No ‘bypass' in adult ruminants: Passage of fluid ingested vs. fluid inserted into the rumen in fistulated muskoxen (Ovibos moschatus), reindeer (Rangifer tarandus) and moose (Alces alces)

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Running head: Fluid passage in large ruminants
Abstract

In young ruminants, the reticular groove ensures that ingested milk is channelled past the forestomach to avoid malfermentation. It has been speculated that some adult wild ruminants, in particular browsing species, maintain a functional oesophageal (reticular) groove, that soluble nutrients can thus bypass the rumen, and that thus the energetic gain from the diet can be increased. We inserted a fluid marker (Co-EDTA) via cannula into the rumen and simultaneously fed a diet that contained a second fluid marker (Sm-EDTA), and analysed the faecal marker excretion patterns, in muskoxen (*Ovibos moschatus*, n=4 in two experiments each), reindeer (*Rangifer tarandus*, n=4 in a total of six experiments) and moose (*Alces alces*, n=1 in one experiment). In no case was the orally fed marker excreted distinctively earlier than the marker inserted into the rumen, which indicates that substantial bypass did not occur in these animals. However, differences between the three species in the excretion of the two markers from the rumen are consistent with hypothetical differences in the stratification of rumen contents. We suggest that effects previously ascribed to a “rumen bypass” in wild ruminants most likely reflect differences in the passage from the rumen.

Key words: ruminant, reticular groove, bypass, passage, saliva, intake, stratification
Introduction

All mammals undergo a dramatic ontogenetic shift in diet from milk to solid food. In foregut-fermenting herbivores, this represents a particular challenge because these animals must prevent the milk from reaching their foregut fermentation chamber in order to avoid serious malfermentation (Breukink et al. 1988). In order to channel the milk past the foregut, these animals have evolved a bypass structure – the ‘oesophageal groove’ (Langer 1993). This groove consists of muscular ridges that contract during sucking, form a hose-like channel, and direct the milk past the foregut into the glandular stomach.

In ruminants, it has been observed that the oesophageal groove appears to be still ‘well-developed’ in adult individuals (Hofmann 1973). Actually, the groove, which in ruminants is called the ‘reticular groove’, can be easily observed as prominent muscular ridges during dissection of the rumen of adult individuals (Hofmann 1973; Langer 1988), on the one hand. On the other hand, there are reports that ensalivation during mastication effectively brings soluble diet components into solution in cattle (Bailey 1961), and that the reticular groove can retain its ability to close completely in conditioned domestic ruminants (Orskov et al. 1970; Ruckebusch and Kay 1971; Dobarganes Garcia et al. 2005). In combination, these observations led to the hypothesis that nutrients dissolved in saliva bypass the rumen via the reticular groove even in adult individuals - especially in browsing ruminants (Hofmann 1989). Such a mechanism would provide the digestive advantage of easily digestible, soluble nutrients being used auto-enzymatically without the energetic losses associated with bacterial fermentation. Several findings suggesting the escape of certain nutrients from the rumen were considered indicative of such a bypass: Correlative reports of rumen bypass in browsing ruminants include an increased occurrence of unsaturated fatty acids in body lipids, and the expression of enzymes for simple carbohydrates digestion and transport of glucose in the small intestine (Meyer et al. 1998; Rowell-Schäfer et al. 1999; Wood et al. 2000; Rowell-Schäfer et al. 2001). These indirect indications notwithstanding, the functionality of the
The functionality of the reticular groove can be assessed in different ways. In domestic ruminants, radiographic studies after the application of a contrast medium (mostly barium sulfate) have been used (Sargison et al. 1998), and a special breath test including the application of a marker isotope and repeated sampling of exhalate has been validated for the study of reticular groove closure (McLeay et al. 1988), and groove closure has been tested by measuring serum glucose after feeding a glucose solution (Lousse and Ronsse 1950). In fistulated animals, presence or absence of an ingested marker in the ruminal contents (Waghorn and Shelton 1994) can be used as an indication for groove closure, as well as temperature recording at different sites of the gastrointestinal tract following the application of cold drinking water (Paragon and Hachet 1980), or simple visual or manual inspection of the groove (Hegland et al. 1957).

However, in wild ruminant species, the methods mentioned above require substantial manipulation of the animal, even in fistulated individuals. In contrast, two liquid markers in fistulated individuals – one inserted into the rumen via the cannula, and one ingested by the animal itself (Daniel et al. 2007) – can be used. If markers are subsequently measured in faeces to determine gastrointestinal and reticuloruminal retention times, no particular manipulation beyond the marker insertion is necessary. Actually, because results on fluid retention in roe deer (*Capreolus capreolus*) from trials in which a fluid marker (cobalt-EDTA or chromium-EDTA, respectively) had either been ingested by the animals (Holand 1994) or inserted into the rumen via a cannula (Behrend et al. 2004) indicated no difference, Behrend et al. (2004) concluded that there was no evidence for a functional reticular groove in this species. However, these results were combined from different studies using different individuals and different food intakes. Because food intake is a major determinant of ingesta fluid and particle passage (Spalinger et al. 1993; Clauss et al. 2007a; Clauss et al. 2007b),
comparisons of ingested and inserted fluid markers should be made simultaneously in the same individual.

We studied the passage of two fluid markers in captive, fistulated muskoxen (Ovibos moschatus), reindeer (Rangifer tarandus) and moose (Alces alces), comparing the excretion patterns of an ingested marker and a marker inserted into the rumen at the same time. Based on observations in roe deer outlined above (Behrend et al. 2004), we expected a simultaneous marker excretion; in particular, we did not expect the ingested marker to be excreted faster than the inserted marker.

Materials and Methods

We used four fistulated adult reindeer and four fistulated adult muskoxen of the Robert G. White Large Animal Research Station, Institute of Arctic Biology, University of Alaska Fairbanks, and two adult fistulated moose of the Alaska Department of Fish and Game (Table 1). All animals were weighed prior to the study. With the exception of one reindeer, all animals had received the rumen fistulas for other studies more than one year before this experiment. All animals were kept individually in outdoor pens with ad libitum access to water, shade, and their respective food. Adaptation periods to a food lasted for a minimum of 14 days. Muskoxen received either a diet of mixed browse (n=4; Salix spp.) or grass hay (n=4; Bromus sp.); reindeer received either a diet of mixed browse (n=4; Salix spp.) or a pelleted compound feed (n=2); moose received only one diet of mixed browse (n=4; Salix spp.).

Cobalt (Co) and Samarium (Sm) were used as fluid markers bound to EDTA. Co-EDTA was prepared according to Udén et al. (1980); Sm was prepared in a similar way: 25 g of Sm(III)-acetate hydrate and 28.4 g EDTA were dissolved in 153 ml of distilled water by heating and stirring for 24 hours. The solution was allowed to cool to room temperature and
rest for 3 hours. Then, 229 g of 96% ethanol were added and the solution was incubated in a freezer at -20°C for 12 hours. The crystallized material was retrieved on a paper filter, washed twice with 80% ethanol, and dried at 40°C in a ventilated drying oven for 48 hours. The resulting white solid dissolved easily in water.

Co-EDTA is a purple substance that has, in our experience, an aversive taste for humans and many animals; voluntary intake of this marker in feeding trials, though possible, is always unpredictable. In contrast, no aversive smell or taste was evident in the colourless Sm-EDTA. Therefore, we decided to always apply the Co-EDTA intraruminally in frozen form via the cannula, and feed the Sm-EDTA dissolved in water and sprayed onto pellets immediately prior to feeding (i.e., the pellets were not ‘dried’ after application). Nevertheless, one moose rejected the Sm-marked pellets, and had to be excluded from the study.

Although in dairy calves, the position of the head plays no role in the triggering of groove closure (Wise et al. 1942), the position when feeding has been suggested to be important (Hofmann 1989); therefore, the Sm-marked pellets were offered to the moose in its usual elevated feeding trough (1.4 m height). Muskoxen and reindeer received the Sm-pellets at ground level, with the exception of one reindeer that received them either in its elevated feeding trough (1 m height). Co-EDTA (dissolved in water and frozen; 2.25 g Co-EDTA/muskox, 0.8 g/reindeer, 3.33 g/moose) was dosed through the cannula into the rumen; in doing so, the frozen marker was pushed into the upper to layer of the rumen contents in the middle (neither cranial or caudal) region. Immediately after this application, the animals were offered the Sm-marked pellets (0.3 g Sm-EDTA/muskox, 0.1 g/reindeer, 0.5 g/moose; 100 g pellets/animal; the dose of Sm was lower than that of Co because Co occurs at higher levels in the environment, and hence a higher dose is necessary to achieve a reliable signal above baseline values). One moose refused the pellets, and one reindeer only consumed them within the following hour. All other animals ingested the pellets immediately.

After marker dosing, faeces were sampled for 13 days in total at defined increasing
intervals of 4 hours (day 1-2), 6 hours (day 3), 8 hours (day 4-5), 12 hours (day 6-9) and 24
hours (day 11-13), stored frozen at -20°C until analysis.

Samples were dried to constant weight at 60 °C and ground (1 mm pore size), and 0.2 g
of each sample was digested using 3 mL nitric acid (HNO₃, 65%, Merck analytical grade,
purified by duplicate subboiling distillation) and 2 mL hydrogen peroxide (H₂O₂, 30%,
Traceselect, Fluka, Germany). Digestion was carried out in a high pressure microwave system
(Ultraclave II, MLS GMBH, Germany) at a final temperature of 250°C and a pressure of 35
bars. After digestion the solutions were transferred into clean flasks, diluted to a volume of 30
mL with de-ionized water (> 18 MΩ, Millipore, France) and stored for analysis. Two blanks
were included in each digestion run to assess the potential contribution from contamination in
the reagents and containers used. 0.5 mL of the digested samples was finally diluted to a
volume of 10 mL with de-ionized water before analysis by inductively coupled plasma mass
spectrometry (ICPMS). An Elan 6000 ICPMS instrument (Perkin Elmer / Sciex, Norwalk,
USA), was used for the analyses. The instrument was optimized daily for best sensitivity
while maintaining a CeO⁺/Ce⁺ ratio below 2%. Cross calibration of the pulse and analog
detection system was carried out before each run in order to extend the dynamic range to
cover the expected peak concentrations in the samples without requiring further dilution.
Calibration was carried out using external standards, prepared from single element stock
solutions in a range between 0 and 100 µg/L. Rh was added to all samples and standards at a
concentration of 10 µg/L to monitor and correct for instrument drift over the course of the
analysis. Typically > 100 samples were analysed in a single run, which included automatic re-
calibration every 30 samples. Limits of detection based on the blanks were 0.01 µg/L for Co
and 0.005 µg/L for Sm, corresponding to 0.06 mg/kg or 0.03 mg/kg dry mass for a typical
sample digest respectively. These were at least a factor of 50 lower than the background
levels determined in the faeces without the tracers present. Combined measurement
uncertainties were always < 2 % of the relative standard deviation (RSD), while results from
Repeat digests of the same sample resulted in average RSD’s of 5% caused by heterogeneity of the dried faeces.

Transit times (the time of first marker appearance) and mean retention times (MRT) were recorded. The MRT for the whole gastrointestinal tract (MRT\_GIT) was calculated according to Thielemans et al. (1978) as

\[ \text{MRT}_{\text{GIT}} = \frac{\sum t_i C_i dt_i}{\sum C_i dt_i} \]

With \( C_i \) = marker concentration in the faecal samples from the interval represented by time \( t_i \) (hours after marker administration) and \( dt_i \) = the interval (hours) of the respective sample.

\[ dt_i = \frac{(t_{i+1} - t_i) + (t_i - t_{i-1})}{2} \]

Liquid MRTs for the reticulorumen (MRT\_RR) were calculated as by Grovum and Williams (1973a); this calculation is based on the decrease of the faecal liquid marker concentration \( C_i \) with time according to the equation

\[ C_i = a e^{-kt_i} \text{ or } \ln C_i = -kt_i + b \]

Liquid MRT in the RR then is \( k^{-1} \). Differences in marker excretion between the ingested and the inserted marker was tested by paired t-test within species using SPSS 17.0 (SPSS Inc., Chicago, IL).

Results

The excretion patterns for intraruminally applied Co-EDTA and orally fed Sm-EDTA were similar within the three species by visual inspection (Fig. 1); however, in muskoxen, Sm-EDTA appeared to be excreted later than Co-EDTA. Transit times and mean retention times for Sm were either equal to, or higher than, those for Co (Table 2); in muskoxen, Sm was excreted significantly later than Co; this difference was not significant in reindeer. Across
Species, MRT\textsubscript{GIT} measurements of the two fluid markers showed a close correlation, with no apparent difference between the species; MRT\textsubscript{GIT}Sm were invariably longer than MRT\textsubscript{GIT}Co (Fig. 2a). When comparing individual MRT\textsubscript{RR} measurements, values of Co and Sm from reindeer and moose lie on the x=y line, but values from muskoxen indicated the longer 195 MRT\textsubscript{RR}Sm (Fig. 2b).

Discussion

The results indicate that among the species investigated here, a rumen bypass due to a solubilisation of fluid marker, and a channelling of fluid via the reticular groove directly into the omasal canal and the abomasum, did not occur to any relevant degree.

A similar pattern had already been suggested in roe deer by Behrend et al (2004) who compared their own measurements of an intraruminally applied fluid marker to those obtained with a similar marker, but fed orally, from another study (c.f. Table 2). The uncertainty inherent in that interpretation, due to potential differences in food intake between the experiments, could be ruled out in the present study, because both fluid markers were applied simultaneously in the same animals. If chewing and ensalivation in the oral cavity would have led to a solubilisation (not only of soluble nutrients, but also of the soluble marker), with a subsequent transport of these solutes past the rumen via the reticular groove, shorter transit times and MRTs would have been expected for the orally fed fluid marker.

Some limitations of the study need to be mentioned. Ideally, the fluid marker inserted into the rumen should have been applied in a similar form (fluid, not frozen), on a similar carrier (on pellets), and placed underneath the cardia. Due to the small size of the cannulae with which the animals were fitted, the latter was not possible. However, both the placement in the middle rumen, within the dorsal layer of the contents, and the frozen form, could only have delayed, not accelerated, Co excretion. The fact that Co was not excreted later than the Sm suggests that these limitations were not crucial to our study. Behrend et al. (2004) also
had also inserted the Co-EDTA in frozen form in their study, whereas the Co-EDTA fed by Holand (1994) had not been frozen; the similarity in the respective excretion (Table 2) again suggests that the frozen marker thaws very rapidly. Actually, a thawing test with the Co-EDTA marker in its dissolved and frozen form in a 38 °C water bath resulted in complete thawing after 80 seconds only, suggesting that the frozen application had a negligible impact on the results. In theory, it would be possible to actually insert the intraruminal marker exactly at the same moment that the animals ingest the oral marker. In our case, the animals were habituated to receiving a treat immediately after manipulation of their cannulae, and we therefore fed the oral marker within minutes after inserting the intraruminal one. Because the resolution of the retention time determination is within the scope of hours, not minutes, this should have no influence on the results. The passage markers used in this study can be recommended for further research. One interesting aspect would be a test of the groove function by applying three fluid markers (Co-EDTA, Sm-EDTA, Cr-EDTA) to both pellets fed to the animals, to pellets inserted into the rumen via a cannula, and to water fed to an habituated animal via a bottle fitted with a nipple, which forces the animal to suckle and hence potentially activate the reticular groove. Additionally, different physiologic conditions (e.g. well-fed animals vs. nutritionally challenged animals) could be investigated.

The concept of forestomach bypass has been proposed not only in ruminants, but also in foregut fermenting primates (Cork 1994; Chivers 1995). Foregut fermenters in general appear limited in their food intake capacity, because a high food intake would lead to a comparatively quick passage of ingesta through the forestomach. This would entail microbial modification and fermentation of soluble nutrients but insufficient fermentation of plant fibre (Clauss et al. 2008). A bypass mechanism is therefore an appealing nutritional concept. However, similar to findings in this study, indications for a bypass of soluble markers in foregut fermenting primates are lacking so far because in this group, orally applied fluid and particle markers are excreted together (Nijboer et al. 2007; Schwarm et al. 2009).
In adult ruminants, a certain degree of rumen bypass does occur during drinking (but note that the majority of fluid still enters the rumen; Woodford et al. 1984). This mechanism has been used repeatedly for the administration of fluid drugs that should ideally bypass the rumen and enter the abomasum directly (Sargison et al. 1998; Sargison et al. 2000a; Sargison et al. 2000b). However, it should be noted that the bypass mechanism originally proposed by Hofmann (1973, 1989) and investigated in this study is not linked to drinking water intake, but to solid food ingestion, mastication, and the concomitant hypothetical solubilisation of nutrients.

In addition to our findings, two different reasons could potentially make the proposed concept of a rumen bypass problematic. On the one hand, the proposed mechanism of bypassing dissolved nutrients via the reticular groove would, in theory, require a biphasic swallowing mechanism, by which the animal first swallows saliva and dissolved nutrients only, and afterwards swallows the solid part of the masticated bolus. Detailed observations on the comparative swallowing behaviour in wild ruminants are lacking to our knowledge. Evidence in domestic ruminants is also lacking, and the sparse information existing is ambiguous. Asplund (1994) cites a personal communication from 1957 that describes biphasic ingestive swallowing in cattle. However, in other studies, such a biphasic swallowing is not reported (Carr et al. 1983; Forwood et al. 1985).

On the other hand, at least one of the findings that has been used to support the argument of a rumen bypass in browsing ruminants might not stand closer scrutiny. Browsing ruminants, such as the roe deer or moose, have higher contents of polyunsaturated fatty acids in their body tissue than grazing ruminants (Meyer et al. 1998; Rowell-Schäfer et al. 2001). While this finding indicates that ingested fatty acids undergo less bacterial modification in the browsing species investigated as compared to the grazers, a solubilisation of fatty acids by saliva (which does not have a detergent action) and subsequent bypass via the reticular groove appears unlikely. In order to accept such a hypothetical mechanism, lipases (Nelson et al. 2011).
would have to be demonstrated in the saliva of adult browsing ruminants that break
down fats into hydrophilic units.

The data generated in this study hint at one interesting difference between the species
investigated. Whereas in reindeer and moose, the excretion of the two fluid markers from the
RR followed a similar kinetic, indicating no difference in the outflow pattern between a
swallowed and an inserted fluid, the excretion of the swallowed fluid marker from the RR was
significantly slower in muskox than the inserted fluid marker (Table 2, Fig. 2b). These
findings do not indicate differences with respect to a functional reticular groove between the
species, as transit time and MRTs were never shorter for the orally fed marker; however, they
probably reflect differences in the physical structure of the RR contents. Several publications
indicate that the rumen contents of moose and reindeer are rather homogenous, with no clear
stratification of different layers (Westerling 1970; Hobson et al. 1976; Renecker and Hudson
1990; Clauss et al. 2009a; Clauss et al. 2009b), and a relatively simultaneous excretion of
fluids and particles from the RR (Clauss et al. 2006b). In contrast, the comparatively large
omasum of muskoxen (Clauss et al. 2006a) and their ruminal papillation pattern (Hofmann
1999) suggest a more distinct stratification of RR contents in this species with a distinctive
fibre mat. In the unstratified RR contents of moose or reindeer, the two different fluid markers
should achieve a similar distribution irrespective of their method of application, leading to the
pattern of similar RR excretion displayed in Fig. 2b. In contrast, the fluid marker applied as a
(frozen) liquid (Co-EDTA) could reach the fluid pool in the stratified RR contents of
muskoxen much sooner than the fluid marker in the ingested bolus (Sm-EDTA); the latter is
likely to be first retained on the fibre mat, from which it will reach the liquid pool more
slowly, leading to the observed delay in excretion (Fig. 2b). However, further studies on the
stratification of RR contents of muskox, reindeer and moose, including deliberate deposition
of markers in different layers of the rumen contents, are required to corroborate this
explanation.
The present study increases our knowledge on the potential function of the reticular groove in adult wild ruminants. Differences between wild ruminants in the degree that ingested material is submitted to microbial modification in the reticulorumen should rather be interpreted as a function of differences in RR passage (Rowell-Schäfer et al. 2001), but not as a consequence of RR bypass.

Acknowledgements

This project was supported by SNF grant 3100A0-115958/1 to MC. We thank Bill Hauer, Peter Reynolds, Sandy Garbowski, Tabitha Hughes, Betsy Wagner for support in animal husbandry, Felix Zelder for support in fluid marker preparation, and Olga Martin Jurado for the translation of a Portuguese article. Experiments and handling procedures for animals were approved by the Institutional Animal Care and Use Committee, University of Alaska Fairbanks under protocols #07-23 (muskoxen and reindeer) and #07-21 (moose).

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Table 1. Experimental animals used in this study.

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<th>Sex</th>
<th>Age years</th>
<th>Body mass kg</th>
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<td>m, castrated</td>
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<td>254</td>
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<td>306</td>
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<tr>
<td>Muskox</td>
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<td>f</td>
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Table 2. Average (±SD) transit times (TT) and mean retention times (MRT) in the gastrointestinal tract (GIT) or the reticulorumen (RR) of intraruminally dosed Co-EDTA and orally fed Sm-EDTA in four wild ruminant species

<table>
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<th>TT</th>
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<th>MRT RR</th>
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<td></td>
<td></td>
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<td>Sm</td>
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<td>17 ± 2</td>
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<td>4</td>
<td>Pellets</td>
<td>12 ± 2</td>
<td>16 ± 6</td>
</tr>
<tr>
<td>Reindeer</td>
<td>Rangifer tarandus</td>
<td>5</td>
<td>Browse</td>
<td>14 ± 2</td>
<td>15 ± 2</td>
</tr>
<tr>
<td>Reindeer</td>
<td>Rangifer tarandus</td>
<td>6</td>
<td>Grass</td>
<td>15 ± 2</td>
<td>16 ± 6</td>
</tr>
<tr>
<td>Reindeer</td>
<td>Rangifer tarandus</td>
<td>7</td>
<td>Pellets</td>
<td>12 ± 2</td>
<td>16 ± 6</td>
</tr>
<tr>
<td>Reindeer</td>
<td>Rangifer tarandus</td>
<td>8</td>
<td>Pellets</td>
<td>12 ± 2</td>
<td>16 ± 6</td>
</tr>
<tr>
<td>Moose</td>
<td>Alces alces</td>
<td>9</td>
<td>Browse</td>
<td>12 ± 2</td>
<td>16 ± 6</td>
</tr>
</tbody>
</table>

Significant differences between Co and Sm measurements within a species are indicated by different superscripts; (a) denotes a trend towards significance (p=0.06 to 0.08).

*This animal received the Sm marker from an elevated trough and ingested the marker within 1 h after being dosed with the Co marker.

Time of first marker appearance in faeces. Calculated according to Thielemans et al. (1978) and Grovum and Williams (1973). Due to n=2, no statistics performed.
Figure 1. Excretion patterns of fluid markers in (a) muskoxen (*Ovibos moschatus*), (b) reindeer (*Rangifer tarandus*) and (c) moose (*Alces alces*) for intraruminally applied Co-EDTA and orally fed Sm-EDTA.
Figure 2. Association of the mean retention time (MRT) of two fluid markers (intraruminally applied Co-EDTA and orally fed Sm-EDTA) in muskoxen (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*) for (a) the whole gastrointestinal tract (GIT) and (b) the ruminoreticulum only.