis*), regrowth	47-49	Mid-January	3
13	6.5	Meadow grass silage (*Poa pratensis*), regrowth	61-62	Beg. December	-
14	8.5	RF-80 (pelleted feed, commercial)	70-71	Beg. February	3
15	7 (6[3])	Renfôr BAS (pelleted feed, commercial)	52 (30[3])	Mid-December	-

[1] Timothy (*Phleum pratense*), bent-grass (*Agrostis tenuis*) and poa species (*Poa* spp).

[2] One animal slaughtered after 25 days, due to animal welfare (low feed intake, large bulky rumen and a slightly lethargic appearance made us fear that the calf was starving to death).

[3] One animal slaughtered after 30 days because of total anorexia for the last 8 days, possibly associated with subclinical ruminal acidosis due to high feed intake in the beginning of the feeding period.

Sampling and measuring

Samples of the rumen wall, about 6x10 cm, were taken from 4 sites (Fig 1): *Atrium ruminis* (ATR), ventral rumen (VEN), dorsal rumen (DOR) and the caudodorsal blind sac (CDO). The samples were fixed in 10% formalin within one hour aftet the death of the animal. A rectangular subsample, 2.0 x 3.0 cm, was taken from the central area of the original sample. This subsample was used for measurements. The length of 20 papillae - 10 from the edge of each short side of the subsampled rectangle - was measured, using a dissecting microscope with eyepiece graticule. 1 cm^2 was cut out of the central area of the subsample and used for perimeter measurements. From the remaining 5 cm^2 all papillae were cut off with a scalpel, dispersed in water, and counted in a counting chamber.

The cm^2 for perimeter measurements was embedded in paraffin, and cross-sections, 8 μm thick, were made at the approximate middle of the papillae (Before paraffin embedding the approximate papillar length was measured, using a slide caliper). The sections were stained with hematoxylin-eosin, and the cross-sectional perimeter of at least 20 randomly chosen papillae was measured using a video-image analysing system (Quantimet 500, Leica Cambridge

Table 2. Chemical composition of the experimental diets fed to different groups of reindeer calves in this study (Gr. = Group No; see Table 1).

	Timothy silage[1] (Gr.6&7)	Timothy silage[1] (Gr.8&9)	Timothy silage[2] (Gr.10)	Mixed grass silage[3] (Gr.11)	Meadow fescue silage[4] (Gr.12)	Meadow grass silage[5] (Gr.13)	Lichen[4] (Gr.5)	RF-80[5] (Gr.14)	Renfôr BAS[5] (Gr.15)
Dry matter (%)	21.0	22.6	24.0	33.3	24.9	21.0	34.7	89.8	88.0
% of dry matter:									
Ash	7.0	7.8	6.3	6.6	9.2	10.0	1.2	7.9	7.6
Crude protein	12.3	14.3	12.0	14.8	13.1	20.8	2.7	15.5	12.3
True protein	6.3	8.1	7.8	7.1	7.1	8.9		13.3	10.6
Ether extract	3.8	4.7	4.7	4.4	4.0	5.2	3.1	7.2	
Cellulose	30.4	18.7	25.4	24.5	27.3	23.8	4.3	13.2	15.4
Hemicellulose	25.3	18.4	22.9	26.7	22.5	21.9	74.9	21.3	22.5
Lignin	2.1	1.6	2.5	2.6	1.6	1.4	3.2	2.8	2.8
WSC[6]	6.2	30.0	19.6	10.1	10.8	15.7	1.2	6.5	12.4
NH_3-N, % of total N	2.0	2.2	2.6	8.2	3.5	6.3			
Butyric acid	<0.05	<0.05	<0.04	<0.04	<0.05	<0.05			
pH	3.6	3.7	3.8	4.6	3.8	3.8			

[1] Data from Aagnes *et al.* (1996).
[2] Data from Olsen *et al.* (1995).
[3] Data from Aagnes & Mathiesen (1995).
[4] Data from Øksendal (1994).
[5] Data from Mathiesen, S. D. (unpublished).
[6] Water Soluble Carbohydrates

Table 3. Overall papillar length (mean of four sample sites), overall cross-sectional perimeter, overall papillar density (number/cm^2) and overall surface enlargement factor (SEF) in the ruminal mucosa of reindeer calves on different diets. Mean (SD) of groups (n=3).

Group No	Length (mm)	Perimeter (mm)	Number of papillae/cm^2	SEF
1	3.4 (0.25)	2.8 (0.28)	189 (16.2)	18.6 (1.77)
2	2.8 (0.21)	2.3 (0.24)	149 (22.7)	10.3 (0.61)
3	3.4 (0.07)	3.0 (0.28)	110 (18.1)	12.2 (2.07)
4	2.5 (0.28)	2.6 (0.03)	135 (22.5)	9.7 (0.57)
5	2.9 (0.31)	3.0 (0.44)	150 (27.0)	13.5 (1.40)
6	2.5 (0.35)	2.4 (0.17)	99 (15.6)	7.0 (2.20)
7	2.3 (0.10)	2.2 (0.35)	96 (4.8)	5.8 (0.70)
8	3.4 (0.30)	3.5 (0.29)	139 (13.0)	17.8 (0.62)
9	2.8 (0.19)	3.3 (0.11)	143 (16.7)	13.9 (1.40)
10	2.7 (0.15)	3.3 (0.17)	102 (14.0)	9.9 (1.37)
11	2.7 (0.10)	3.4 (0.15)	114 (15.0)	11.4 (1.30)
12	2.6 (0.24)	3.2 (0.20)	94 (4.1)	8.9 (0.99)
13	2.6 (0.08)	2.9 (0.12)	85 (10.7)	7.3 (0.41)
14	2.8 (0.20)	2.8 (0.06)	156 (13.7)	13.1 (1.66)
15	3.0 (0.37)	2.6 (0.14)	124 (18.2)	10.4 (0.99)

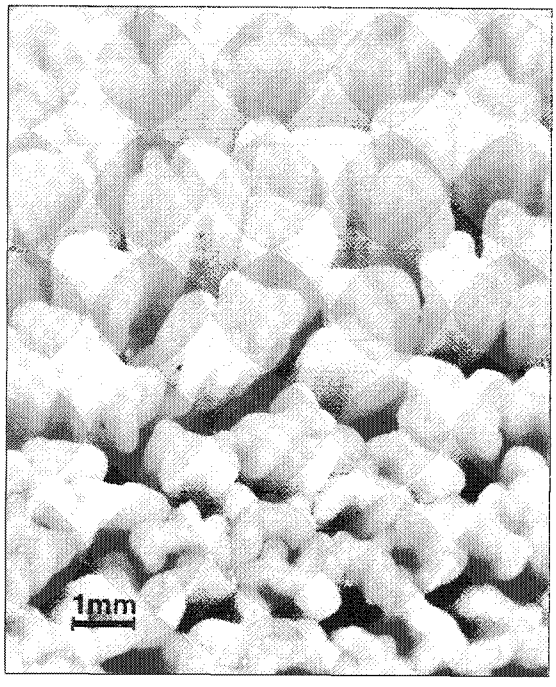

Fig. 2. Formalin fixed papillae from ventral rumen of an 8 month old male reindeer calf, showing the typical "cornered" morphology of the reindeer ruminal papillae. (Calf from Group 11, fed mixed grass silage as the only feed for 47 days before slaughtering).

Ltd., Cambridge, England). Papillae obviously cut on the bias were omitted.

Parameters

Mean papillar length, mean cross-sectional perimeter and the mean number of papillae/cm^2 ("the basic parameters") were used to calculate the surface enlargement factor (SEF) at each sample site, using the formula (length and perimeter in mm):

SEF =
(Length x perimeter x number/cm^2 + 100) /100

The SEF expresses how many times the surface is enlarged compared to a smooth, unpapillated surface.

The mean of the four sample sites, called the "overall" value, was calculated for each animal and parameter.

Statistics

Selected groups and sample sites were compared by unpaired two-tailed *t*-tests. Pearson's r was used to assess correlations between the basic parameters.

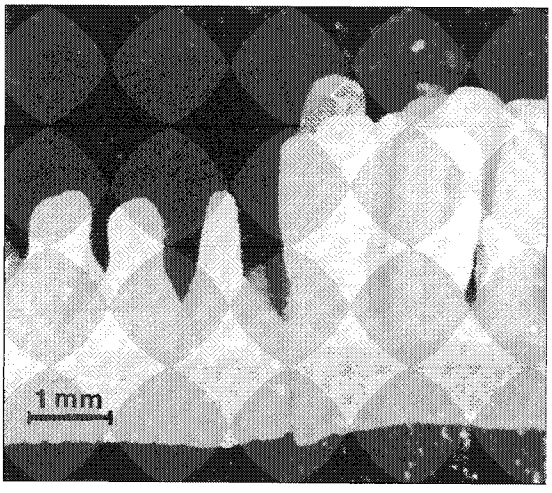

Fig. 3. Formalin fixed ruminal papillae from caudodorsal blind sac of two 5.5 months old male reindeer calves, fed timothy silage with high (Group 6, left) and low (Group 8, right) content of cellulose (30.4 and 18.7% of dry matter, respectively) as the only feed for 47 days before slaughtering. Note short papillae with coneshaped morphology to the left, compared to the typical, slightly clubshaped papillae to the right.

Multiple regression was used to assess the influence of the basic parameters on variation in SEF. Level of significance chosen was $P < 0.05$ in all tests.

Results

The ruminal mucosa of all animals was covered with the typical cornered papillae of reindeer (Fig. 2). Deviation in shape was seen only in CDO of 5 animals from Groups 6, 7 and 13, where short, coneshaped, atrophied papillae were observed (Fig. 3, left). Unpapillated areas were not observed outside the ruminal pillars.

Overall papillar length of the different groups ranged from 2.3 to 3.4 mm, overall cross-sectional perimeter ranged from 2.2 to 3.5 mm, while overall papillar density ranged from 85 to 189 papillae/cm^2 (Table 3). The variation in the basic parameters partly added up in the overall SEF, resulting in values ranging from 5.8 to 18.6 (Table 3). The highest SEF recorded in a single sample was 29.0 in ATR from an animal in Group 8. The mean SEF in ATR of this group was 28.3, which was the highest mean SEF recorded from a single sample site. The lowest SEF recorded in a single sample was 3.1 in CDO of an animal in Group 6. Mean SEF from CDO of this group was 4.3, which was the lowest mean SEF from a single sample site.

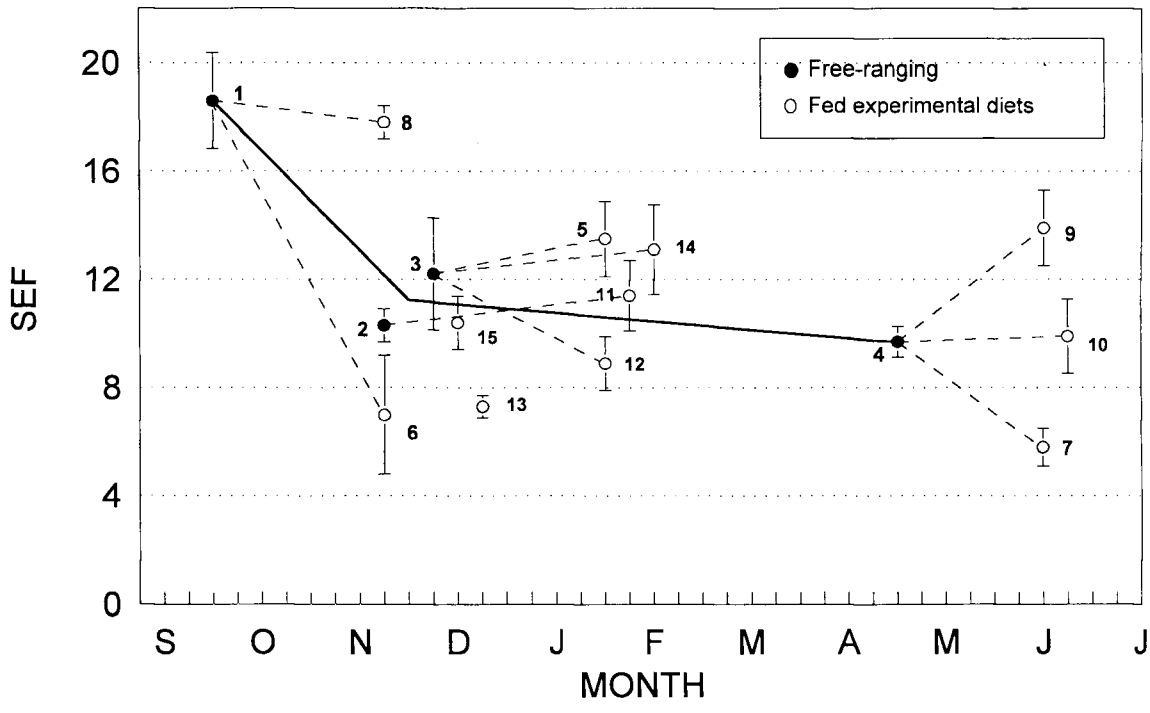

Fig. 4. Overall surface enlargement factor (SEF) (group mean and SD, $n=3$) in the ruminal mucosa of free-ranging and captive, experimentally fed reindeer calves. The solid line indicates the trend of SEF in free-ranging animals from September to April. Dashed lines show connections between free-ranging groups ("reference groups") and groups of experimentally fed animals, and indicate the trend in SEF change during the feeding period. Numbers refer to Group No (Table 1).

Free-ranging animals (Groups 1-4) showed highest overall SEF in September (late summer) and lowest in April (late winter) (Fig. 4). The reduction in SEF from September to November was larger than from November to April. The September animals (Group 1) showed the highest overall SEF of all groups.

Groups 8 and 9, fed regrowth timothy with 18.7% cellulose and 30% water soluble carbohydrates, showed the highest overall SEFs among fed animals (17.8 and 13.9, respectively), while Groups 6 and 7, fed first cut timothy with 30.4% cellulose and 6.2% water soluble carbohydrates, showed the lowest overall SEFs (7.0 and 5.8, respectively) (Fig. 4). Low overall SEFs (< 9) were also found in Group 12, fed meadow fescue silage with 27.3% cellulose, and Group 13, fed meadow grass silage with 23.8% cellulose.

ATR had the longest papillae and the highest papillar density, resulting in the largest SEF, 25% higher than overall SEF, even if the smallest papillar perimeter was also found at this site (Fig. 5). DOR had the lowest density of papillae, but SEF at this site still was at about the same level as in VEN, due to the long papillae in DOR (nearly as long as in ATR, difference not statistically significant). CDO had the shortest papillae, with relatively low papillar density and short perimeter, resulting in the lowest SEF, 24% below overall SEF (Fig. 5).

The relative proportions of the parameters between sample sites remained relatively constant through different overall SEFs. The only marked difference was found for high overall SEFs (from approx. 15 and upwards), where SEF in ATR seemed to increase more than SEF at other sample sites. This increase was due to a larger increase in cross-sectional perimeter and partially also in papillar density in ATR relative to the other sample sites.

Papillar length and number of papillae per cm² had largest influence on SEF, and these two parameters together accounted for 76–84% of the variation in SEF. The influence of perimeter was lower, and showed variation between sample sites, being highest in ATR and lowest in DOR.

Length and perimeter showed significant positive correlation in ATR and CDO ($r=0.59$ and 0.39,

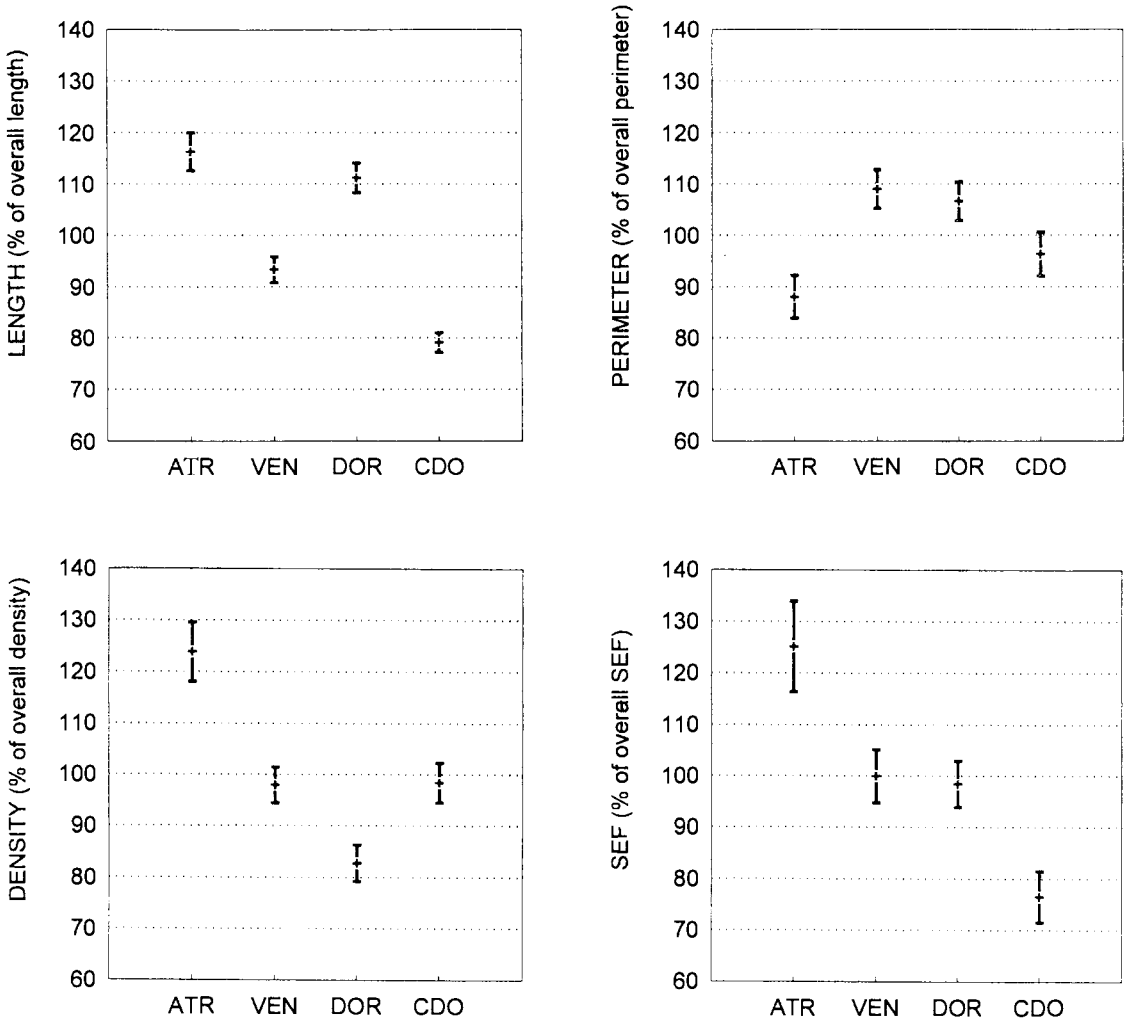

Fig. 5. Relative proportions between ruminal sample sites for papillar length, cross-sectional perimeter, papillar density (number/cm^2) and ruminal surface enlargement factor (SEF) in 45 reindeer calves on different diets. Each sample site is expressed as percentage of the mean of all four sample sires (the "overall" value). Figure shows mean percentage for each sample site (n = 45) and 95% confidence limits of the mean. ATR = *atrium ruminis*, VEN = ventral rumen, DOR = dorsal rumen, CDO = caudodorsal blind sac.

respectively), but not in VEN and DOR. Length and density showed positive correlation, but significant only in DOR (r=0.40). No significant correlation was found between perimeter and papillar density.

Discussion

The ruminal mucosa of reindeer seems to be characterized by an even distribution of a high number of small papillae that show high degree of uniformity throughout the ruminal surface. Differences between sample sites are distinct, but relatively small (Fig. 5). Similar size, density and uniform distribution of ruminal papillae are reported in small concentrate selecting African antelopes like Günther's dik-dik (*Madoqua guentheri*), Kirk's dik-dik (*Madoqua kirki*) and grey duiker (*Sylvicapra grimmia*) (Hofmann, 1969; Hofmann, 1973), and in roe deer (*Capreolus capreolus*) (Hofmann *et al.*, 1976; Müller, 1990). The density of papillae observed in this study (85–189) is compatible with the results of Soveri & Nieminen (1995), who found 98–113 papillae/cm^2 in reindeer calves on natural winter diet. These papillar densities are in part very high compared to other ruminants. Overall papillar density in the small African antelopes is about 80-100 (Hofmann, 1973), in roe deer 74 (SD = 16, n = 58) (Müller, 1990). The very high density of papillae in

this study may be explained by the young age of the animals. In a random material of young animals (6–12 months) from different species of African ruminants Hofmann (1969; 1973) observed higher density of papillae (often up to 100%), but smaller size of each papillae, compared to adult animals. Berg *et al.* (1986) did the same observation on the ruminal papillae of 4–5 month old pygmy goats when compared to adult animals, though the difference was smaller.

Irrespective of group ATR tended to have the highest SEF (Fig. 5), indicating this area to be the main site of absorption in reindeer, as in all other ruminants studied so far (Hofmann & Schnorr, 1982). The difference between ATR and other sample sites increased when overall SEF was high, as also seen in moose (Hofmann & Nygren, 1992). The relatively high SEF in DOR and VEN of reindeer calves agrees with earlier results (Soveri & Nieminen, 1995), and seems to be a unique feature of the reindeer ruminal mucosa. In most ruminants DOR and VEN have shorter papillae and lower SEF than CDO. Long papillae in DOR and short in CDO is also found in roe deer (Hofmann *et al*, 1976; Müller, 1990), but in this species the SEF in CDO still is larger than in DOR and VEN, due to high density of papillae in CDO. The large degree of uniformity of reindeer ruminal papillae, with high SEF in DOR and VEN, suggests a homogenous ruminal content, without the stratification seen in grass- and roughage eating ruminants like domestic cattle and sheep.

The "cornered" morphology of reindeer ruminal papillae (Fig. 2) is reported by several authors (Sablina, 1960; Langer, 1973; Westerling, 1975; Soveri & Nieminen, 1995), and seems to be unique to reindeer. The "corners" may serve to increase the absorptive surface of the papillae, but still, the absorptive area of each papilla is not particularly large. The overall cross-sectional perimeter found in this study (2.2–3.5 mm) corresponds to 1.1–1.8 mm width of a conventional tongueshaped papilla, and the significans of the "cornered" morphology is unknown.

The SEF measurements in free-tanging reindeer calves indicate a fast reduction in SEF in the autumn (from September to November), followed by a continued, but slow decrease through the winter (from November to April). A similar pattern of seasonal changes in SEF is reported in moose (*Alces alces*) (Hofmann & Nygren, 1992) and chamois (*Rupicapra rupicapra*) (Hofmann, 1984), and can be explained by the seasonal variation in feed quality and availability.

The ruminal SEF in animals fed experimental diets demonstrates that an *ad libitum* diet not necessarily results in higher SEF than the naturally selected, often sparse, winter diet of reindeer. The quality of the experimental diets seems to be crucial: Diets low in cellulose and rich in soluble carbohydrates (especially Groups 5, 8, 9 and 14) seemed to fulfil the demands of the reindeer, and gave ruminal SEFs only slight to moderate below September pasture. Silage diets rich in cellulose (especially Groups 6 and 7) gave a substantial reduction in ruminal SEF. The animals in these groups were characterized by large, bulky rumens and reduced muscle and fat indices (Aagnes & Mathiesen, 1996). These results indicate that reindeer have limited ability to utilize roughage rich in cellulose.

Groups 8 and 9 were given the same diet, but mean overall SEF in Group 8 still was significantly highet than in Group 9 (17.8 versus 13.9, $P < 0.05$). This difference in SEF was due to the size of the papillae, as papillar density was the same in both groups (Table 3). The difference seems to depend on SEF when feeding was started. Group 8, taken from September pasture, would be expected to have a SEF at the same level as Group 1 (18.6) at the start of the feeding, and this SEF is more or less maintained through the feeding period. Group 9, taken from winter mountain pastures in April, would be expected to have SEF at the same level as Group 4 (9.7) at the start of the feeding, and even though this SEF is increased by 43% during the feeding period, it still does not reach the SEF of Group 8. One explanation could be that the feeding period (6-7 weeks) was too short for the papillae to grow out. However, other authors report that mucosal adaptation takes place within 4-6 weeks (Hofmann & Schnorr, 1982; Dirksen, 1985). Another explanation might then be that the concentrations of VFA necessary to maintain ruminal SEF at a certain level are lower than the VFA concentrations required to stimulate growth of papillae up to the same level.

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