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The dissociation of the fluid and particle phase in the forestomach as a physiological characteristic of large grazing ruminants: an evaluation of available, comparable ruminant passage data

Abstract Whether differences in digestive physiology exist between different ruminant feeding types has been an ongoing debate. In this regard, potential differences in ingesta retention have been understood to be of particular importance. We analyzed a data pool in which only mean retention time (MRT) data for the ruminoreticulum (RR) were collated that were obtained using comparable techniques with either chromium or cobalt EDTA as a fluid marker and/or with chromium-mordanted fiber of less than 2 mm in size as a particle marker. Data were compared using one averaged value per species. In general, the paucity of species in such a collection is striking and does not allow—in contrast to earlier statements—any final conclusions regarding the influence of body weight (BW) or feeding type on ruminant MRTs. In particular, there was no significant correlation between $MRT_{particles}RR$ or $MRT_{fluid}RR$ and BW, neither in the interspecific nor in the intraspecific comparison, and no difference between the feeding types. The trend that indicates longer $MRT_{particles}$ RR in grazers is based on too few species to be conclusive.

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Small browsers seemed to have shorter $MRT_{fluid}RR$ than similar-sized grazers. In contrast, there was a trend for large grazers to have shorter $MRT_{fluid}RR$ than large browsers. In direct pair-wise comparisons between cattle and the browsers giraffe, moose, and okapi, the latter difference was significant. Cattle also had the highest relative RR fluid outflow rates among the species investigated. This is in accord with the observation that grazers have larger omasa, a major function of which is water-reabsorption distal to the RR. Grazers seem to have longer $MRT_{particles}$ RR per unit $MRT_{fluid}RR$, and cattle are particular outliers in this respect. It is hypothesized that potentially shorter $MRT_{fluid}RR$ in large grazers and higher relative outflow rates are linked to a higher saliva production and a lesser viscosity of both saliva and RR fluids. A constant supply of a fluid phase of low viscosity is proposed to be the prerogative for the physical mechanisms of flotation and sedimentation that result in the stratification of RR contents and its selective particle retention typical for large grazing species.

Introduction

In the debate on physiological consequences of the differentiation of ruminants into feeding types, the question whether there are differences in ingesta passage rate between the feeding types has been a major focus of attention (Hofmann 1989; Gordon and Illius 1994; Robbins et al. 1995; Clauss and Lechner-Doll 2001). Researchers supporting or contradicting potential morphophysiological differences have both emphasized that a quantitative understanding of ingesta retention mechanisms is pivotal for a comprehensive view of ruminant ecophysiology (Kay 1987a; Illius and Gordon 1992; Owen-Smith 1996; Jiang and Hudson 1996). This is due to the fact that there are probably systematic differences between grass and browse, insofar as a longer retention of grass will result in a

significant increase in energy gain, whereas this is much less the case for browse (Demment and Van Soest 1985). To gain insight on the correlation of ingesta passage rates and body size on the one hand, and feeding types on the other hand, different data collections were compiled. Gordon and Illius (1994) collated data on particle mean retention time (MRT) in the whole gastrointestinal tract (GIT) of ruminants and concluded that there was a strong correlation to body weight (BW), but no difference between the feeding types for this parameter. In a similar way, Robbins et al. (1995) collated data on liquid outflow from the ruminoreticulum (RR) and RR fluid passage rates; they did not find any difference between the feeding types and liquid RR outflow was highly correlated to BW. In contrast, RR fluid passage rates did not correlate to BW, but neither these nor other authors commented further on this finding. Clauss and Lechner-Doll (2001) criticized the methods of data compilation in these studies. They collated literature evidence on physiological measurements that indicate a faster particle passage in browsers and proposed the use of the "selectivity factor," originally defined as the ratio of $MRT_{particles}RR/MRT_{fluid}RR$ by Lechner-Doll et al. (1990), and thereby demonstrated potential differences between the feeding types with grazers displaying high and browsers low values for this quotient. However, these authors did not investigate whether this effect was due to longer $MRT_{particles}RR$ or shorter $MRT_{fluid}RR$ in grazers, or a combination of both.

To differentiate between different classes of forestomach physiology when comparing passage rates in ruminants, it is important to only use data for the MRT in the RR, not in the total GIT. Total GIT MRT may differ significantly with respect to a species' adaptation to water conservation in the distal colon. This was exemplified, for instance, by Behrend et al. (2004), comparing values for mouflon from a temperate and sheep from an arid environment. Fecal dry matter concentrations can vary drastically between ruminant species (Clauss et al. 2004), and Woodall and Skinner (1993) showed that this correlates to the length of the distal colon where water reabsorption occurs. Thus, e.g., desert species would be expected to have longer total tract MRTs compared to species of similar RR physiology from temperate environments.

An important aspect of comparing MRT data is the method by which it was derived. Different marker systems can yield different estimates. Particle size is an important determinant of $MRT_{particles}RR$ in ruminants (Lechner-Doll et al. 1991), and therefore, only data referring to a (standardized) similar particle size should be compared. Particles for the measurement of ingesta retention can be labeled by different substances, which differ in their binding characteristics and hence in the results they yield. These differences were discussed in detail by Warner (1981). For ruminants, Poncet and Al Abd (1984) showed that the two most common marker systems for particles, chromium (Cr) mordants, and ytterbium-labeled particles yield results that are not comparable. The same authors showed that results for the two most common liquid markers—polyethylene glycol and a combination of EDTA

and a metal (Cr- or Co-EDTA) are not comparable. The sampling regime can also influence the results: If feces are collected as often as possible, mostly shorter MRTs will be calculated compared to studies where only one or two pooled fecal sample per day are analyzed (as in Foose 1982). Finally, a variety of mathematical models for the calculation of MRT exists (e.g., Amici et al. 1997).

Another important aspect in comparing MRT data is the effect of the feeding level and food characteristics on the measured results. For example, animals of different digestive tract systems all had faster total tract passage rates on alfalfa as opposed to grass hay (Foose 1982); however, in that study, intake was also invariably higher on the alfalfa hay diet. If interspecific comparisons are attempted, the paucity of existing data leads to the inclusion of measurements made on very variable diets.

In this collation of comparable data we intended to test whether the available data allowed any conclusions with regard to quantitative differences in retention mechanisms between grazing and browsing ruminant species. In particular, we intended to elucidate whether the high ratios of particle to fluid retention observed in grazers are the result of longer particle or shorter fluid retention times, or both. Finally, we propose a hypothetical explanation of our findings that emphasizes a parameter that has received little attention in the comparative literature so far: the viscosity of ruminant saliva and rumen fluid.

Materials and methods

Data were collected only from studies that gave at least average values or ranges for the BWs of the animals used, that measured retention times in the RR, that used Cr- or Co-EDTA as fluid marker, and/or that used Cr-mordanted fiber of a particle size <2 mm, prepared according to Udén et al. (1980), as a particle marker. These choices automatically excluded the one major comparative study on wild herbivores in which MRT data for the whole GIT was generated by analyzing one or two pooled fecal samples per day (Foose 1982).

In publications in which no direct values for retention time and outflow rate were given, fluid MRT in the RR was calculated as the reciprocal of the fractional outflow rate (k), and rumen outflow rate was calculated by multiplying RR fluid volume with k. In publications in which the total tract MRT for fluids and particles was given, $MRT_{fluid}RR$ and $MRT_{particles}RR$ were calculated according to Lechner-Doll et al. (1990) by first calculating the fluid MRT for the tract distal to the RR by the subtraction of $MRT_{fluid}RR$ from $MRT_{fluid}GIT$, and then by subtracting the resulting value from $MRT_{particles}GIT$. This procedure assumes that no significant difference in distal tract MRT exists between particles and fluids, an assumption that was principally confirmed by Grovum and Williams (1973), Kaske and Groth (1997), Mambrini and Peyraud (1997).

Data were available for domestic cattle (*Bos taurus*), water buffalo (*Bubalus bubalus*), domestic sheep (*Ovis ammon aries*), mouflon (*Ovis ammon musimon*), wapiti

Fig. 1 Correlation between BW and MRT$_{particles}$RR in different ruminant feeding types—one average value per species. Regression lines: *dotted*, grazer and *solid*, browser. There is no significant correlation with BW within any feeding type or for the whole data set; the number of species is too low to allow a reasonable comparison between the feeding types
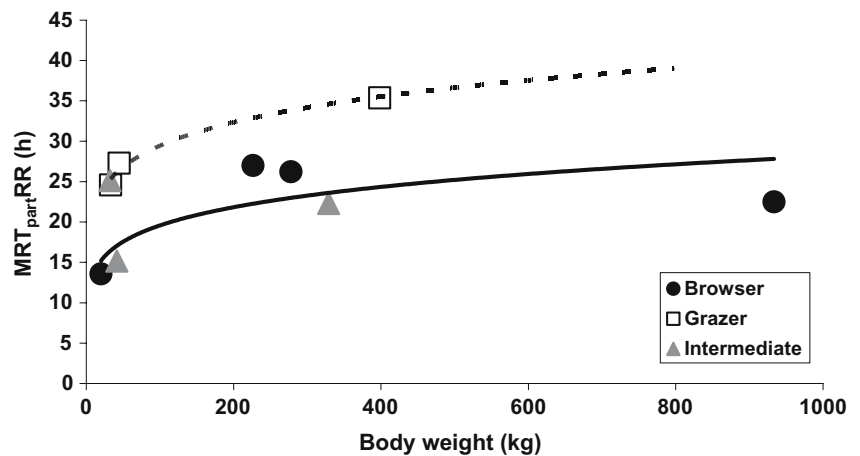
(*Cervus elaphus wapiti*), red deer (*Cervus elaphus elaphus*), domestic goat (*Capra hircus*), giraffe (*Giraffa camelopardalis*), moose (*Alces alces*), okapi (*Okapia johnstoni*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), and roe deer (*Capreolus capreolus*) and was collated from the following sources:

1. MRT$_{particles}$RR
   We used data from Udén et al. (1982), Van Bruchem et al. (1984, read from graph), Kennedy (1985), Lindberg (1985, read from the graph), Okine et al. (1989), Renecker and Hudson (1990), Burns et al. (1997), Clauss et al. (1998), Behrend (2000), Hummel (2003), and the original datasets from Lechner-Doll et al. (1990) and Gross et al. (1996).

2. MRT$_{fluid}$RR
   We used data from Faichney and Griffiths (1978), Faichney (1980), Hendricksen et al. (1981), Poppi et al. (1981a,b), Goetsch and Galyean (1982), Hjeljord et al. (1982), Udén et al. (1982), Varga and Prigge (1982), Colucci et al. (1984), Poncet and Al Abd (1984), Prigge et al. (1984), Van Bruchem et al. (1984, read from graph), Kennedy (1985), Ledoux et al. (1985), Lindberg (1985, read from the graph), McCollum and Galyean (1985), Majak et al. (1986), Merchen et al. (1986), Funk et al. (1987), Krysl et al. (1987), Shaver et al. (1988), Jacques et al. (1989), Okine et al. (1989), Branine and Galyean (1990), Renecker and Hudson (1990), Moore et al. (1990), Tatman et al. (1991),

Arthun et al. (1992), Kattnig et al. (1992), Kennedy et al. (1992), Spalinger et al. (1993), Freudenberger et al. (1994), Holand (1994), Robbins et al. (1995, citing Spalinger and Murden, unpublished article, read from graph), Hatt et al. (1998, individual data from Hatt 1996), Bartocci et al. (1997), De Vaga and Poppiof (1997), Burns et al. (1997), Kaske and Groth (1997), Clauss et al. (1998), Behrend (2000), Tafaj et al. (2001, 2002), Hummel (2003), and the original datasets from Lechner-Doll et al. (1990) and Gross et al. (1996).

3. RR fluid outflow rates
   We used data from Poppi et al. (1980a,b), Goetsch and Galyean (1982), Varga and Prigge (1982), Colucci et al. (1984), Prigge et al. (1984), Dixon and Milligan (1985), McCollum and Galyean (1985), Merchen et al. (1986), Funk et al. (1987), Krysl et al. (1987), Jacques et al. (1989), Renecker and Hudson (1990), Tatman et al. (1991), Arthun et al. (1992), Spalinger et al. (1993), Robbins et al. (1995, citing Spalinger and Murden, unpublished article, read from graph), Kaske and Groth (1997), Behrend (2000), and the original dataset from Lechner-Doll et al. (1990).

According to Illius and Gordon (1992) and McNab (2002), MRTs were assumed to correlate allometrically to BW. As an allometric analysis of the correlation between RR outflow and BW tended to yield an exponent equal to 1, a linear correlation between these two parameters was assumed.

Table 1 Correlation analysis (Pearson's correlation coefficient, PCC) for MRT$_{particles}$RR and BW for the available literature data of different ruminant species and feeding types

n_g is the number of groups included (see Materials and methods), e.g., n=13 and n_g=2 means: this correlation is based on 11 measurement pairs of single animals and 2 group mean pairs

Feeding type/species	n	n_g	PCC	p
One average value per species				
Grazer	3	–	0.977	0.137
Browser	4	–	0.292	0.708
(Groups of) individuals within a species				
Cattle	13	2	−0.140	0.647
Sheep	16	3	−0.377	0.150
Ibex	8	0	0.595	0.120
Goat	11	0	−0.446	0.170
Giraffe	3	0	0.994	0.070
Okapi	8	0	−0.603	0.397

Fig. 2 Correlation between BW and MRT$_{fluid}$RR in different ruminant feeding types—one average value per species. Regression lines: *dotted*, grazer and *solid*, browser. There is no significant correlation with BW within any feeding type or for the whole data set; the number of species is too low to allow a reasonable comparison between the feeding types
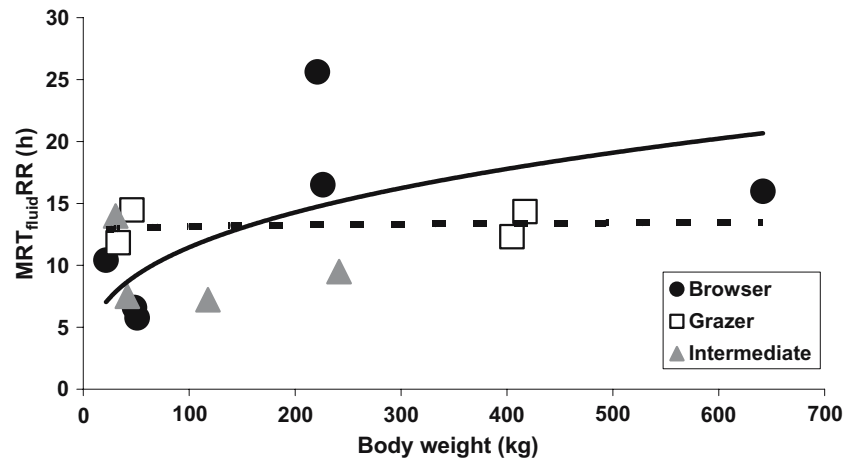
Data were compiled for individual animals whenever possible and only one average value per individual was used for the further calculation of a species average. If data were available for a group of animals only, its average was used for the calculation of the species average after multiplication with its number of individuals in that respective animal group. Such groups were also included in the calculation of Pearson's correlation coefficient (PCC) between retention time and BW or MRT$_{fluid}$RR and MRT$_{particles}$RR in the intraspecific comparisons. In the latter calculations, however, each group contributed just a single data pair (like a single animal), because considering the group's multiplicity would potentially distort the respective p value. The t test was used to compare animals of different species concerning their retention time. In case of multiple tests, the significance was evaluated according to the Dunn/Sidak method (Sokal and Rohlf 1997). ANOVA or analysis of covariance served to compare groups of species assigned to different feeding types. The significance level was always set to 5%. All calculations were performed using the Statistical Package for the Social Sciences 9.0 (SPSS Inc., Chicago, IL, USA) statistical software package.

Results

MRT$_{particles}$RR

Data on MRT$_{particles}$RR were available for the following species:

Species	Animal	Number of publications from which the data were derived from
Browsers	Roe deer	1
	Okapi	1
	Moose (one animal only)	1
	Giraffe	1
Intermediate feeders	Goats	2
	Ibex	1
	Wapiti	1
Grazers	Mouflon	1
	Sheep	5
	Cattle	5

The data are visualized in Fig. 1. They are not numerically sufficient to statistically evaluate differences between the feeding types. The tendency of grazing ruminants to have longer MRT$_{particles}$RR than browsing species cannot be

Table 2 Correlation analysis (Pearson's correlation coefficient, PCC) for MRT$_{fluid}$RR and BW for the available literature data of different ruminant species and feeding types

Feeding type/species	n	n_g	PCC	p
One average value per species				
Grazer	4	–	0.108	0.892
Browser	6	–	0.479	0.337
(Groups of) individuals within a species				
Cattle	33	22	−0.113	0.532
Sheep	33	22	−0.042	0.816
Ibex	8	0	0.771	0.025*
Goat	12	1	−0.243	0.447
Wapiti	3	1	0.950	0.203
Giraffe	6	0	0.461	0.357
Okapi	4	0	−0.881	0.119
Moose	5	4	−0.365	0.546
White-tailed deer	3	0	−0.699	0.507
Roe deer	5	1	0.871	0.055

n_g is the number of groups included (see legend of Table 1)
*p<0.05

Table 3 Correlation analysis (Pearson's correlation coefficient, PCC) for $MRT_{fluid}RR$ and $MRT_{particles}RR$ for the available literature data of different ruminant species and feeding types

Feeding type/species	n	n_g	PCC	p
One average value per species				
Grazer	3	–	−0.106	0.933
Intermediate	3	–	0.894	0.296
Intermediate + grazer (without cattle)	5	–	0.926	0.026*
Browser	4	–	0.763	0.237
(Groups of) individuals within a species				
Cattle	13	2	0.841	<0.001*
Sheep	16	3	0.711	0.002*
Mouflon	5	0	0.909	0.032*
Ibex	8	0	0.914	0.001*
Goat	11	0	0.374	0.257
Giraffe	3	0	1.000	0.020*
Okapi	4	0	0.847	0.123
Roe deer	4	0	0.994	0.006*

n_g is the number of groups included (see legend of Table 1)
*p<0.05

regarded as evidence. The allometric equation derived from these data,

$$MRT_{particles}RR(h) = aBW^b,$$

was neither significant for any feeding type (grazer: $p=0.109$, intermediate feeder: $p=0.876$, browser: $p=0.205$) nor for all ruminant species combined ($p=0.156$). In species in which several animals with given BWs were measured, there was no significant correlation between BW and $MRT_{particles}RR$; the calculated correlation coefficients were not even consistently positive (Table 1). Even if feeding types generally could not be compared because of the data situation, it was possible to compare individual species against each other by the use of t tests. When comparing representatives of browsers and grazers, there was only the tendency for a difference in $MRT_{particles}RR$ between giraffe (22.5 ± 7.0 h) and cattle (35.4 ± 10.4 h, $p=0.055$), no difference between giraffe and sheep (27.3 ± 8.8 h, $p=0.372$) or giraffe and mouflon (24.6 ± 2.6 h, $p=0.552$), and no significant difference between okapi (27.0 ± 3.0 h) and cattle ($p=0.132$), sheep ($p=0.949$), or mouflon ($p=0.230$), respectively. In contrast, roe deer

(13.6 ± 2.0 h) showed significantly shorter values than cattle ($p=0.001$), sheep ($p=0.005$), or mouflon ($p<0.001$).

$MRT_{fluid}RR$

Data on $MRT_{fluid}RR$ were available for the following species:

Species	Animals	Number of publications from which the data were derived from
Browsers	Roe deer	2
	White-tailed deer	1
	Mule deer	1
	Okapi	1
	Moose	2
	Giraffe	2
Intermediate feeders	Goats	3
	Ibex	1
	Wapiti	2
	Red deer	1
Grazers	Mouflon	1
	Sheep	19
	Cattle	25
	Water buffalo	1

Fig. 3 Correlation between $MRT_{fluid}RR$ and $MRT_{particles}RR$ in different ruminant feeding types; the only data used were those where both values were determined simultaneously in individual animals, and one value per species was calculated. Regression lines: *dotted*, intermediate feeders and grazer (without cattle), and *solid*, browser. The outlying value of grazers is domestic cattle
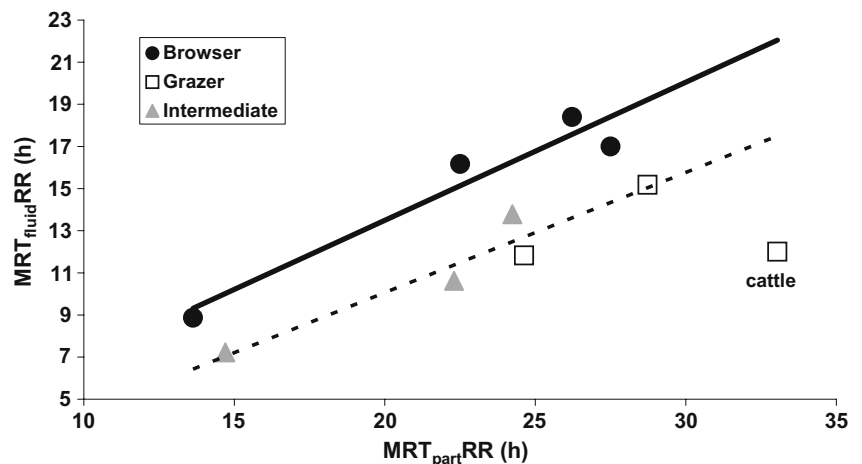
The data are visualized in Fig. 2. The allometric equations derived from these data were neither significant for any feeding type (grazer: $p=0.830$, intermediate feeder: $p=0.621$, browser: $p=0.125$) nor for all ruminant species combined ($p=0.122$). In only one of the 11 species in which several individuals with given BWs were measured was there a significant correlation between BW and $MRT_{fluid}RR$; the calculated correlation coefficients were not even consistently positive (Table 2). The uncertainty concerning the correlation between $MRT_{fluid}RR$ and the BW and the BW gaps in the set of available species do not allow a valid comparison between the feeding types.

Without inclusion of BW (i.e., presuming no correlation), the comparison of feeding types yielded no significant difference between them (ANOVA, $p=0.501$). The tendency of large grazing ruminants to have shorter $MRT_{fluid}RR$ than browsing species cannot be regarded as evidence. Given the situation, it was, however, possible to compare individual species against each other by the use of t tests. Cattle (12.3 ± 3.0 h) had significantly shorter $MRT_{fluid}RR$ than the large browsers giraffe (16.0 ± 3.1 h, $p=0.004$), moose (25.6 ± 3.2 h, $p<0.001$), and okapi (16.5 ± 3.2 h, $p=0.006$), and significantly longer $MRT_{fluid}RR$ than white-tailed deer (6.6 ± 1.2 h, $p=0.0001$); there was no

Fig. 4 Correlation between $MRT_{fluid}RR$ and $MRT_{particles}RR$ in different ruminant species of **a** browsers, **b** intermediate feeders, and **c** grazers; the only data used were those where both values were determined simultaneously in individual animals
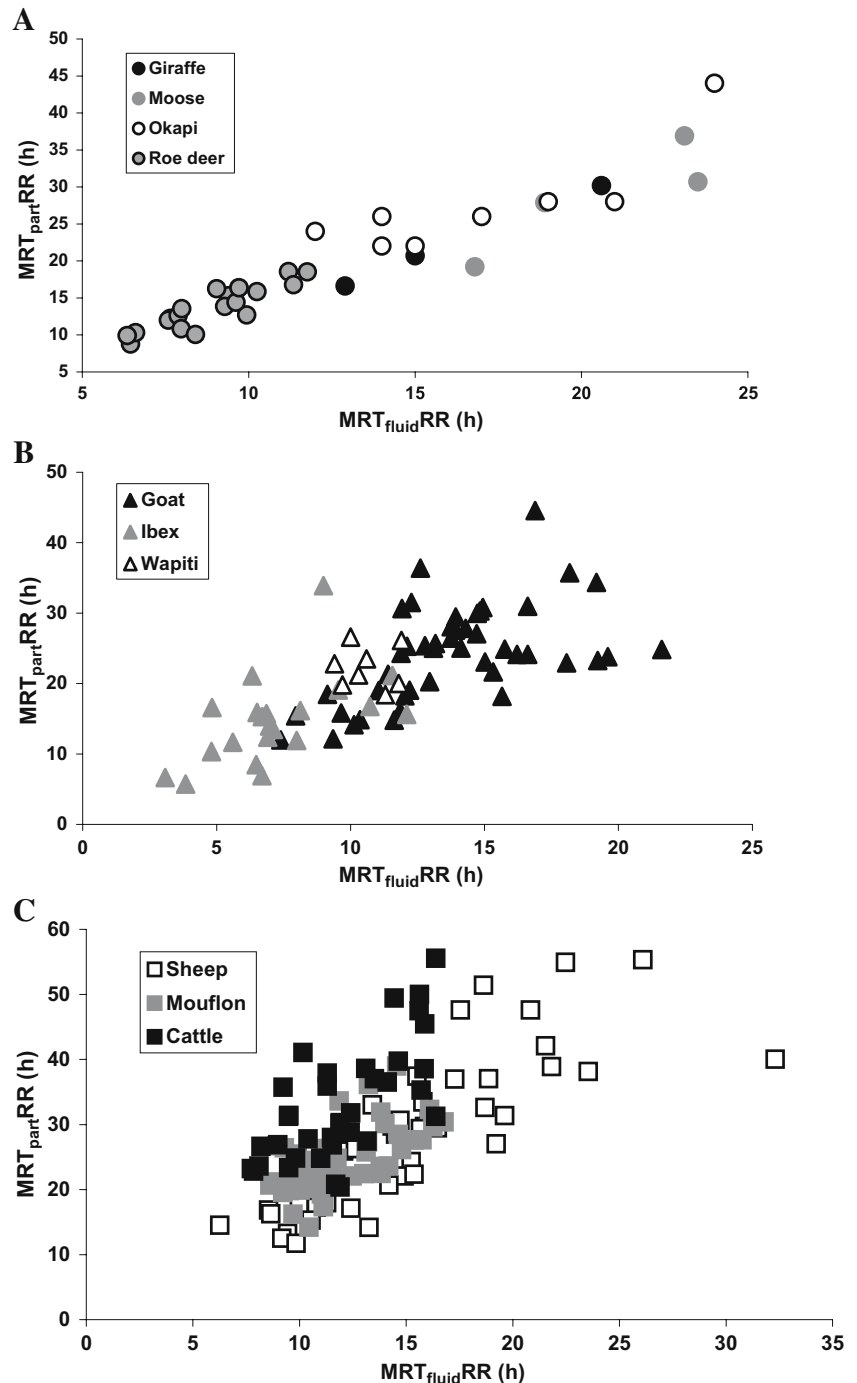
Fig. 5 Correlation of RR outflow and BW in ruminant species of different feeding type, using one value per species. Regression lines: *dotted*, grazer and *solid*, browser
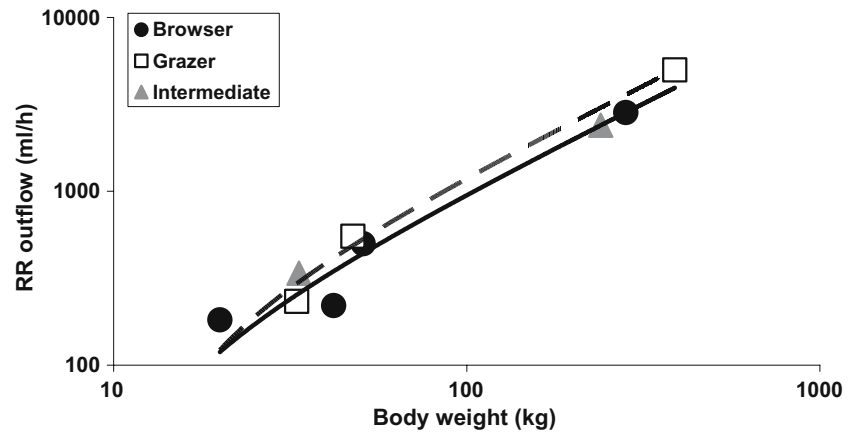
difference between cattle and roe deer (10.4±2.5 h, p=0.125). Moose had significantly longer $MRT_{fluid}RR$ than sheep (14.5±4.1 h, p<0.0001) or mouflon (11.8±1.1 h, p<0.001) and white-tailed deer had significantly shorter $MRT_{fluid}RR$ than sheep (p=0.001) or mouflon (p=0.001). There were no differences between giraffe, okapi or roe deer on the one hand, and sheep or mouflon on the other hand.

For all measurements in which $MRT_{fluid}RR$ and $MRT_{particles}RR$ were simultaneously measured in the same individual (or group of individuals), there were strong correlations between $MRT_{fluid}RR$ and $MRT_{particles}RR$ within species, with the exception of goat and okapi (Table 3). The correlation was stringent in browsers and intermediate feeders, but for the three grazing species available in this study combined, there was no such correlation due to the outlying value for cattle (Fig. 3). When the data for sheep and mouflon were added to that of the intermediate feeders, a stringent correlation resulted again (Table 3). In general, measurements in browsing species tended to be more uniformed (less scattered) across species than measurements in both intermediate feeders and grazers (Fig. 4). When cattle were excluded, the intercepts of the regression lines of $MRT_{fluid}RR$ on $MRT_{particles}RR$ differed significantly between browsers and grazers+intermediate feeders (p=0.026, see also Fig. 3). This means that $MRT_{fluid}RR$ was significantly lower for grazers or intermediate feeders than for browsers if species with similar $MRT_{particles}RR$ are compared. This was all the more true in comparison to cattle, which were excluded from this analysis for formal reasons (parallelity of slopes).

RR fluid outflow

Data on fluid outflow from the RR were available for the following species:

Species	Animal	Number of publications from which the data were derived from
Browsers	Roe deer	1
	White-tailed deer	1
	Mule	1
	Moose	1
Intermediate feeders	Goat	1
	Wapiti	2
Grazers	Mouflon	1
	Sheep	9
	Cattle	12

The data are visualized in Fig. 5. They are not numerically sufficient to statistically evaluate differences between the feeding types. In both browsers and grazers, BW was highly correlated with RR fluid outflow (browsers: PCC=0.998, p=0.002; grazers: PCC=0.999, p=0.015). An interesting tendency was that the regression lines of browsers and grazers without cattle did not differ significantly in their slope (p=0.392); if, however, cattle were included in the grazers, the difference in slope became significant (p=0.018). This could indicate a disproportionately high rumen fluid outflow in cattle. Expressed on a per BW basis, cattle had the highest average relative RR fluid outflow rate (12.7±2.4 ml h^{-1} kg^{-1} SD) when compared to sheep (11.6±3.8 ml h^{-1} kg^{-1}), goats (10.4±1.7 ml h^{-1} kg^{-1}), wapiti (10.3±1.0 ml h^{-1} kg^{-1}), moose (10.0 ml h^{-1} kg^{-1}, SD not available), mule deer (9.8 ml h^{-1} kg^{-1}), roe deer (9.1±0.2 ml h^{-1} kg^{-1}), mouflon (7.1±0.4 ml h^{-1} kg^{-1}), or white-tailed deer (5.2 ml h^{-1} kg^{-1}).

Discussion

Any discussion of results on passage characteristics between species that does not address the issue of potential differences in rations fed and food intake levels will automatically lack explanatory power. However, given the fact that earlier publications on the influence of BW or feeding type on passage characteristics did not address this question either (Illius and Gordon 1992; Gordon and Illius 1994; Robbins et al. 1995), we feel it is justifiable to assess what conclusions can be drawn from a data collection on retention times, which were at least controlled for the consistency of experimental setups used. Undoubtedly, any conclusion would have to be corroborated by more controlled studies that account for differences of both diet ingested and level of intake.

The most striking feature of the data sets compiled in this investigation is the paucity of data on both the species and

the individual level. Many measurements available on the few browsing species were from one publication only, using only very few individuals. However, what is even more striking is the complete absence of measurements on medium-sized and large wild grazer species. In this respect, effects of domestication on the conclusions derived from such data sets cannot be ruled out, and any conclusion regarding the digestive physiology of large grazers that is based on data from cattle only must be regarded with caution. The paucity of comparable data rules out earlier claims (Gordon and Illius 1994; Robbins et al. 1995) that differences between the feeding types do not exist. They may very well exist, but we cannot test on them yet. As it is, the prediction that browsers have faster RR particle passage rates than grazers (Hofmann 1989) remains effectively untested to date (cf. Ditchkoff 2000).

An equally common claim, namely that particle retention time is a function of BW in ruminants (Illius and Gordon 1992; Gordon and Illius 1994), cannot be confirmed for the RR on the basis of comparable data, either. From the data compiled here, it cannot be decided whether $MRT_{particle}RR$ or $MRT_{fluid}RR$ are a function of BW or not. The lack of significance could indicate both a lack of data from more species, or the absence of such a correlation. While the general correlation between BW and $MRT_{particles}RR$ could not be confirmed on an interspecies level, presumably because of a lack of data, such a correlation could not be demonstrated either if individual data within a species are analyzed. In some cases this might be due to low sample size and a narrow BW range. However, such a correlation could also not be detected for species for which a larger number of measurements for a broader range of body sizes were available.

A surprising finding of this study is that large browsers seem to have longer fluid retention times in the RR than the representative of the large grazers—cattle. This is also reflected in higher relative RR outflow rates in cattle than in moose. Up to now, whenever differences in passage rates between the feeding types have been postulated, particles and fluids have been assumed to differ in the same way between grazers and browsers (Kay 1987a; Hofmann 1989). Shorter $MRT_{fluid}RR$ in large grazers as compared to large browsers and its higher relative RR outflow rates would be in accord with the observation of Hofmann (1973, 1989) that grazers have generally larger omasa than browsers of comparable size. A major function of the omasum is the reabsorption of water from the ingesta (Hauffe and von Engelhardt 1975; Edrise and Smith 1979). If it is assumed that relative RR outflow of fluids is higher in grazers than in browsers, a larger omasum in the former with a larger absorptive surface would make sense.

The fact that $MRT_{fluid}RR$ does not correlate with BW was already demonstrated by Robbins et al. (1995); in the data generated by Udén et al. (1982), $MRT_{fluid}RR$ in cattle was even shorter than in sheep and goats on a similar diet, and Colucci et al. (1984) noted that "the rate of passage of Co-EDTA was faster in cows than in sheep for all diets at both levels of intake." These observations already hint at a particular position of cattle among ruminant species. It is evident that $MRT_{fluid}RR$ does not follow a strict allometric pattern to BW over the body size range of ruminants.

Thus, no concluding statement on differences in passage rates between similar-sized grazers and browsers can be made, and only new hypotheses can be put forward. The data compiled in this study indicate that grazers and intermediate feeders retain particles longer in their RR *per unit fluid retention time* than browsers, and that cattle are particularly exceptional in this respect with very long particle retention times per unit fluid retention—or with very short fluid retention times per unit particle retention (Fig. 3). The similar value for $MRT_{fluid}RR$ in cattle and water buffalo (Fig. 2) suggests that in this respect, cattle are representative for other large members of the *Bovinae*. The observation of this dissociation of the fluid and the particle phase leads to the questions: (1) By what mechanism it is caused and (2) What are the potential consequences.

The stratification of rumen contents, i.e., the dissociation of fluids and particles, is a major prerogative for the selective retention of particles in the ruminant forestomach (Lechner-Doll et al. 1991). Differences in forage morphology were used to explain potential differences in the stratification behavior of RR ingesta between browsers and grazers (Clauss et al. 2003). However, considering the data measured by Renecker and Hudson (1990) in cattle and moose on a variety of diets, the dissociation of fluid and particle phase in cattle compared to moose seems to be unaffected by diet composition. Therefore, an intrinsic "animal factor" that determines the stratification behavior of the ingesta in the RR could be suspected to operate as well. In tradition, postulated differences in the size of intraruminal apertures were regarded as such a factor (Kay 1987a; Hofmann 1989), although the physical efficacy of such differences was not explained. A factor with more explanatory power could be the consistency of the RR fluid: For a stratification to occur, the RR fluid needs to be of a low viscosity that allows particles to move in the liquid phase—either float or sink; the lower the viscosity of the fluid, the easier movement of the particles therein. A low viscosity of RR fluid in grazing ruminants would explain why fluid MRT is more detached from particle MRT in these animals. In contrast, a higher viscosity of RR fluid in browsers could be a reason why fluid MRT is more closely associated to particle MRT in this feeding type (Table 3, Fig. 4) and why a stratification of RR contents is less prominent (Hofmann 1973; Clauss et al. 2001). A low RR fluid viscosity in grazers will explain why fermentation gases can gather easily in the dorsal rumen where their concentrated presence (and the corresponding absence of volatile fatty acids) leads to a reduction in papillation and the typical unpapillated dorsal rumen wall (Hofmann 1973). In contrast, a high RR fluid viscosity in browsers would prevent any gathering of fermentation gases, leading to the typical "frothy" RR contents consistence; the absence of a dorsal gas dome would also explain why the dorsal rumen wall of browsers is usually evenly papillated (Hofmann 1973).

One of the major determinants of RR fluid viscosity is saliva viscosity. Larger parotid salivary glands were doc-

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umented in browsing as compared to grazing ruminants (Kay 1987b; Hofmann 1989; Robbins et al. 1995). From this morphological finding, it was deducted that browsers could have higher salivary flow rates than grazers (Hofmann 1989). In contrast, Robbins et al. (1995) did not find a difference in resting salivary flow rate between mule deer, wapiti, and cattle. Regarding the statement of Edrise et al. (1986) that "it appears that the omasum helps to counteract the very great drain on body water imposed by high saliva production…," a smaller omasum in browsers than in grazers (see above) would not make sense if these animals had higher salivary flow rates. Saliva viscosity was not investigated quantitatively in different ruminant species. The only observation stems from Robbins et al. (1987, 1995) who noted that "mule deer saliva…was very viscous with a gelatinous consistency similar to raw egg albumen, whereas cow and sheep saliva was thin and watery." Saliva from mule deer contained 2–3 times as much nitrogen as sheep and cow saliva (Robbins et al. 1987). Investigations of the parotid gland of domestic sheep and cattle led Van Lennep et al. (1977) and Suzuki et al. (1981) to the conclusion that the respective glands' ultrastructure reflected its role in excreting large amounts of fluid with little protein. Likewise, Stolte and Ito (1996) found that the parotis ultrastructure of a series of grazing ruminants (Père David's deer *Elaphurus davidianus*, European mouflon *O. ammon musimon*, African buffalo *Syncerus caffer*, and sable antelope *Hippotragus niger*) was typical for the secretion of large amounts of fluid with very little protein. The intercellular spaces and secretory canaliculi were well developed and the cells possessed numerous large mitochondria. In browsers (roe deer *C. capreolus*, nyala *Tragelaphus angasii*), the same authors found that the secretory canaliculi and intercellular spaces were not as predominant, and the organelles of the parotid acinar cells were more typical of protein-secreting cells. Considering the difference in the recorded parotid gland size, one could speculate that the larger glands of browsers do not produce a larger volume but a more proteinaceous, viscous saliva.

The hypothesis that fast liquid passage from the RR and the production of less viscous saliva are physiological adaptations typical for grazing ruminants, gains circumstantial support from investigations on a digestive problem in domestic ruminants—frothy bloat. The consistency of the RR contents of browsing ruminants was repeatedly described as an unstratified, homogenous, and frothy mass (Hofmann 1973; Nygren and Hofmann 1990; Renecker and Hudson 1990; Clauss et al. 2001); this description suggests that the RR contents of browsers and domestic ruminants with frothy bloat could be similar to a certain degree. Cattle susceptible to bloat were demonstrated to have longer MRT_{fluid}RR and a less distinct selective particle retention (Majak et al. 1986; Okine et al. 1989), lesser saliva production (Mendel and Boda 1961; Gurnsey et al. 1980), and higher RR contents viscosity (Meyer and Bartley 1971, 1972; Clarke and Reid 1974; Sakauchi and Hoshino 1981). The application of substances that prevent bloat lead, at least partially, to faster MRT_{fluid}RR (Branine and Galyean 1990) and a reduced viscosity (Meyer and

Bartley 1972; Stanford et al. 2001). Hence, faster MRT_{fluid} RR, increased relative RR outflow and an increased production of a less viscous saliva might be characteristic physiological adaptations of the digestive tract of large grazing ruminants. These characteristics might be more prominent in the *Bovinae* than in other grazing ruminants.

The consequence of these adaptations would be the distinct RR contents stratification with a "raft" or "mat" floating on top of a fluid layer. Both a high saliva production/fluid throughput and a low saliva viscosity guarantee that the RR fluid is of a consistently low viscosity that allows flotation and sedimentation processes to occur. Thus, the tendency of the longish, fiber-shaped particles into which grasses disintegrate (Clauss et al. 2003), and which display a distinct change in functional density when being digested (Nocek and Kohn 1987; Bailoni et al. 1998) to either cohere in a raft/mat layer or sink to the bottom of the RR according to digestion status, is reinforced. This mechanism ensures a distinct selective particle retention in grazers with its high fiber digestibilities (Iason and Van Wieren 1999; Pérez-Barbería et al. 2004) and very effective particle size reduction (Clauss et al. 2002), but necessitates a larger omasum (Hofmann 1973, 1989) with a larger surface for water reabsorption.

Further research on wild ruminant species is necessary to corroborate or modify these assumptions and to generate sufficient data for a phylogenetically controlled statistical analysis. Any further experimental work should aim at comparing passage characteristics between species consuming their natural forage at both ad libitum and at the same intake level (i.e., for species with the higher ad libitum intake levels, a second run with a restricted feeding period should follow). In particular, MRTs should be determined in a larger variety of species, and the comparative viscosity of saliva and/or RR fluid of different ruminant species should be investigated.

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