RUMINAL MUCOSA AS INDICATOR OF NUTRITIONAL STATUS IN WILD AND CAPTIVE MOOSE

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ABSTRACT: Ruminal mucosa samples were collected at four homologue sites from two subadult and 23 adult wild moose (booth sexes) belonging to one Swedish and two Finnish populations, and compared with samples from 7 moose kept in Zoos or Zoo Parks. Rumen papillary numbers were counted and measured and the absorptive mucosal surface enlargement factors (SEF) calculated. The four standardized sample sites (1-4) are reflecting sites of intensive (2,3) and reduced (1,4) VFA concentration. Wild moose were shot between 6 June and 3 March. The overall average SEF was 10.64 (SD 3.85), the summer average SEF was 17.02 (SD 3.37), the autumn average SEF was 10.31 (SD 3.44) and the winter average SEF 8.76 (SD 1.38); max. at 21.28, min. at 6.16. Surface reduction from summer to autumn was c. 50%! Average papillary number / 100 mm2 of all animals in all seasons was 40.7 (SD 9.2); summer: 50.4 (SD 7.4), autumn : 44.5 (SD 6.5), winter : 34.7 (SD 6.5); maximal number reduction was 31%. Average overall papillary length was 6.63 mm (SD 1.1); summer 8.01 mm (SD 0.9), autumn 6.19 mm (SD 0.9), winter 6.51 mm (SD 1.0); length reduction amounted to 25%. All differences were statistically highly significant, reduction / increase were cyclic. Moose have in summer c. 250% absorptive surface (enlarged 17 x) of grazing cattle (7 x).

In captive moose, overall average SEF was only 4.01, i.e. 31% of wild moose (49% of winter average); average papillary number was 30.5 (regionally destroyed by acidosis), average papillary length was 4.14 mm. Captive moose lack selectivity, diversity of forage plants and accordingly balanced VFA stimulation of mucosal blood flow. They usually suffer from acidosis, due to wrong feeding.

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It has been established in both domestic and wild ruminants by numerous morphological and physiological studies over the last fifty years that the ruminal mucosa is the main site of absorption of bacterial fermentation products, in the first place volatile fatty acids (VFA). It was first established in domestic ruminants (Schnorr and Vollmerhaus 1967) and subsequently in 29 East African species (Hofmann 1973) that different ways of feeding or of food selection are the cause of differences and changes in the mucosal surface enlargment.

After testing seven rumen wall samples (Hofmann 1973) and then collecting samples from only five sites in two cervid species (Hofmann *et al.* 1976), it was found sufficiently representative to collect rumen wall samples from only four homologue sites. The method was standardized and finally tested in Rupicapra rupicapra, Capreolus capreolus and Cervus nippon (Hofmann *et al.* 1982). Comparisons were made with test material from nomadic East African goats and Somali blackhead sheep (Hofmann *et al.* 1987), free ranging Chinese water deer, Hydropotes inermis (Hofmann *et al.* 1988). Wild and captive giraffes were compared, using this method (Hofmann and Matern 1988) which showed extreme differences.

All this provided sufficient evidence for mucosal changes being closely related to seasonal changes in forage quality and availability. The moose in its northern environment with pronounced seasonal changes was expected to show comparable signs of rumen mucosal adaptations which had not yet been studied in detail. Captive moose, on the other hand, were known for a long time to be difficult in their nutritional maintenance.

In order to establish the assumed seasonality of the ruminal mucosa, its changes

both in wild and captive moose, and to compare moose with ruminants of the same and other feeding types, we investigated the material collected over several years in Sweden and Finland.

METHODS

We collected rumen wall samples from four homologue sites (Fig.1). Two came from the central stratum of the rumen exposed to high concentrations of volatile fatty acids (VFA), i.e. the left lower wall of the atrium ruminis (region 2) and the left lower wall of the dorsal blindsac (region 3). These are main absorptive sites, well vascularised. Two samples came from the extreme strata receiving lower concentrations of VFA, i.e. the central dorsal wall of the dorsal ruminal sac (region 1) and the central ventral wall of the ventral ruminal sac (region 4).

Samples cut out were appr. 6 x 4 cm, marked for identification by cutting off 1 to 4 corners as shown (either after formalin fixation - 4 % formaldehyde solution, i.e. dilution 1 : 9 - of the entire stomach via oesophagus plus total immersion, or formalin fixation of the samples only, after cooling off, to prevent post mortal contractions). At least two random sub-samples were later on stencilled out (using a scalpel) for counting and measuring the rumen papillae, each subsample 10 x 10 mm (1 cm^2).

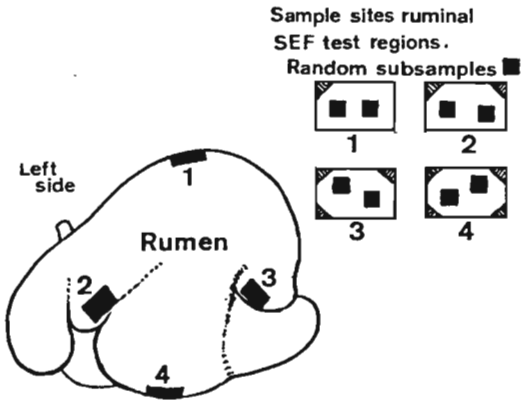

Fig.1. Moose stomach showing the standardized test regions 1-4. Each sample marked by cutting off corners according to site. Subsamples for counting papillary number, measuring papillary length and width and calculating SEF were cut out randomly.

Papillae were cut off for counting and measuring on a glass plate, using a magnifying glass. Papillary height was measured irrespective of shape and papillary width was measured at half level of maximal length.

The surface enlargment factor (SEF) is taking into account the papillary microstructure: each flat papilla has two absorptive surfaces with their own vascular pattern. Calculations were based on the formula:

$$SEF = \frac{2 \times \text{pap.surface (length x width)} \times \text{pap.no.} + \text{base surf.}}{\text{Base surf.}}$$

Results of the sub-samples were averaged and entered in a table containing the variables as shown on Fig. 2-5. The following table shows the results of the two-factorial variance analysis with repeated measurements related to the four ruminal regions (standard test sites, Hofmann *et al.* 1982) as tested in 25 wild moose:

Parameter (regions 1-4 aver.)	Main effects: Season	Region	Interrelationship
SEF	$p < 0.001$	$p < 0.001$	$p < 0.01$ (regional differences seasonally maintained)
Papillary number	$p < 0.01$	$p < 0.001$	n.s.
Papillary length	$p < 0.05$	$p < 0.001$	n.s.
Papillary width	n.s.	$p < 0.05$	n.s

RESULTS

A. Wild Moose

A total of 25 wild moose (Table 1) were grouped into three samples according to season: group 1 (summer) was sampled between 8 June and 6 September; group 2 (autumn/rut) sampled between 20 September and 21 October; group 3 (winter) sampled between 1

Table 1. Wild Animals Investigated

No	Origin	Sex	Age	Weight	Date sampled	Remarks
1	SF	f	4-5	190	8 June 87	spec.lic.
2	SF	f	3	203	3 July 87	" "
3	SF	m	4-5	312	3 August 87	" "
4	SF	m	2-3	232	6 September 87	" "
5	S	f	6-7	192	10 September 83	rut
6	SF	f	4-5	230	1 October 89	"
7	SF	m	5-6	330	1 October 89	"
8	SF	m	3,5	275	3 October 89	"
9	SF	f	3-4	210	3 October 89	"
10	SF	m	4-5	352	15 October 88	postrut
11	S	f	3-4	173	11 October 76	"
12	S	m	4-5	214	11 October 76	"
13	SF	m	5-6	338	21 October 87	"
14	SF	m	3-4	319	1 November 87	spec.lic.
15	SF	f	5-6	232	14 November 89	" "
16	SF	f	4-5	207	17 November 87	" "
17	SF	f	8-9	198	22 November 87	" "
18	SF	f	2-3	193	29 November 87	" "
19	SF	f	4,5	280	17 January 88	" "
20	SF	m	2,5	308	17 January 88	" "
21	SF	f	2,5	238	17 January 88	" "
22	SF	f	6,5	288	17 January 88	" "
23	SF	f	4,5	c.310	16 Feb.87	traffic acc.
24	SF	m	5,5	c.370	17 February 90	bear kill
25	SF	f	5,5	335	7 March 88	spec.lic.

November and 7 March.

The overall average SEF of all 25 animals from all four rumen site regions was 10.64 (SD 3.85; min. 6.16, max. 21.28)(Fig. 2).

The summer average SEF was 17.02 (SD 3.37; min. 13.02; max. 21.28) The autumn average was 10.31 (SD 3.44; min 6.16; max. 16.79). The winter average SEF was 8.76 (SD 1.38; min. 6.24; max. 11.54).

The differences between the seasons were highly significant, so were the differences between each of the four region samples and all samples in relation to the season (see table, in Methods).

The greatest absorptive surface reduction occured between summer and autumn; the overall reduction from summer to winter amounts to almost 50%!

In all groups, region 2 (atrium ruminis) showed the highest SEF, especially pronounced in summer, followed by region 3 (bottom of dorsal blindsac); lowest values were recorded in region 4 (floor/ventral ruminal wall), followed by region 1 (roof/ dorsal ruminal wall).

Main factor for the reduction of the surface enlargment between summer and autumn, more so (due to continued reduction) between summer and winter, is the number of ruminal papillae per cm^2 (Fig.3). This reduction is highly significant.

Average number of papillae per square cm in all regions of all 25 animals over all seasons was 40.7 (SD 9.2; min. 27.8; max. 57.8). Average number in summer was 50.4 (SD 7.4; min. 44; max. 57.3); in autumn 44.5

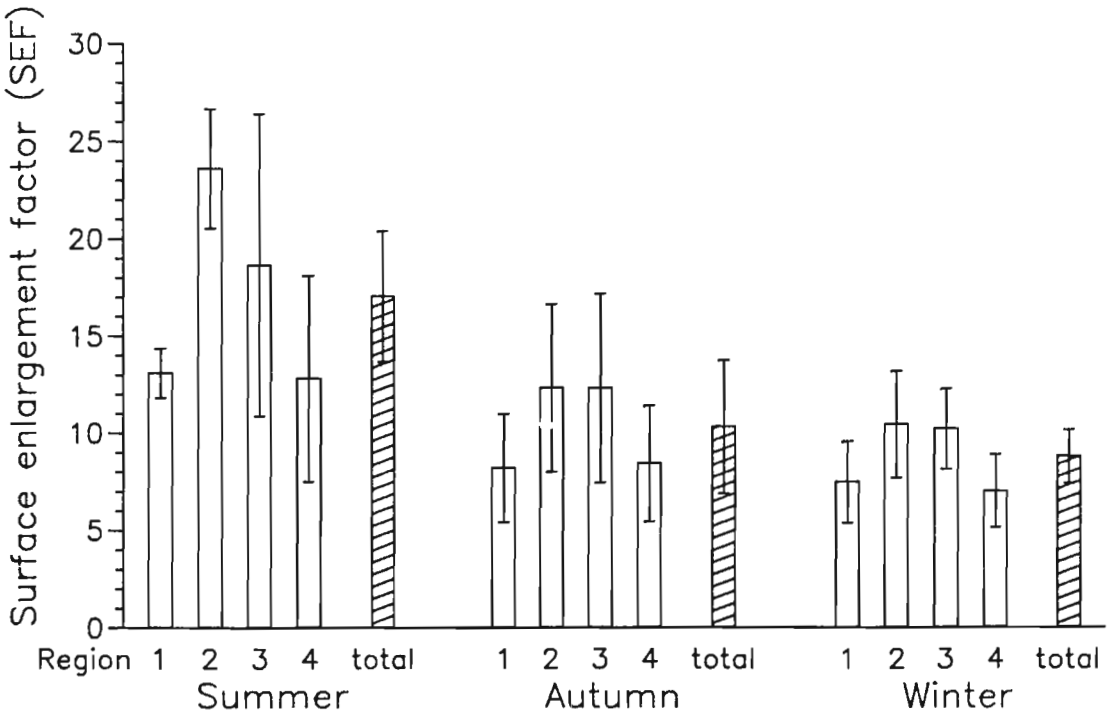

Fig. 2. Surface enlargement of the ruminal mucosa of 25 wild moose as calculated from four standardized test regions and sampled during three defined seasons.

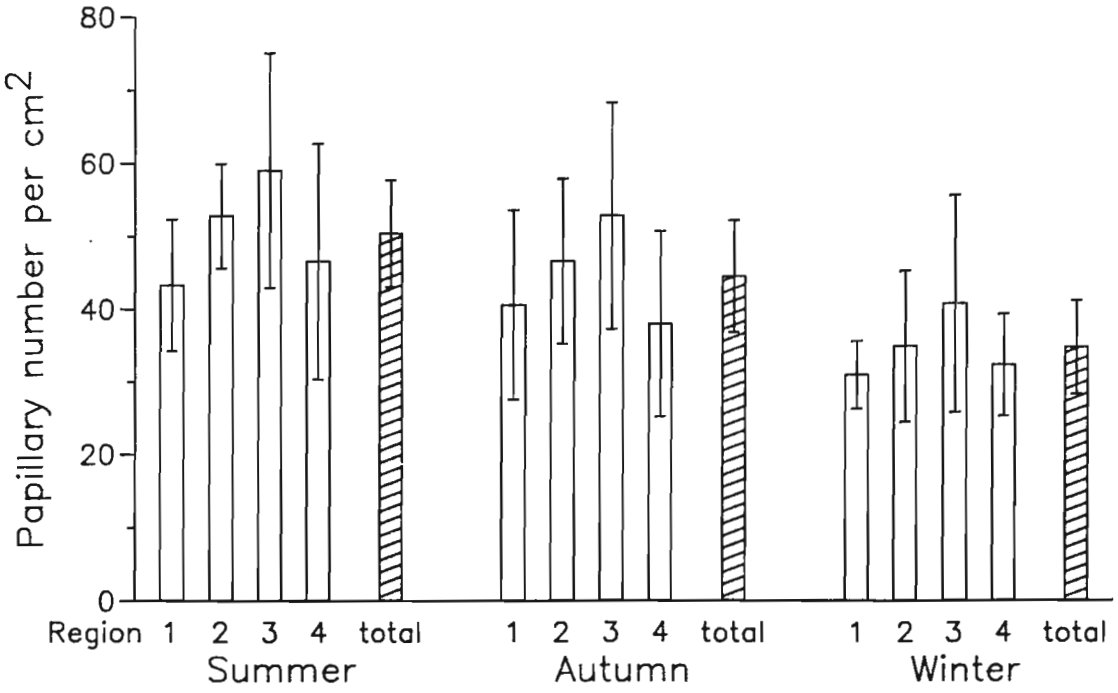

Fig. 3. Papillary number per cm2 in samples from four standardized moose rumen wall test regions grouped according to defined seasons.

(SD 7.7; min, 32,3; max.57,8); in winter 34.7 (SD 6.5; min. 27.8; max.46.5). Papillary reduction from summer to winter was 31%. Highest number of papillae, irrespective of season, was in region 3. The papillary number differs significantly between all four regions and all three seasonal periods.

The second surface reduction factor is papillary length (Fig.4). It was most pronounced between summer and autumn. Average papillary length in all 25 animals over all regions and over all seasons was 6.63 mm (SD 1.1; min. 4.9; max 9.1).

Average length in summer was 8.01 mm (SD 0.9; min. 7.0; max. 9.1); in autumn 6.19 mm (SD 0.9; min. 5.2; max.7.9); in winter 6.51 mm (SD 1.0; min 4.9; max 8.8). Length reduction from summer to autumn was 23 % (highly significant).

Less variation was observed in papillary width (Fig.5). Average papillary width in all 25 animals over all regions and seasons was 1.77 mm (SD 0.27); summer width: 2.03 mm, autumn: 1.64 mm; winter 1.75 mm. The widest papillae were found in region 2.

B. Captive Moose

A total of 7 captive moose were grouped into one sample due to their heterogenic origin (Kronberg Zoo/FRG 1, Whipsnade Zoo Park/GB 3, Saarbrücken Zoo/FRG 3) collected between 1984 and 1989.

The overall average SEF of all seven captive animals from all four regions was 4.01 (range 2.82 - 4.92); this is 38% of the overall average SEF as derived from 25 wild moose (10.64 x) and not more than 49% of the winter average (8.76 x) of wild moose. Highest single SEF value (region 2, Saarbr. I/89) was 8.63 x, as compared to 27.19 x (region 2, PK 159/87, shot 6 June).

Overall average papillary number was 30.5 as compared with 40.0 in wild moose. In regions 1 and more so in regions 4, a pathological reduction to only 1, 5, 9, 12 etc. papillae/cm^2 was observed due to acidosis. Maxi-

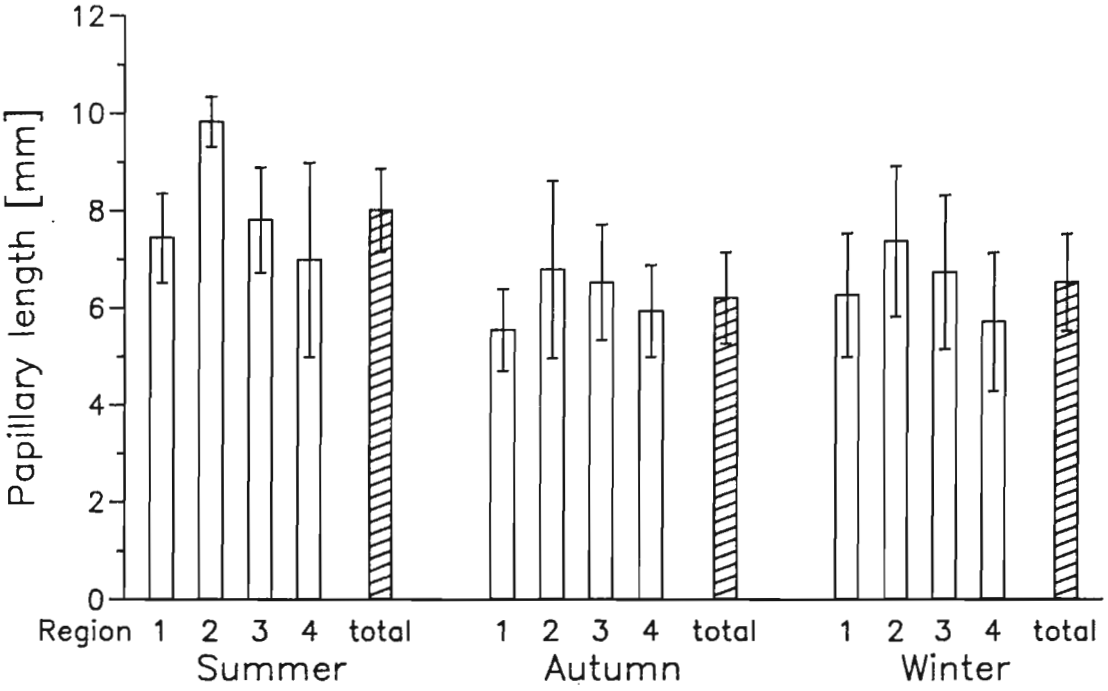

Fig. 4. Papillary length in samples from four standardized moose rumen wall test regions grouped according to defined seasons.

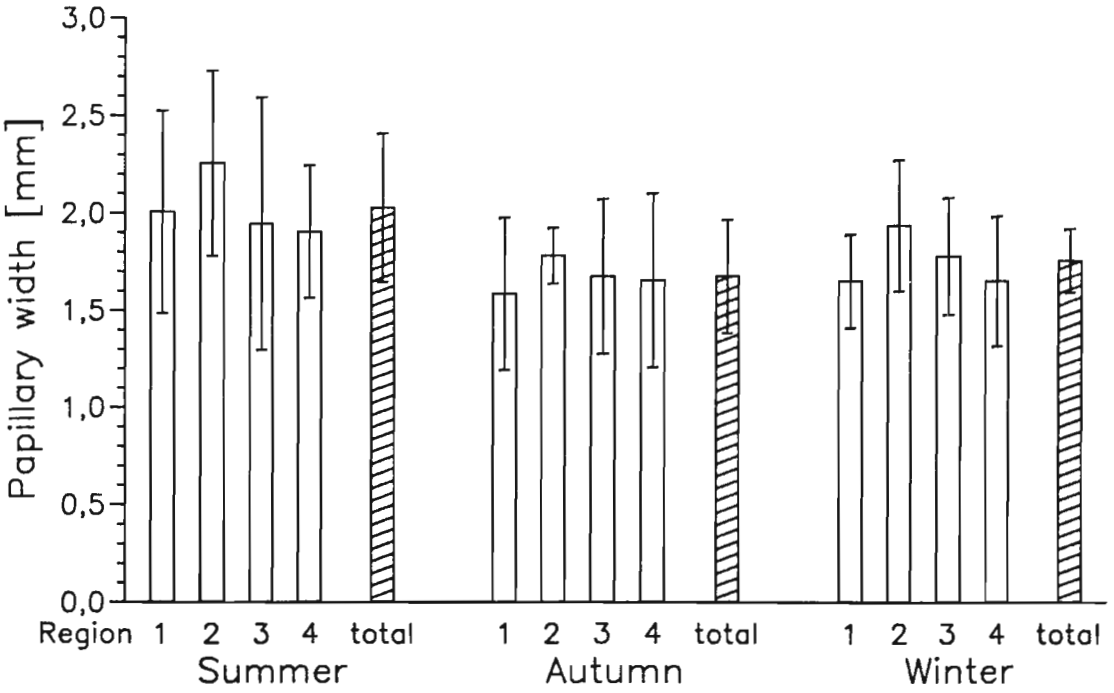

Fig. 5. Papillary width in samples from four standardized moose rumen wall test regions grouped according to defined seasons.

mal number was 58 (in stomachs recovering after changes in feeding; max. number in wild moose: 84).

Overall average papillary length was 4.14 mm as compared with 6.63 mm in wild moose. Minima were at 1 mm, as opposed to 4.9 mm in wild animals; maxima were at 7.43 mm (region 2) as opposed to 10.57 mm (region 2, wild).

Captive moose, irrespective of origin, show a similar drastic mucosal surface reduction when compared with wild moose, mainly caused by partly eroded and by less absorptive papillae (25 % below average of wild papillary number) all of which are, on average, also 25 % shorter than those of wild moose. In addition, many of these papillae are transformed in their shape from flat/tongue-shaped to biconvex/round and their microstructure is distinguished by various degrees of parakeratosis, which further reduces absorption.

DISCUSSION AND CONCLUSION

The ruminal mucosa of Northern European moose is completely, densely and apparently evenly papillated. Its tongue shaped papillae (ø 6.6 mm long, 1.8 mm wide) provide an absorptive surface which, under optimal summer foraging conditions (extreme selectivity for easily digestible plant parts rich in nutrients), is enlarged 2´ times more than that of the cattle rumen (c. 17 x vs 7 x)! It is even under nordic winter conditions slightly greater (ø 8.8 x) than the overall cattle surface enlargement, on average 7 x (Schnorr and Vollmerhaus 1967) which points to continued selectivity/forage plant diversity of moose also in winter.

At birth, evenly dense and evenly long papillae soon become regionally differentiated under increasing VFA stimulation of their blood vascular system. They are largest and most numerous at rumen midlevel, slightly shorter and less dense on roof and floor of the fermentation chamber, in all seasons.

The ruminal mucosa responds in wild moose significantly to seasonal changes in forage quality, intake and availability. The most drastic reduction of the absorptive surface (c. 50%) occurs from summer to autumn during the rut period, with reduced food intake (more in mature males, less in mature females, however significant in both sexes). This results primilary in a reduction of papillary number (31 %), secondly in a reduction of the papillary length, on average 23 % (both caused by reduced blood flow due to decreased fermentation/VFA stimulation, i.e. whole papillae, or their tips only retract or fall off). Wild moose apparently are able to stabilize a relatively large mucosal surface over winter. This process is cyclic, i.e. papillary number and length increases again when nutritious forage becomes available during April/May; the adaptation/transformation period is between 10 and 20 days (in all ruminants; Hofmann 1973).

Captive moose from different feeding regimes show amazingly similar deficiencies. Their ruminal mucosa shows various stages and degrees of acidosis and overall reduction of papillary dimensions causing an anaturally small SEF. Apparently it is not sufficient to feed captive moose nutritious rations ("concentrate"); they obviously suffer from being prevented to perform their behavioural selectivity upon a great diversity of forage plants and plant parts, which change seasonally and to which their digestive system responds with regulated changes of particle retention/rumen outflow and changes of both ruminal and intestinal fermentation and absorption.

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