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ORIGINAL PAPER

Surface enlargement in the rumen of free-ranging muskoxen (*Ovibos moschatus*)

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Abstract The intraruminal papillation pattern indicates the degree of rumen contents stratification and is related to the feeding niche of a ruminant. Muskoxen (*Ovibos moschatus*) display a variety of morphophysiological adaptations typical for grazers. We investigated the intraruminal papillation of 22 free-ranging muskoxen from five different months by comparing the surface enlargement factor both between seasons and between individual rumen regions. The seasonal pattern of rumen papillation indicated a distinct seasonality in food quality. The intraruminal papillation indicated a moderate degree of rumen contents stratification typical for intermediate feeders. The nutritional ecology of muskoxen is characterised by specific morphophysiological adaptations to a grass-dominated diet that nevertheless allow extensive seasonal use of browse forage.

Keywords Papillation · Intermediate feeder · Grazer · Browser · Stratification

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Introduction

The papillation of the ruminal mucosa varies among ruminants—both with seasons or diets and between feeding types (Hofmann 1973; Hofmann and Schnorr 1982; Clauss et al. 2009c). Most likely due to differences in the way the rumen contents are stratified, the rumen mucosa can show a completely, homogenously papillated pattern in animals with unstratified contents or a very heterogenous papillation with papillae-free areas in the dorsal and ventral rumen in animals with particularly stratified contents (Clauss et al. 2009a, b). To date, it remains unclear whether animal factors, such as the viscosity of the saliva and, hence, of the rumen fluid, or plant factors, such as higher water-binding capacities and, hence, rumen contents viscosity, are responsible for the observed differences in stratification. The degree of contents stratification is most likely linked to other morphological and physiological characteristics of the ruminant fore-stomach and has been suggested to be at the core of the browser–grazer differentiation (Clauss et al. 2008).

Although grasses and sedges represent the major part of the diet of muskoxen (Klein and Bay 1990; Larter and Nagy 1997), significant consumption of browse forage has also been reported in this species, in particular during summer (Staaland and Olesen 1992). Nevertheless, anatomical characteristics of the digestive tract of muskoxen have been interpreted as consistent with a classification of this species as a grazer (Staaland and Thing 1991; Staaland et al. 1997; Hofmann 2000; Mathiesen et al. 2000; Knott et al. 2004, 2005; Clauss et al. 2006a), and measurements of physiologic parameters suggest digestive efficiencies and ingesta retention times in muskoxen that are similar to those found in other grazers (Adamczewski et al. 1993, 1994a, b; Peltier et al. 2003; Barboza et al. 2006). These findings suggest that the rumen papillation of muskoxen should show evidence for a stratification of rumen contents as suggested qualitatively by Hofmann (2000).

Methods

Rumen samples of the mucosa of free-ranging female muskoxen were taken during different seasons (April, May, July, September, November) at the southern end of Victoria Island in the Canadian Arctic (104–107° W longitude, 69–69.5° latitude) as part of a larger study between 1989 and 1993 (Adamczewski et al. 1992, 1997) in which also the body mass, mass of rumen contents and the backfat depth of the same animals were measured. Samples were taken from the dorsal and ventral rumen, from the *Atrium ruminis* and from the bottom of the dorsal blindsac, preserved in formalin, and the surface enlargement factor (SEF) due to the papillae was determined by measuring the number of papillae, and their mean height and width per square centimetre (Schnorr and Vollmerhaus 1967). In order to characterise the difference in papillation between different rumen regions, the SEF of the dorsal and the ventral rumen were expressed in% of the SEF of the *A. ruminis*. Differences between seasons were tested by one-way ANOVA and post hoc tests with Sidak adjustment for multiple comparisons; differences between rumen regions within a season were tested by repeated measurements ANOVA and paired *t* tests with Dunn–Sidak adjustment for multiple comparisons; all statistical calculations were performed with SPSS 16.0 (SPSS Inc., Chicago, IL). The significance level was set to 0.05.

Results

All measurements showed a distinct seasonal pattern (Table 1). Body mass and backfat depth were lowest at the end of winter (May) and highest in September, indicating an accretion of body reserves during the summer period. Rumen fill was lowest during summer and highest in early winter. The SEF of the different rumen regions was highest in summer and decreased until the end of the winter period (May; Table 1). The dorsal rumen SEF was always numerically lower than the SEF of the *A. ruminis*, but the difference was only significant in May and September (Table 1). The ventral rumen SEF showed a similar pattern as that of the dorsal rumen, but the difference to the SEF of the *A. ruminis* was significant in May only (Table 1). Across all seasons, the dorsal rumen SEF averaged at 54% of the SEF of the *A. ruminis*.

Table 1 Mean (±SD) age, body mass, backfat depth, reticulorumінal content mass (also expressed in % of body mass) and the SEF of the dorsal and ventral rumen, the *A. ruminis*, and the dBS, and the SEF of the dorsal and ventral rumen in% of the SEF of the *A. ruminis*, in free-ranging female muskoxen (*Ovibos moschatus*)

Season	Parameter (*n*)	Age	Body mass	Back fat	RR contents	RR contents	SEF				SEF dorsal	SEF ventral
			kg	cm	kg	% BM	Dorsal	Ventral	Atrium	dBS	% Atrium	
Apr	5	4.4±0.6	192.4ab±10.7	2.0a±0.1	32.7ab±5.1	17.0ab±2.0	2.81ab±0.49	2.41a±0.22	5.90ab±1.06	3.61a±0.68	50.9±10.6	43.6±13.2
May	4	4.5±0.6	155.6a±10.7	0.8a±0.1	30.3ab±5.1	19.4ab±2.0	2.32bA±0.49	2.17aA±0.22	5.03abB±1.06	4.17aB±0.68	47.2±10.6	45.2±13.2
July	4	4.0±0.0	159.3a±5.1	0.9a±0.4	24.7a±1.3	15.5a±0.4	5.85c±1.66	8.15b±4.24	11.17c±1.17	11.11b±1.60	53.1±17.6	74.9±43.8
Sept	5	4.8±0.3	212.7b±5.3	4.3b±0.7	33.9ab±3.8	16.0a±2.0	4.68acA±0.61	6.09abAB±0.98	9.66acBC±4.00	12.55bC±1.43	59.1±32.3	78.9±48.1
Nov	4	3.6±1.0	170.9ab±45.9	3.8b±1.4	35.6b±4.9	21.5b±3.5	2.53abA±0.34	2.57aA±0.61	4.31bAB±0.92	4.55aB±0.48	60.1±9.6	64.7±31.7

Within columns, lower case letters indicate significant differences; within lines, upper case letters indicate significant differences in SEF between the rumen regions (adjusted for multiple testing); there were no significant differences in the relative dorsal or ventral SEF between seasons, nor in SEF between rumen regions in April or July

SEF surface enlargement factor, *dBS* dorsal ruminal blind sac

Discussion

The results corroborate numerous other studies that document the strong seasonal influence on the digestive physiology of muskoxen. Muskoxen have to accumulate body reserves in the form of adipose tissue during the brief summer period in which high-quality forage is available. In our dataset, this is reflected in the dramatic fluctuation of backfat depth between the end of winter (May) and the end of the summer period (September), with a similar but less drastic variation in total body mass.

Although particularly high food intakes have to be assumed for the summer period, rumen contents were lowest in summer. This is in contrast to findings in captive muskoxen, which showed, in parallel to their summer hyperphagia, particularly high rumen volumes in this season (Barboza et al. 2006). Actually, a similar discrepancy between different sets of rumen content measurements can be found between different reports for other species as well, such as roe deer (*Capreolus capreolus*; Holand 1992 vs. Hofmann et al. 1976 and Behrend et al. 2004) and reindeer (*Rangifer tarandus*; Adamczewski et al. 1987 vs. Tyler et al. 1999). In general, low levels of intake of lower-quality forage with longer ruminal retention times appears to lead to higher gut fill in many ruminants during the winter or the dry season, respectively—such as in moose (*Alces alces*; Gasaway and Coady 1974), domestic sheep, goats (Lechner-Doll et al. 1990), cattle (McCollum and Galyean 1985; Schlecht et al. 2003), as well as for hartebeest (*Alecelaphus buselaphus*; Stanley Price 1978), kudus (*Tragelaphus strepsiceros*; Owen-Smith 1994) or Mongolian gazelles (*Procapra gutturosa*; Jiang et al. 2002). If the measurements are performed on animals that receive the same food around the year (Behrend et al. 2004; Barboza et al. 2006), then lower gut fill in winter probably reflects a reduced food intake due to seasonally reduced energy budget that have been described in temperate ruminants even at ad libitum food availability (e.g. Schwartz et al. 1984). If the measurements are taken from animals on natural, seasonally variable forage, then at first, a higher gut fill in the dormant period will most likely reflect a reduced diet quality, with increasing fibre levels. Later, a reduced gut fill might reflect a lower quantity of available food. The case of the muskoxen of this study, with low rumen contents in summer, increasing rumen contents towards the beginning of winter and then decreasing rumen contents towards the end of winter, might represent an example of such a shifting pattern in forage quality and quantity.

The rumen SEF due to differences in papillation in these muskoxen also indicates a seasonal pattern of forage quality. The highest SEF values were measured in summer, supporting the interpretation that the diet was of the highest quality here, yielding high amounts of volatile fatty acids and, hence, stimulating papillae growth. Similar differences in the papillation pattern across the seasons have been reported in many wild ruminant species (complied in Clauss et al. 2009c). Similar to other ruminants of the intermediate feeding type, the papillation pattern of the muskox indicates a moderate degree of rumen contents stratification, with the dorsal and ventral rumen sites having lower SEF than the typical high-SEF rumen regions (which contrasts with strict browsers), but nevertheless, the SEF of the dorsal and ventral sites reach values between 40% and 70% of the high-SEF rumen sites (which contrasts with strict grazers; Clauss et al. 2009c). As in other intermediate feeders (Hofmann 1973; Clauss et al. 2009c), the SEF of the different rumen regions of muskoxen indicates a lower degree of rumen contents stratification in the season where a high intake of browse can be assumed (in July, with no significant difference in SEF between the rumen regions) and the highest degree of stratification towards the end of winter (May). Given the correlation between the degree of rumen content stratification as indicated by the intraruminal papillation patterns and the "selectivity factor"—the ratio of particle vs. fluid retention in the rumen—in other ruminants (Clauss et al. 2009c), the selectivity factor of muskoxen can be predicted from the results of this study (Fig. 1). With an average SEF of the dorsal rumen of 54% of the SEF of the *A. ruminis*, muskoxen should display a selectivity factor of 1.6, which is in the range of other intermediate feeders (Hummel et al. 2005; Clauss et al. 2006b). To date, the only simultaneous measurements of fluid and particle retention that have been performed in muskoxen (Barboza et al. 2006), however, were done with a marker set that is not compatible with the one regularly used to determine the selectivity factor (cobalt-EDTA and chromium-mordanted fibre). Therefore, this prediction regarding ingesta retention in muskoxen will have to be tested in future studies.

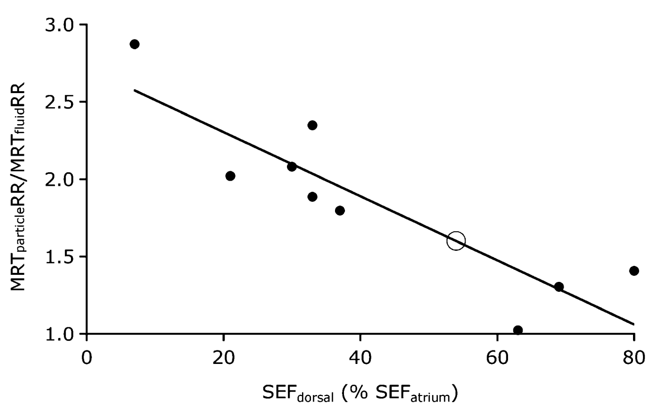

Fig. 1 Relationship between the intraruminal papillation pattern, expressed as the *SEF* of the dorsal rumen in% of the SEF of the *A. ruminis*, and the ratio of the mean retention time (*MRT*) in the reticulorumen (*RR*) of particles and fluids (from Clauss et al. 2009c). The ratio of $MRT_{particles}RR/MRT_{fluid}RR$ in muskoxen as predicted by papillation measurements taken in this study is indicated by the *open circle*

In contrast to a variety of anatomical and physiological observations that suggest a classification of muskoxen as a typical 'grazer' (see "Introduction"), the intraruminal papillation of the species resembles that of other intermediate feeders. It has been suggested that morphophysiological adaptations typical for grazers should not constrain the use of browse forage, as long as toxicity of secondary plant compounds is not limiting (Clauss et al. 2003). In this respect, investigations of salivary gland size in muskoxen (Hofmann et al. 2008) and the presence of tannin-binding proteins in their saliva (Fickel et al. 1998) would be particularly interesting as well as investigations into the evolutionary history of the muskox feeding niche (Codron et al. 2008). In contrast to moose, which show a set of morphophysiological characteristics typical for a strict browser (Hofmann and Nygren 1992; Clauss et al. 2009b), muskoxen use a range of morphological and physiological adaptations usually considered typical for grazers to exploit the niche of a mixed feeder; in this respect, muskoxen might be convergent to other larger (European bison *Bison bonasus*) or smaller (Mouflon *Ovis ammon musimon*) ruminants of a similar set of morphophysiological and dietary adaptations.

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