ORIGINAL ARTICLE

Retention of solutes and particles in the gastrointestinal tract of a grazing cervid: Père David's deer (*Elaphurus davidianus*)

Jill Derix[1,2] · Sylvia Ortmann[3] · Lisa Wiegmann[4] · Arne Lawrenz[4] · Geert Paul Jules Janssens[1] · Marcus Clauss[5]

Abstract

Ruminants are classified into three groups, according to their feeding behaviour: browsers, intermediate feeders and grazers. Corresponding to their dietary preferences, multiple morphological and physiological adaptations have been described, resulting in another classification: 'moose-type' and 'cattle-type' ruminants. Digesta retention patterns in the gastrointestinal tract (GIT) and reticulorumen (RR) are considered major criteria to distinguish these types, as cattle-type ruminants show shorter retention of fluids (measured by a solute marker) than of particles, while in moose-type ruminants, both are retained for more similar periods. To what extent these digestive types are specific to phylogenetic lineages is still unclear. We measured mean retention times (MRTs) of solutes and particles (2 and 20 mm) in the strictest grazing cervid: the Père David's deer (*Elaphurus davidianus*; $n = 5$; body mass $= 155.0 \pm 14.5$ kg). The MRTs of solutes, small and large particles in the GIT were 34 ± 4, 60 ± 7 and 69 ± 9 h, respectively. The ratio of the MRT of small particles versus solutes in the RR was 2.0 ± 0.1, similar to other cattle-type ruminants. The results confirm the hypothesis that Père David's deer can be classified as cattle-type ruminants, corresponding to both dietary preferences and previously described morphological traits. The results complement previous findings, showing that both cattle-type and moose-type physiologies are found among bovids as well as cervids, indicating that these digestion types can be considered convergent adaptations.

Keywords Browser-grazer dichotomy · Digestive physiology · Père David's deer · Reticulorumen · Selectivity factor

Introduction

Ruminants have been classified into three feeding types (browser, intermediate feeders and grazers) (Hofmann and Stewart 1972) and two digestion types ('moose-type' and 'cattle-type') (Clauss et al. 2010). Moose-type ruminants are typically browsers, whereas cattle-type ruminants cover the spectrum of intermediate feeders and grazers (Codron and Clauss 2010). Some important morphological differences between moose- and cattle-type ruminants are associated with the function of the rumen. The moose-type's ruminal mucosa shows papillation that is more homogeneously distributed over the whole surface, while the papillation in cattle-types is less distinct in the dorsal and ventral, but prominent in the middle rumen (Clauss et al. 2009b). The uneven papillation is an indication for stratified rumen contents, which are seen in cattle-type ruminants, with more moisture in the ventral part of the rumen (Clauss et al. 2009a; Codron and Clauss 2010; Tahas et al. 2017). Stratified rumen contents are linked to a higher rumen fluid throughput in cattle-type ruminants, and therefore, a major physiological difference between moose-type and cattle-type ruminants is that in the former, fluids and particles leave the rumen nearly in parallel, whereas in the latter, particles are retained much longer and hence 'washed' by rumen fluid (Dittmann et al. 2015a). Across ruminant species, the difference in moisture content between

✉ Marcus Clauss
    mclauss@vetclinics.uzh.ch

[1] Department of Nutrition, Genetics and Ethology, Faculty of
     Veterinary Medicine, Ghent University, Heidestraat 19,
     9820 Merelbeke, Belgium

[2] Department of Pathology, Bacteriology and Avian diseases, Faculty
     of Veterinary Medicine, Ghent University, Salisburylaan 133,
     9820 Merelbeke, Belgium

[3] Leibniz Institute for Zoo and Wildlife Research (IZW),
     Alfred-Kowalke-Str. 17, 10315 Berlin, Germany

[4] Zoological Garden Wuppertal, Hubertusallee 30,
     42117 Wuppertal, Germany

[5] Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty,
     University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland

dorsal and ventral rumen (content stratification), the papillation gradient (papillation stratification) and the degree by which fluids leave the rumen sooner than particles (digesta washing) appear to be interrelated (Tahas et al. 2017).

Lechner-Doll et al. (1990) called the difference in mean retention time (MRT) of fluids and particles the 'selectivity factor' (SF), expressed as the ratio of $MRT_{particle}/MRT_{solute}$ in the reticulorumen (RR). Low SF values are present in tragulids (Darlis et al. 2012), giraffids (Hummel et al. 2005), a number of cervids (Behrend et al. 2004; Lechner et al. 2010) and some bovid species (Clauss et al. 2011), suggesting either a convergence in this characteristic in browsing species, or that this characteristic represents the plesiomorphic state in ruminants. While high SF values have been reported in a variety of bovid species (Dittmann et al. 2015a), few SFs have been reported for cervid species that are not considered strict browsers, namely the wapiti (Cervus elaphus) with a SF_{RR} of 2.1 (Renecker and Hudson 1990) and the reindeer (Rangifer tarandus) with a SF_{RR} of 1.7 (Lechner et al. 2010). Notably, data on MRT and SF in a cervid species that is considered a grazer has been lacking so far.

One reason might be the general lack of truly grazing species among cervids. According to Hofmann (1985), some deer species are browsers and all other are intermediate feeders, with no strict grazing species. Others disagree and count for example the hog deer (Axis porcinus) (Asher 2011) and the axis deer (Axis axis) (Pérez et al. 2015) among grazers, as they primarily graze during the summer. In a later publication, Hofmann (1991) himself considered the Père David's deer (Elaphurus davidianus) a grazer. While the literature is divided on whether Père David's deer should be considered grazers or intermediate feeders (Beck and Wemmer 1983; Van Wieren 1996; Jiang and Takatsuki 1999), with a diet that contains approximately 75% of grass, they are considered the 'most grazing' species amongst cervids (e.g. Cantalapiedra et al. 2014), although this information most likely only derives from a very general statement in Nowak and Paradiso (1999). In addition, Père David's deer show morphological traits that suggest that they are ruminants of the cattle-type, with a stratified rumen papillation (Clauss et al. 2009b). In the present study, the MRTs of solute and particle markers in the GIT of Père David's deer were investigated, to test whether its digestive physiology matches the ruminal morphology and the vague botanical classification.

Materials and methods

This study was performed under animal experiment licence 84-02.04.2016.A363 at the Zoological Garden of Wuppertal, Germany. Five female Père David's deer (body mass BM 155.0 ± 14.5 kg) were adapted to a diet of only grass hay, fed for ad libitum consumption, in their usual group enclosure. Animals had been weighed recently during immobilisation for the application of ear tags and for a general clinical examination. They were sequentially assessed in individual housing between September 20th and November 6th of 2017. Individual housing was either achieved in a 4.2×4.0 m compartment with paved floor (animals 1–2) or a 5.7×4.7 m compartment with concrete floor (animals 3–5), which were both located in larger stables and had empty neighbouring enclosures to allow a shifting of the animals during feeding, cleaning and faeces collection. The enclosure floors were covered with sawdust. Throughout the whole study, the animals had ad libitum access to clean drinking water and the grass hay. New hay was offered every day at the same hour, to maintain a constant feeding routine. In the individual compartments, animals were maintained first for an adaptation period of 7 days and a subsequent collection period of 8 days. During the adaptation period, animals were habituated to being offered, always at the same hour of the day, a separate meal of 80 g wheat bran mixed with small hay particles, water and red beet juice (imitating the colour of Co-EDTA), in order to habituate them to this meal and thus guarantee unproblematic ingestion when the passage markers were to be applied in a meal on the last day of adaptation. During the collection period, hay intake was monitored by weighing offered and refused hay on a daily basis. Every day, hay samples (offered and refused) were taken and kept at room temperature for later analysis.

Three markers were used to measure retention times: Co-EDTA as a solute marker for the fluid digesta fraction, Cr-mordanted fibre for small particles (< 2 mm) and La-mordanted fibre for larger particles (~ 20 mm), prepared according to Udén et al. (1980) and Schwarm et al. (2009). The particle markers contained 36.9 g Cr and 20.9 g La/kg dry matter, respectively. The markers were fed at approximately 0.1 g/kg BM for the fibre mordants and 0.02 g/kg BM for the Co-EDTA. The marker meal was offered at the last day of the adaptation period and was consumed within 15 min by all animals.

For faeces collection, animals were shifted from the main compartment to the neighbouring pen. All faeces were collected in toto from the compartment, cleaned of sawdust, and weighed. Thereafter, a representative sample of approximately 200 g fresh weight was stored in a tared aluminium dish at − 20 °C until further processing. Prior to marker feeding, three faecal samples were taken on 48 h, 24 h and 12 h before the marker was fed, to determine baseline concentrations of Co, Cr and La. After marker feeding, faeces were collected regularly for 8 days, with intensive sampling during the first 2 days (every 4 h) and increasing time intervals thereafter: on the third day every 6 h, on the fourth and fifth days every 8 h, and on the sixth, seventh and eighth days every 12 h. It was assumed that the markers would be excreted completely

within 8 days. As this was not always the case (see 'Results'), the resulting MRT values represent slight underestimates.

Representative samples of the offered and refused hay were ground to pass through a 2-mm mesh sieve. Thereafter, samples were subjected to standard nutrient analyses (AOAC 1995) for dry matter (DM) and total ash (AOAC no. 942.05), crude protein (AOAC no. 977.02), crude fibre (AOAC no. 930.10), crude fat (AOAC no. 920.39, only the hay offered), and neutral detergent fibre (NDF, AOAC no. 2002.04; corrected for residual ash). For each animal, a portion of every faecal sample (representing a constant proportion of the daily faeces output) was pooled, dried at 60 °C and then ground using a blender and analysed for DM, crude ash, crude protein, crude fibre, NDF) with the same methods.

The individual faeces samples were dried at 105 °C, ground with a blender and used for marker analysis by inductively coupled plasma optical emission spectrometer (model Optima 8000, PerkinElmer, Rodgau, Germany) according to Frei et al. (2015). The MRT in the whole digestive tract was calculated according to Thielemans et al. (1978) as:

$$\mathrm{MRT} = \frac{\Sigma t_i C_i dt_i}{\Sigma C_i dt_i}$$

with C_i = marker concentration in the faecal samples from the interval represented by time t_i (h after marker administration, using the midpoint of the sampling interval) and dt_i = the interval (h) of the respective sample

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

Complete excretion of the markers was assumed once the faecal marker concentrations were similar to the background levels determined in pre-dose faecal samples. Mean retention time in the RR was estimated following Lechner-Doll et al. (1990). The $\mathrm{MRT_{solute}RR}$ is determined by estimating the rate constant of the descending part of the marker excretion curve via an exponential equation:

$$y = A \times e^{-k \times t}$$

with y = faecal marker concentration at time t (mg/kg DM), A = a constant, k = rate-constant ($\mathrm{h^{-1}}$) and t = time after marker dosing (h); the reciprocal of k represents the MRT for the RR. The $\mathrm{MRT_{particle}RR}$ is calculated based on the assumption that fluid and particles do not differ in passage characteristics distal to the RR (Mambrini and Peyraud 1997) and that ruminal dilution rate is covered by the rate constant of the decreasing part of the marker excretion pattern alone:

$$\mathrm{MRT_{particle}RR}$$
$$= \mathrm{MRT_{particle}GIT} - (\mathrm{MRT_{solute}GIT} - \mathrm{MRT_{solute}RR})$$

The selectivity factor (SF, the ratio of $\mathrm{MRT_{particle}}$/ $\mathrm{MRT_{solute}}$) was calculated for both the total GIT and the RR.

Results

Nutritional values of the feed are presented in Table 1. Differences between offered and leftover hay reflect selective feeding. Of the total amount of offered hay, $52 \pm 10\%$ was refused on a dry matter basis. The refused hay contained more crude fibre (-0.3–6.4%) and NDF (0.6–6.9%) and less protein (-1.0–-0.3%) than the offered hay. Daily food intake averaged at 2002 ± 247 g DM, and faecal excretion at 769 ± 34 g DM. The resulting apparent digestibility coefficients for dry matter, organic matter, crude protein, crude fibre and NDF were 61.0 ± 6.0, 62.4 ± 6.1, 52.2 ± 6.4, 54.4 ± 10.9 and $55.0 \pm 6.9\%$.

Table 1 Nutrient composition of the offered hay, leftovers and faeces as well as the nutrient digestibility for five Père David's deer (*Elaphurus davidianus*)

Animal		1	2	3	4	5
Offered hay						
Dry matter (DM)	(% as fed)	90.6				
Crude ash	(% DM)	5.4				
Crude protein		5.4				
Ether extracts		1.6				
Crude fibre		29.9				
Neutral detergent fibre		62.2				
Hay leftovers						
Dry matter (DM)	(% as is)	90.3	89.4	90.9	90.8	91.4
Crude ash	(% DM)	5.1	5.4	4.8	5.0	4.5
Crude protein		4.9	5.1	4.5	4.4	4.7
Crude fibre		36.3	34.3	30.2	30.9	29.6
Neutral detergent fibre		65.7	67.7	64.7	69.1	62.8
Ingested diet						
Crude ash	(% DM)	5.7	5.4	6.3	5.9	6.6
Crude protein		5.9	5.6	6.8	6.6	6.4
Crude fibre		23.8	27.4	29.4	28.7	30.3
Neutral detergent fibre		58.8	59.1	58.3	53.9	61.4
Faeces						
Dry matter (DM)	(% fresh)	33.7	28.2	29.2	30.8	29.1
Crude ash	(% DM)	10.0	9.8	9.2	9.9	7.4
Crude protein		7.2	8.2	7.9	7.4	7.6
Crude fibre		32.8	29.5	31.5	33.0	34.2
Neutral detergent fibre		64.8	65.7	68.9	65.2	71.7
Apparent digestibility (%)						
Dry matter		55.0	69.0	58.1	65.9	57.2
Organic matter		57.0	70.4	59.4	67.3	57.6
Crude protein		44.8	54.3	51.4	61.8	48.8
Crude fibre		37.8	66.6	55.2	60.8	51.7
Neutral detergent fibre		50.4	65.5	50.5	58.7	50.1

The excretion patterns of the passage markers are shown in Fig. 1. Approximately 16 h after marker administration, the excretion started, for both fluid and particles. Thereafter, maximum concentrations of Co-EDTA, Cr-mordanted fibre and La-mordanted fibre were detected 20.8 ± 3.3, 32.8 ± 3.3 and 50.4 ± 14.5 h after the marker was consumed, respectively. Complete excretion of the fluid marker was finished after an average of 6.3 days, while both particle markers were still detected in the faeces after the full experimental phase of

8 days. Yet, at that point, they were present at very low concentrations ($4 \pm 4\%$ of peak concentration).

On average, the $MRT_{particle}$ in the GIT was 59.8 ± 6.8 h for small particles (2 mm) and 69.3 ± 9.1 h for large particles (20 mm). Shorter retention times were measured for solutes, with an average $MRT_{solute}GIT$ of 33.8 ± 4.4 h. This was also found to be true for retention in the RR, where small particles, large particles and fluids were excreted approximately after 52.9 ± 6.6, 62.4 ± 8.7 and 26.9 ± 4.2 h. Based on MRT values
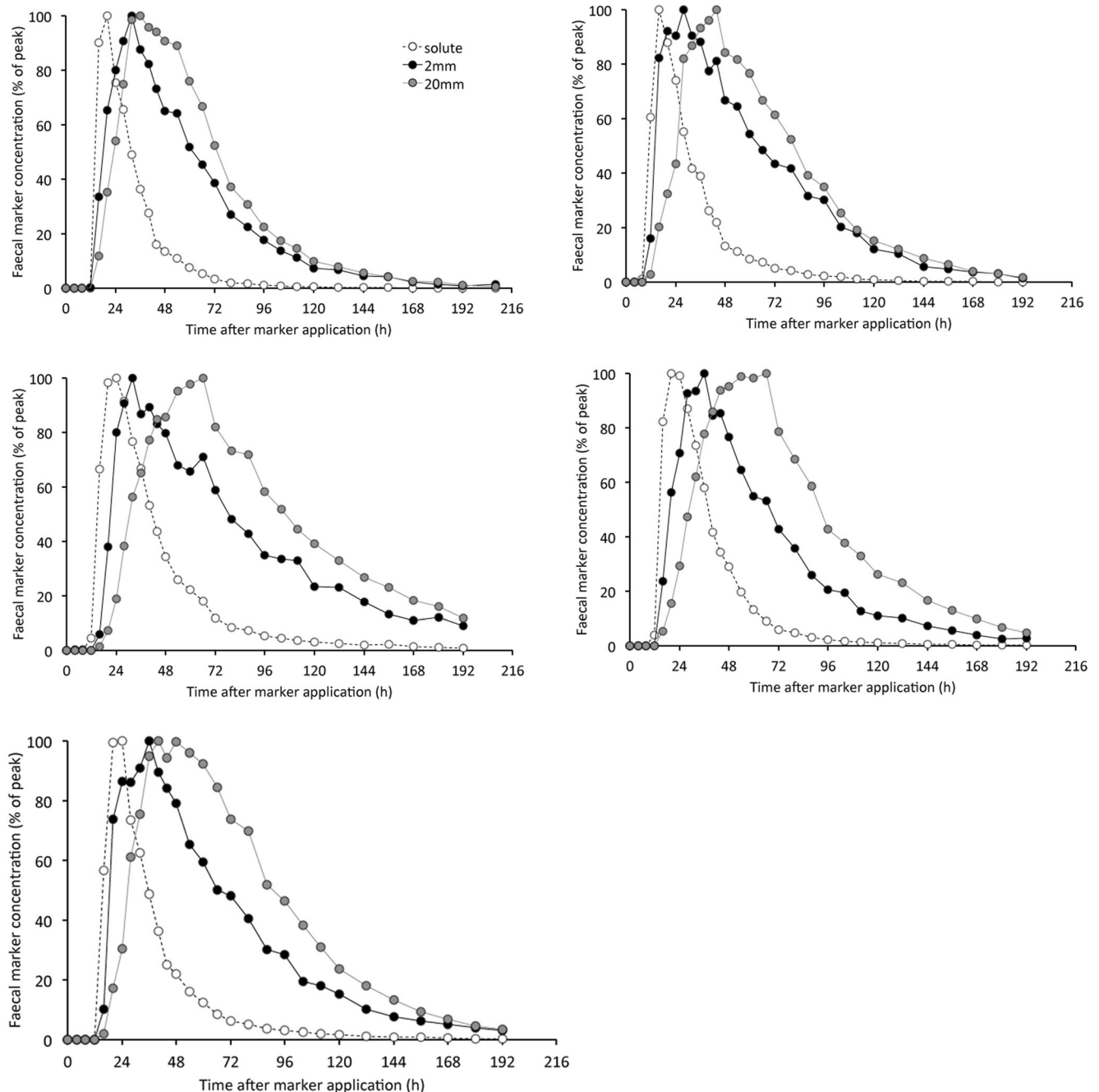

Fig. 1 Faecal excretion patterns for solute, small particle (2 mm) and large particle (20 mm) markers in five Père David's deer (% of peak concentration)

of small particles versus those of solutes, the SF was 1.8 ± 0.1 for the whole GIT and 2.0 ± 0.1 for the RR (Table 2).

Discussion

The present study shows that the SF in Père David's deer corresponds to values described for other grazing ruminants. This confirms the occurrence of cattle-type digestion in a cervid species, strongly suggesting that ruminant digestion types are convergent adaptations.

Typical constraints for zoo-based research apply: The number of animals was limited, and it was not considered justifiable to assess individual animals more than once, for example on different diets, different feed intake levels, or on the same diet to evaluate the repeatability of the results. Therefore, the results must be considered with caution, although the similarity between the five individuals at least suggests that the results could be representative for the species. It should be noted that in ruminants, apparent protein digestibilities do not mainly indicate protein degradability, but simply protein intake.

An important constraint of this study is the method of marker administration via voluntary consumption. This might have had an effect on particle markers, if the mordanted fibres were chewed on by the animal. Options to circumvent this situation were not given in the present study: On the one hand, the use of fistulae (Lechner et al. 2010) is rarely possible for wild ruminants, and fistulation for such just a single experiment does not appear ethically justified. On the other hand, the practice of feeding a marked forage whole (i.e., not chopped

or ground) and determining the mean retention times of different faecal particle size fractions does not allow an estimation of large particle retention in ruminants (Hummel et al. 2018). Their comminution during rumination makes them indistinguishable from smaller particles that are excreted sooner. Another possible limitation could exist in the accuracy in faeces and leftover hay collection. To minimise errors in precision, collection was carried out by the same person during the whole trial. A third problem is the possible effect of the unusual stress of the experimental setup, including the fact that animals normally kept in a group are kept individually. While the adaptation period, which also included habituation to the investigators' presence and the management routines of feeding and faeces collection, most likely reduced such stress to a considerable extent, its effect cannot be excluded or reasonably assessed.

As the animals were fed ad libitum hay with ample amounts of leftovers each day (2211 ± 641 g), they had the opportunity to feed selectively. The ingested hay had slightly lower levels of crude fibre and NDF and higher protein levels, indicating that the animals used this opportunity to a certain extent. In the present study, animals digested $55.0 \pm 6.9\%$ of NDF. In a data collection of 37 studies on 24 ruminant species, the NDF digestibility of very strict browsers ranged approximately between 25 and 50%, whereas grazers had a range of 50–65% (Pérez-Barbería et al. 2004). The values of our Père David's deer therefore fall into the 'grazer' category. The difference in NDF digestibility between species is most likely a result of differences in retention time of the fibre, as longer retention facilitates a more thorough digestion by the commensal rumen bacteria (Hummel et al. 2006).

Table 2 Body mass (BM), dry matter intake (DMI), dry matter excretion (DME) and parameters for feed retention for gastrointestinal tract (GIT) and reticulorumen (RR) in captive *Elaphurus davidianus*

Animal	1	2	3	4	5
BM (kg)	174	155	150	163	146
DMI (g/day)	1783	2377	1829	2122	1896
Leftovers (% of offered)	49	36	61	56	58
DMI (g/kg BM$^{0.85}$ day)	22	33	26	28	27
DME (g/day)	803	738	766	724	811
MRT$_{solute}$GIT [h]	29.2	29.5	41.2	33.4	35.5
MRT$_{particle}$GIT (2 mm) [h]	53.4	55.0	72.5	58.0	60.0
MRT$_{particle}$GIT (20 mm) [h]	57.6	62.4	83.8	73.3	69.5
SF GIT (2 mm)	1.8	1.9	1.8	1.7	1.7
MRT$_{solute}$RR [h]	21.8	24.4	33.9	25.1	29.2
MRT$_{particle}$RR [h] (2 mm)	46.1	49.9	65.2	49.7	53.8
MRT$_{particle}$RR [h] (20 mm)	50.2	57.4	76.5	64.9	63.2
SF RR (2 mm)	2.1	2.0	1.9	2.0	1.8

Small particle marker (2 mm, chromium (Cr)); large particle marker (20 mm, lanthanum (La))

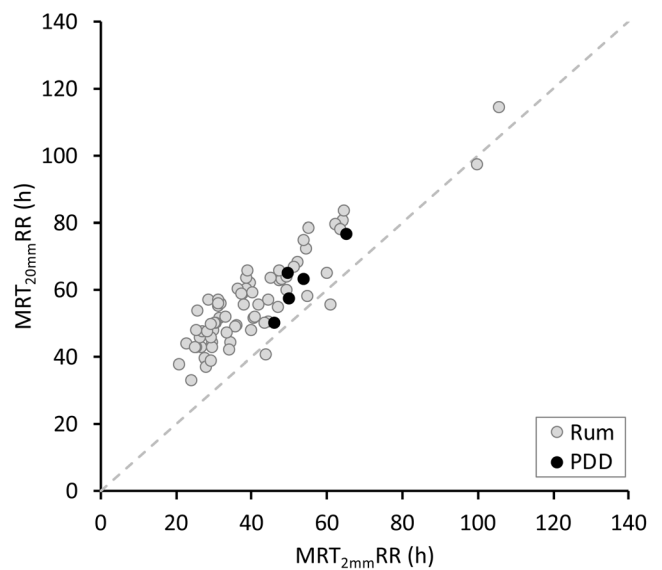*MRT* mean retention time, *SF* selectivity factor

Fig. 2 Relationship of the mean retention time (MRT) between small and large particles. Data collection for ruminants (RUM) from Dittmann et al. (2015b) with data from the current study on Père David's deer (PDD, *Elaphurus davidianus*). The dotted line denotes $y = x$

Fig. 3 Relationship between the mean retention time (MRT) of small particles and a solute marker in the reticulorumen (RR) of various ruminant species (from Dittmann et al. 2015a). Among the species consuming more than 20% grass in their natural diet, cervids are in grey
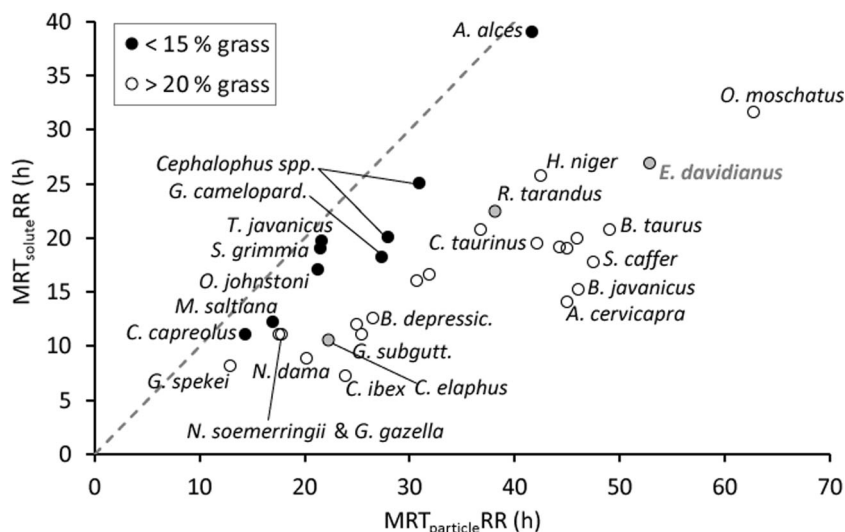
With respect to particle sorting, combining the results of the present study with the data collection of Dittmann et al. (2015b) (Fig. 2) indicates that the particle size discrimination mechanism in Père David's deer is similar to that observed in other ruminants. For absolute retention times, Dittmann et al. (2015a) noticed that the $MRT_{particle}RR$ was significantly related to the percentage of grass (%grass) in the natural diet across ruminant species, although significance became only marginal once BM was also accounted for in the analysis. In our Père David's deer, $MRT_{particle}RR$ were relatively high compared to values measured in other ruminants with comparable %grass in their natural diet, such as *Oryx gazella* (46.0 h) or *Antilope cervicapra* (45.0 h) (Dittmann et al. 2015a). An extended particle retention
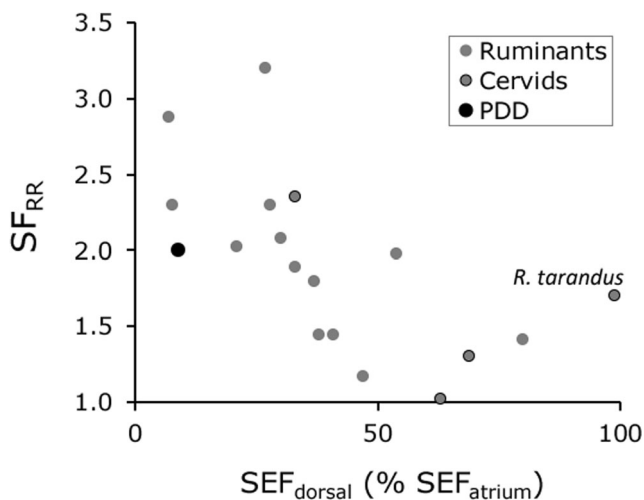
Fig. 4 Relationship between the ruminal papillation gradient (expressed as the surface enlargement factor SEF of the dorsal rumen in % of the SEF of the atrium ruminis) and the selectivity factor (SF) in the reticulorumen (RR) in ruminant species from Tahas et al. (2017) and the Père David's deer (PDD, *Elaphurus davidianus*) of the present study. Note that a lower SEF percentage indicates a more stratified ruminal papillation, and a higher SF a more distinct difference in the retention of particles and fluids in the RR

has often been suggested to be a logical consequence of a grass diet. Grass contains a higher content of digestible fibre, and therefore long retention times in the RR are an expected adaptation of grazing ruminants (Hummel et al. 2006; Dittmann et al. 2015a). This does not seem to be the case for the retention of fluid. $MRT_{solute}RR$ itself is neither linked to %grass in the diet nor to BM, but is likely species-specific (Dittmann et al. 2015a). In particular, the relationship between $MRT_{solute}RR$ and $MRT_{particle}RR$ is considered an indicator for digestion type (with a higher difference in cattle-type ruminants) (Clauss et al. 2010): Cattle-type ruminants show SF values in the reticulorumen from 1.7 to 4.6, whereas the SF of moose-type ruminants is much lower (1.1–1.8) (Hummel et al. 2005). The relationship between $MRT_{solute}RR$ and $MRT_{particle}RR$ has been qualitatively linked to categorical feeding types (Clauss and Lechner-Doll 2001), shown to differ quantitatively between categorical feeding types (Clauss et al. 2006), as well as shown to correlate significantly with the %grass in the natural diet as a continuous variable for feeding types (Dittmann et al. 2015a). Adding our data of the Père David's deer to the data collection of Dittmann et al. (2015a) (Fig. 3) shows that Père David's deer represent the most extreme cervid investigated so far and that cervid species are distributed across the whole data range covered by bovid ruminants. When plotting the average SF measured in our Père David's deer against data from other animals on the intraruminal papillation pattern (Fig. 4), Père David's deer match the overall ruminant pattern of an increased difference in intraruminal papillation with a higher SF. This has been explained by the triggering of rumen contents stratification by a high SF, consequently resulting in a stratification of the intraruminal papillation pattern (Tahas et al. 2017).

It remains unclear whether the moose-type or the cattle-type morphophysiology represents the original or a derived set of characteristics. Browsing ruminants have been considered the 'original' ruminants (Hofmann 1989), which was also

based on the fact that many families that hold only few species (such as tragulid, giraffid, pronghorn and musk deer) involve browsers. However, various lines of evidence from analyses of the cervid and bovid families that include many more species have insinuated that current information is more compatible with considering the state of mixed feeders (and therefore, by derivation, a cattle-type digestive physiology) as the ancestral state of ruminants, with strict browsing and strict grazing both representing secondary adaptations (Codron et al. 2008; DeMiguel et al. 2008; Cantalapiedra et al. 2014; Cerling et al. 2015). At present, it cannot be decided whether high or low SF is the ancestral condition, but the fact that both occur in cervids and bovids opens the possibility that a high SF, aimed at microbial harvesting, was an early adaptation of ancestral ruminants.

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