



Digesta passage in nondomestic ruminants: Separation mechanisms in ‘moose-type’ and ‘cattle-type’ species, and seemingly atypical browsers

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ABSTRACT

Ruminants have been classified as having a ‘moose-type’ or ‘cattle-type’ digestive physiology. ‘Cattle-type’ ruminants have a clear difference in the mean retention time (MRT) of fluid vs. small particles in the reticulorumen (RR), with a high ‘selectivity factor’ ($SF = MRT_{\text{particle}} / MRT_{\text{fluid}} > 1.80$), and are typically grazers and intermediate feeders. ‘Moose-type’ ruminants have lower $SF (< 1.80)$, possibly because of defensive salivary proteins that constrain amounts of (high-viscosity) saliva, and are typically restricted to browsing. To further contribute to testing this physiology-diet correlation, we performed 55 individual passage measurements in 4/6 species that have/have not been investigated previously, respectively. Co-EDTA was used as a solute (fluid) and Cr-mordanted hay particles (< 2 mm) as particle markers. Results are related to the percentage of grass in the natural diet taken from the literature. Moose (*Alces alces*, $n = 4$ on 4 to 5 diets each and $n = 2$ on a single diet, 5% grass, $SF 1.46 \pm 0.22$) and giraffe (*Giraffa camelopardalis*, $n = 3$ on 3 to 5 diets each, 1%, 1.42 ± 0.23) as classical ‘moose-type’, and cattle (*Bos taurus*, $n = 2$, 70%, 2.04) as classical ‘cattle-type’ ruminants yielded results similar to those previously published, as did waterbuck (*Kobus ellipsiprymnus*, $n = 5$, 84%, 2.46 ± 0.49), corroborating that the SF represents, to a large extent, a species-specific characteristic. Results in oryx (*Oryx leucoryx*, $n = 1$, 75%, 2.60) and sitatunga (*Tragelaphus spekii*, $n = 4$, 68%, 1.81 ± 0.21) correspond to the concept of ‘cattle-type’ ruminants being grazers or intermediate feeders. However, European bison (*Bison bonasus*, $n = 1$, 10%, 2.74), nyala (*T. angasii*, $n = 6$, 20%, 1.95 ± 0.25), bongo (*T. eurycerus*, $n = 3$, 13%, 2.39 ± 0.54) and gerenuk (*Litocranius walleri*, $n = 1$, 0%, 2.25) appear as ‘cattle-type’ ruminants, yet have a browse-dominated diet. While the results do not challenge the view that a ‘moose-type’ digestive physiology is an adaptation to browse diets, they indicate that it may not be the only adaptation that enables ruminants to use browse. Apparently, a ‘cattle-type’ digestive physiology with a high SF does not necessarily preclude a browsing diet niche. High- SF browsers might have the benefit of an increased harvest of RR microbiota and grit removal prior to rumination; how they defend themselves against secondary plant compounds in browse remains to be investigated.

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1. Introduction

Ever since the seminal work of Hofmann and Stewart (1972) and Hofmann (1973, 1989), wild ruminants have presented a classic case of niche diversification and convergence by morphophysiological adaptations to diets consisting of browse, grass, or varying intermediate (mixed) stages (Clauss et al., 2008; Codron et al., 2019). Among the many measurements considered in this context is the difference in the mean retention time (MRT) of fluid, as measured by a solute marker, and of small particles, as measured by mordanted fibres (reviewed by Dittmann et al., 2015). In some ruminant species, such as the moose (*Alces alces*), these two digesta phases move more or less in parallel, resulting in ratios of the MRT (particles/fluids) in the reticulorumen (RR) of < 1.80. This ratio has been termed the ‘selectivity factor’ (SF) (Lechner-Doll et al., 1990b). In other species, such as cattle (*Bos primigenius taurus*), the SF is very high, indicating that fluids move much faster through the RR than the fine particle phase. Correspondingly, the two physiological types of ruminants have been termed ‘moose-type’ and ‘cattle-type’ (Clauss et al., 2010b), with ‘moose-type’ ruminants being exclusive browsers, whereas ‘cattle-type’ ruminants occupy both the exclusive grazing and the mixed feeding niche (Codron and Clauss, 2010).

There is distinct appeal in the interpretation focus on the difference in fluid throughput through the rumen. Other narratives that emphasize a putative difference in the fibre content (Hofmann, 1989), or a putative difference in stratification behaviour (Clauss et al., 2003b), between browse or grass are in conflict with empirical data (reviewed by Clauss and Hummel, 2017). In contrast, differences in fluid throughput can be reconciled with other morphological observations. Larger salivary glands in ‘moose-type’ ruminants putatively produce lower amounts of a more viscous saliva due to salivary tannin-binding proteins (Hofmann et al., 2008). A higher fluid throughput should lead to a more distinct stratification of rumen contents and hence a more distinct intraruminal papillation gradient in ‘cattle-type’ ruminants (Clauss et al., 2009c). A viscous rumen fluid could not quickly re-fill the reticulum if that organ contracted completely, which could explain the need for much-reduced reticular crests in ‘moose-type’ ruminants (Clauss et al., 2010a). A higher fluid throughput matches the need for much larger fluid re-absorbing omasa in ‘cattle-type’ ruminants (Ehrlich et al., 2019). Finally, a more viscous rumen fluid in ‘moose-type’ ruminants (Lechner et al., 2010) might prevent a clear separation of fluid and small particles. This narrative shifts the focus away from direct adaptations to either diet type, but stresses the general advantage of having a relatively high fluid throughput through the RR: such fluid movement will likely lead to an increased intensity of the harvest of microbes from the RR (Hummel et al., 2008; Hummel et al., 2015), irrespective of diet. The fluid probably flushes microbes towards the lower digestive tract, harvesting this source of nutrients, and at the same time exerting selective pressure on the remaining microbes for high growth rates (Clauss and Hummel, 2017).

Exclusive browsers, it is suggested, cannot afford this strategy, because they need to defend themselves against the secondary plant compounds in browse with salivary proteins (Austin et al., 1989; Robbins et al., 1991; Hagermann and Robbins, 1993; Fickel et al., 1998). The production of these proteins is thought to require larger salivary glands and to limit the overall saliva output (Hofmann et al., 2008). Additionally, some toxins like alkaloids, or peptids/proteins with deterrent effects, can be modified by rumen microbes (Van Soest, 1994). A lower saliva throughput through the rumen gives microbes more time to de-toxify those plant toxins that are soluble and not neutralized by salivary proteins. Therefore, browse is considered to limit ruminants to a ‘moose-type’ strategy, whereas mixed and grass diets allow ruminants to reap benefits of a ‘cattle-type’ strategy that are not linked to a specific property of these diets (but only the absence of a constraining factor). In particular, this narrative accommodates observations that some apparently ‘extreme’ ‘cattle-type’ ruminants, such

as many Bovini and muskoxen, are not the most extreme grazers (Clauss and Hofmann, 2014).

Several questions with respect to SF in ruminant species remain. Although it has been shown that the SF is comparatively constant with respect to intake levels, diet variation, and age from subadult to adult (Schwarm et al., 2009; Lechner et al., 2010; Clauss et al., 2014; Grandl et al., 2018), many species are so far only characterised by a low number of measurements, with hardly any repetitions. Additionally, a large number of species have not been characterised so far. Absentees include the entire bovid tribe Tragelaphini, unusual browsers such as the gerenuk (*Litocranius walleri*) (in comparison with other gazelle species), and the European bison (*Bison bonasus*) (in comparison with other Bovini). In this contribution, we report hitherto unpublished MRT data from 55 individual passage experiments in captivity, on four species that have previously been investigated (moose *Alces alces*, giraffe *Giraffa camelopardalis*, waterbuck *Kobus ellipsiprymnus*, and cattle) and six species that have not been investigated so far (oryx *Oryx leucoryx*, sitatunga *Tragelaphus spekii*, bongo *T. eurycerus*, nyala *T. angasii*, European bison, and gerenuk). Moose and giraffe are considered exclusive browsers, and waterbuck and cattle as grazers or intermediate feeders with a distinct preference for grass (Dittmann et al., 2015). The estimated percentage of grass in the natural diet is 75% for the oryx, 68% for sitatunga, 13% for bongo, 20% for nyala, and 0% for gerenuk (Gagnon and Chew, 2000). The European bison is usually considered to prefer grass (Kraśnińska and Kraśniński, 2007), but non-grass material represents by far the majority of diet during winter in unsupplemented areas, when the percentage of grasses and sedges is as low as 10% (Kowalczyk et al., 2011).

2. Methods

2.1. General study features

The measurements reported here were either performed in parallel to previously published intake and digestion experiments, or were performed opportunistically with the only aim to gain mean retention time (MRT) data. Animals were kept individually for the respective experiments, with visual and olfactory contact to conspecifics, even if only one animal was assessed. Animals were kept on a constant diet for at least 10 days, and individually at least 3 days, prior to marker feeding. Faeces were collected either after shifting the animal to a neighbour enclosure, or, if the character of the individual and the size of the enclosure permitted, with the animal present in the same enclosure. The individual experiments varied with respect to the sample size (number of animals assessed, from $n = 1$ to $n = 6$), the number of different diets tested per animal (from 1 to 5 diets), indoor or outdoor housing, and the faecal sampling regime (with an interruption during the night time vs. continuous sampling; sampling strictly organized by intervals, with 4 h intervals during the first days of faecal collection, vs. more frequent intervals during daylight hours). When night time sampling was not possible, the passage marker was administered late in the evening, with the next faecal sampling as early as possible the following morning. Note that the method of calculating MRTs used (see below) has been shown to be independent of the sampling regime (Van Weyenberg et al., 2006), and variation in sampling regimes therefore does not affect the results. Feed intake was quantified (as dry matter intake, by weighing all items offered and refused, and determining their dry matter concentration) in all studies except for the two domestic cattle. Body mass was either directly measured by weighing during the experiment, by referring to documentation of the respective facility when animals had been weighed recently during veterinary procedures, or by estimation (using weighed specimens as a guideline). Details of the diets are given in the previous publications of the respective studies cited below when available, or in the description of the individual experiments; compressed information on the diets in terms of ingredient composition (crude protein and neutral detergent fibre levels) is given

in Tables 1–5. The ruminant species were characterised by the percentage of grass in their natural diets (not in the diets of the experiments) based on the literature.

2.2. Markers, marker application, sampling, analyses and calculations

The MRT measurements followed the same methods previously employed in nondomestic species. Cobalt-EDTA served as a solute (fluid) marker, and chromium-mordanted fibre (ground hay particles, < 2 mm) as small particle marker, both prepared according to Udén et al. (1980). The marker dose per animal was calculated as 0.03 g Co-EDTA and 0.2 g mordanted fibre per kg body mass. Markers were offered for voluntary consumption. Across studies, the strategy to ensure voluntary marker consumption included the habituation of the animals, during the adaptation period, to a small daily offering of a particularly palatable feed (mostly, in animals fed forage, a handful of wheat bran), at the same time of day as the intended marker offering. Thus, animals were conditioned to consume this regularly. One to three faecal samples collected within the 3 days prior to marker feeding served to establish baseline concentrations of markers in the faeces. Faeces were collected for 5–8 days after marker feeding, with more frequent collection during the first 2 days, and at increasing intervals in the subsequent days. At each collection interval, all faeces voided into the enclosure were removed completely, mixed, and a subsample was taken and either immediately submitted to drying, or stored frozen before drying and grinding for chemical analysis.

Chemical analysis of faecal samples for markers was performed after wet acid digestion, either using atomic absorption spectroscopy as described in Behrend et al. (2004) or inductively coupled plasma mass spectroscopy as described in Frei et al. (2015). The MRT in the whole gastrointestinal tract (GIT) was calculated according to Thielemans et al. (1978) as

$MRT_{GIT} = \frac{\sum t_i C_i dt_i}{\sum C_i dt_i}$ with C_i = marker concentration in the faecal samples from the interval represented by time t_i (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 reticulorumen (RR) was estimated following (Lechner-Doll et al., 1990a). The $MRT_{soluteRR}$ is determined by estimating the rate constant of the descending part of the marker excretion curve via an exponential equation:

$$y = Ae^{-kt}$$

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

$$MRT_{particleRR} = MRT_{particleGIT} - (MRT_{soluteGIT} - MRT_{soluteRR}).$$

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

2.3. Individual experiments

Measurements on sitatunga and nyala were performed after studies on intake, feeding behaviour and digestion (Górka et al., 2016; Przybyło et al., 2018), with experiments performed by M. P., U. P. and S. S., and the parallel assessment of two waterbuck. The diets differed slightly from those usually fed in that amounts of concentrates and produce were reduced, and consisted of grass hay and a mix of chopped

lucerne, with low amounts of grain (Table 1).

Measurements in giraffe were performed during a study on intake and digestion of different combinations of forages and a pelleted diet (Schaub et al., 2004; Hatt et al., 2005), with experiments performed by D. K. in 2002 as part of her dissertation work (Schaub, 2005). During this work, the measurements in domestic cattle (fed only grass hay) were performed for comparison. The diets of the giraffe were either lucerne hay only, a combination of lucerne hay and a browser pellet, or that combination with two different levels of additional fresh browse (Table 2); their normal diet at the facility consisted of lucerne hay and a browser pellet both for ad libitum consumption, with varying additions of browse and additional produce.

Measurements in moose were performed during a study on intake and digestion of various forages (Clauss et al., 2013a), with experiments performed by G.-M. K. in 2006 and 2007 as part of her dissertation work (Kohlschein, 2011). Two moose received only one diet, fresh grass or fresh browse; four moose received lucerne hay only, lucerne and grass hay, additional dried browse, or dried browse only. During this work, additional data was gained for two European bison on grass hay: a subadult animal 2 years of age, and a juvenile animal barely 1 year of age (Table 3). The normal diet of the moose at this facility consisted of browse, lucerne hay, and a mixture of produce and concentrates; that of the bison consisted of grass pasture, grass hay, and a concentrate component.

Measurements on three bongo and three waterbuck were part of an unpublished MSc, with experiments performed by J. S. in 2007. Animals were fed both grass hay and lucerne hay for ad libitum consumption, and a browser pellet (Table 4), whereas their regular diet also consisted of a grass pasture and occasional produce.

The measurements in the single gerenuk and Arabian oryx were performed by M. C. in 2002 and 2010, respectively, as part of a series of similar experiments with larger numbers of specimens (Hummel et al., 2008; Hebel et al., 2011; Dittmann et al., 2015; Hummel et al., 2015; Hummel et al., 2017). The oryx received grass hay and fresh lucerne at nearly equal proportions (on a dry matter basis), without the concentrate component it was usually fed in addition, and the gerenuk received its regular diet of (in decreasing proportion) a browser pellet, fresh browse (*Ziziphus spina-christi* and *Acacia* spp.), lucerne hay, carrots and fresh lucerne (Table 5).

3. Results

Details of the animals, the ingested diets as well as the measured MRT and SF are given in Tables 1–5.

Marker excretion patterns in moose and giraffe showed a close association of the solute and the particle marker (Fig. 1), corresponding to the low SF RR of 1.20–1.61 in giraffe (Table 2) and 1.26–1.74 in moose (Table 3). In contrast, the marker excretion pattern of cattle showed a clear difference between the solute and the particle marker (Fig. 1), corresponding to the high SF RR of 2.04 (Table 2). The comparison of the two moose individuals that received either fresh browse or a fresh grass pasture, respectively, indicated a more distinct separation between small particle and solute marker excretion in the animal fed freshly cut grass pasture, but the value nevertheless was in the range typical for 'moose-type' ruminants (Fig. 2). The subadult European bison showed a marker excretion pattern similar to that of cattle, with a clear separation of the solute and the particle marker and an SF RR of 2.74, whereas the juvenile animal showed a less distinct marker separation and a lower SF RR of 1.54 (Fig. 3; Table 3).

The three Tagelaphini species, as well as the waterbuck, oryx and gerenuk all showed a distinct separation in the excretion patterns of the solute and the particle marker (Fig. 4), with SF RR between 1.81 and 2.60 (Tables 1, 4, 5).

Across all individuals, the MRT of particles through the GIT decreased with increasing relative feed intake level (Fig. 5A), but within species, the SF RR appeared stable across relative intake levels (Fig. 5B).

Table 1
Body mass, diet composition, dry matter intake and measures of digesta retention in sitatunga (*Tragelaphus spekii*), nyala (*Tragelaphus angasi*) and waterbuck (*Kobus ellipsiprymnus*).

Species	N	Body mass kg	Diet composition % dry matter	CP/NDF (% dry matter)	Dry matter intake kg d ⁻¹	MRT _{solute} GIT		MRT _{solute} RR		MRT _{particle} RR		SF RR
						h	h	h	h	h	h	
<i>T. spekii</i>	4	50 ± 0	*Grass hay 45% Chopped lucerne hay 32% Concentrate mixture 23%	14/51	0.75 ± 0.06	30.1 ± 1.8	44.1 ± 5.7	1.46 ± 0.15	17.0 ± 2.6	31.1 ± 7.1	1.81 ± 0.21	
<i>T. angasi</i>	6	64 ± 7	*Grass hay 48% Chopped lucerne hay 32% Concentrate mixture 20%	13/51	1.18 ± 0.12	22.6 ± 2.9	37.5 ± 7.2	1.65 ± 0.15	15.7 ± 3.6	30.6 ± 7.6	1.95 ± 0.25	
<i>K. ellipsipr.</i>	2	160 ± 0	*Grass hay 77% Chopped lucerne hay 8% Concentrate mixture 15%	11/55	2.76 ± 0.120	19.6 ± 3.6	40.1 ± 7.6	2.05 ± 0.01	13.0 ± 5.2	33.5 ± 9.2	2.65 ± 0.35	

CP/NDF: average percentage of crude protein/neutral detergent fibre in dry matter of the ingested diet. MRT mean retention time, SF selectivity factor (=MRT_{particle}/MRT_{solute}), GIT gastrointestinal tract, RR reticulorumen.

^a diet item offered for ad libitum consumption.

Table 2
Body mass, diet composition, dry matter intake and measures of digesta retention in giraffe (*Giraffa camelopardalis*) and domestic cattle (*Bos taurus*).

Species	N	Body mass kg	Diet composition % dry matter	CP/NDF (% dry matter)	Dry matter intake kg d ⁻¹	MRT _{solute} GIT		MRT _{particle} GIT		MRT _{solute} RR		MRT _{particle} RR		SF RR
						h	h	h	h	h	h	h	h	
<i>G. camelopard.</i>	3	667 ± 29	*Lucerne hay A 100%	14/45	6.67 ± 1.10	41.3 ± 9.1	47.5 ± 6.7	1.17 ± 0.12	20.1 ± 1.6	26.3 ± 2.0	1.32 ± 0.17			
<i>G. camelopard.</i>	3	667 ± 29	*Lucerne hay B 100%	14/45	5.73 ± 0.91	40.5 ± 4.6	50.8 ± 4.5	1.26 ± 0.12	21.2 ± 3.0	31.5 ± 6.4	1.48 ± 0.17			
<i>G. camelopard.</i>	1	650	*Lucerne hay A 37% *Browser pellet 63%	*Fresh browse 15% 15/37	6.90	36.5	43.9	1.20	11.9	19.3	1.61			
<i>G. camelopard.</i>	2	675 ± 35	*Lucerne hay A 20% *Browser pellet 65%;	15/37	9.70 ± 1.41	33.9 ± 1.3	37.6 ± 2.0	1.11 ± 0.10	16.9 ± 5.1	20.5 ± 8.4	1.20 ± 0.14			
<i>G. camelopard.</i>	3	667 ± 29	*Lucerne hay A 14% *Browser pellet 55% ^b Fresh browse 31%	15/38	10.27 ± 1.52	34.5 ± 4.7	44.9 ± 9.0	1.30 ± 0.15	18.3 ± 1.9	28.7 ± 6.2	1.57 ± 0.31			
<i>B. taurus</i>	2	680 ± 198	*Grass hay 100%	na/na	–	21.6 ± 0.6	39.7 ± 0.2	1.84 ± 0.06	17.4 ± 1.6	35.5 ± 2.5	2.04 ± 0.05			

CP/NDF: average percentage of crude protein/neutral detergent fibre in dry matter of the ingested diet (na not analyzed).

MRT mean retention time, SF selectivity factor (=MRT_{particle}/MRT_{solute}), GIT gastrointestinal tract, RR reticulorumen.

^a Diet item offered for ad libitum consumption.

^a Offered as 3 kg fresh leaves.

^b Offered as 6 kg fresh leaves.

Table 3
Body mass, diet composition, dry matter intake and measures of digesta retention in moose (*Alces alces*) and European bison (*Bison bonasus*).

Species	N	Body mass kg	Diet composition % dry matter ^a	CP/NDF (% dry matter)	Dry matter intake kg d ⁻¹	MRT ^{solute} GIT		MRT ^{particle} GIT		SF GIT		MRT ^{solute} RR		MRT ^{particle} RR		SF RR	
						h	h	h	h	h	h	h	h	h	h	h	h
<i>A. alces</i>	1	200	^b Fresh browse leaves 98%	14/49	5.96	20.2	27.4	1.36	11.3	18.5	1.64						
<i>A. alces</i>	1	300	^b Fresh grass pasture 99%	16/51	6.69	23.6	36.7	1.55	17.7	30.8	1.74						
<i>A. alces</i>	2	301 ± 15	^b Lucerne hay 84%	14/59	6.13 ± 0.76	27.8 ± 3.9	34.9 ± 7.5	1.25 ± 0.10	18.6 ± 1.5	25.7 ± 2.2	1.39 ± 0.23;						
<i>A. alces</i>	4	290 ± 22	^b Trough feed	13/43	5.43 ± 0.42	35.3 ± 1.7	43.8 ± 3.4	1.24 ± 0.11	21.5 ± 4.7	30.0 ± 1.3	1.45 ± 0.32;						^b Grass hay 4%
<i>A. alces</i>	4	290 ± 22	^b Lucerne hay 85%	15/56	3.71 ± 0.68	38.2 ± 2.6	44.2 ± 2.8	1.16 ± 0.04	23.5 ± 1.8	29.5 ± 2.8	1.26 ± 0.05						
<i>A. alces</i>	4	290 ± 22	^b Lucerne hay 38%	15/57	6.53 ± 0.29	27.6 ± 3.2	36.3 ± 4.7	1.32 ± 0.05	19.3 ± 4.7	28.1 ± 6.2	1.46 ± 0.06;						^b Grass hay 0%;
<i>A. alces</i>	4	290 ± 22	^b Dried browse leaves 89%	15/55	5.00 ± 0.83	31.5 ± 3.7	43.0 ± 6.2	1.37 ± 0.12	19.6 ± 4.7	31.1 ± 7.0	1.60 ± 0.21						^b Dried browse leaves 54%
<i>B. bonasus</i>	1	130	^b Grass hay 98%	9/52	3.60	23.7	30.8	1.30	13.2	20.2	1.54						
<i>B. bonasus</i>	1	246	^b Grass hay 98%	9/52	6.02	18.5	42.8	2.31	13.9	38.2	2.74						

CP/NDF: average percentage of crude protein/neutral detergent fibre in dry matter of the ingested diet.
MRT mean retention time, SF selectivity factor (= MRT^{particle}/MRT^{solute}), GIT gastrointestinal tract, RR reticulorumen.
^a Difference to 100% represents non-forage items (incl. Those used as bait for shifting).
^b Diet item offered for ad libitum consumption.

Table 4
Body mass, diet composition, dry matter intake and measures of digesta retention in waterbuck (*Kobus ellipsiprymnus*) and bongo (*Tragelaphus eurycerus*).

Species	N	Body mass Kg	Diet composition % dry matter	CP/NDF (% dry matter)	Dry matter intake kg d ⁻¹	MRT ^{solute} GIT		MRT ^{particle} GIT		SF GIT		MRT ^{solute} RR		MRT ^{particle} RR		SF RR	
						h	h	h	h	h	h	h	h	h	h	h	h
<i>K. ellipsiprymnus</i>	3	187 ± 58	^a Lucerne hay 18% ^a Grass hay 56% Browser pellet 25%	12/56	2.63 ± 1.35	28.0 ± 8.8	47.4 ± 16.6	1.70 ± 0.29	14.6 ± 1.4	34.0 ± 9.7	2.33 ± 0.60						
<i>T. eurycerus</i>	3	183 ± 29	^a Lucerne hay 52% ^a Grass hay 14% Browser pellet 34%	14/52	1.93 ± 0.20	26.1 ± 2.7	44.4 ± 7.7	1.71 ± 0.31	13.5 ± 3.1	31.9 ± 9.4	2.39 ± 0.54						

CP/NDF: average percentage of crude protein/neutral detergent fibre in dry matter of the ingested diet.
MRT mean retention time, SF selectivity factor (= MRT^{particle}/MRT^{solute}), GIT gastrointestinal tract, RR reticulorumen.
^a Diet item offered for ad libitum consumption.

Table 5
Body mass, diet composition, dry matter intake and measures of digesta retention in Arabian oryx (*Oryx leucoryx*) and gerenuk (*Litocranius walleri*).

Species	N	Body mass Kg	Diet composition % dry matter (CP/NDF)	CP/NDF (% dry matter)	Dry matter intake kg d ⁻¹	MRT _{solute} GIT		MRT _{particle} GIT		SF GIT		MRT _{solute} RR		MRT _{particle} RR		SF RR
						h	h	h	h	h	h	h	h	h	h	
<i>O. leucoryx</i>	1	70	^a Grass hay 58% Fresh lucerne 42%	14/52	1.15	23.2	51.6	2.22	17.7	46.1	2.60					
<i>L. walleri</i>	1	37	^a Brower pellet 50% ^a Fresh browse 34% ^a Lucerne hay 8% Carrots 6% ^a Fresh lucerne 3%	16/32	0.54	30.5	47.7	1.57	13.8	31.0	2.25					

CP/NDF: average percentage of crude protein/neutral detergent fibre in dry matter of the ingested diet.

MRT mean retention time, SF selectivity factor (= MRT_{particle}/MRT_{solute}), GIT gastrointestinal tract, RR reticulorumen.^a Diet item offered for ad libitum consumption.

4. Discussion

The results of the present study expand both the number of species for which fluid and particulate digesta retention times have been measured for the first time, and the number of species in which previous findings on digesta retention times were corroborated. Therefore, they increase our confidence in the repeatability of such measurements within species, and facilitate a yet more comprehensive assessment of comparative ruminant digestive physiology. However, they also make a re-assessment of the putative link between digestive physiology and the natural diet necessary.

4.1. Limitations

Various limitations apply to the compilation of digesta retention measurements in nondomestic ruminant species. By the necessities of logistics, the compilation does not represent the outcome of one large study in which animals were assessed on a consistent diet, by the same investigator with a consistent sampling regime, and on a consistent husbandry regime. For example, no single zoological institution keeps the many different investigated species. Within individual institutions, the available facilities, for example neighbour enclosures that make a repeated shifting of specimens for faeces collection possible, may allow an experiment with some but not with other species. Institutions may consent to an experiment with some specimens of their collection, but have reservations about the degree to which their usual diet can be changed to resemble a natural diet, and may not consider specimens of other species due to the social structure of the group or the reproductive status of individuals. Such factors lead to a variety of reasons for unexplained scatter in comparative data collections and make a careful selection of data necessary, as often emphasized for comparative datasets. With respect to methodological considerations, the results reported here have all been gained by a comparable set of passage markers, with MRT calculated by a method that makes the result independent of the actual frequency of faecal sample collection (Van Weyenberg et al., 2006; Matsuda et al., 2015).

4.2. Corroboration of previous findings

The degree to which the species-specific data appears reliable depends on the repeatability of measurements for a species; in this respect, the present results on cattle, waterbuck, giraffe and moose are reassuring.

A large number of experiments with domestic cattle have established that this species is characterised by a comparatively high SF RR (reviewed in Hummel et al., 2005: 1.7–4.6). A high SF GIT for waterbuck similar to the present study was reported from an experiment at a different zoological collection and with other specimens (Steuer et al., 2011: 2.3). Clauss et al. (1998) reported similarly low SF RR (1.3–1.5) for three individual giraffe, one of which was also included in the present study. For moose, two studies with different specimens than those included in the present study indicated similarly low SF RR (Renecker and Hudson, 1990: 1.1–1.7; Lechner et al., 2010: 1.0–1.3).

4.3. Effects of intake, diet and age

The observation that digesta retention times decrease with increasing feed intake matches a large number of similar observations (reviewed in Clauss et al., 2013b). Levey and Martínez del Río (1999) stated that intake level is the most important, and oftentimes overlooked, covariable when trying to explain variation in digesta retention in vertebrates.

By contrast, the impression gleaned from the present study that the SF RR is constant across a range of relative intake levels in various ruminant species (Fig. 5B), corroborates similar observations made in different species sets of ruminants (Schwarm et al., 2009; Clauss et al.,

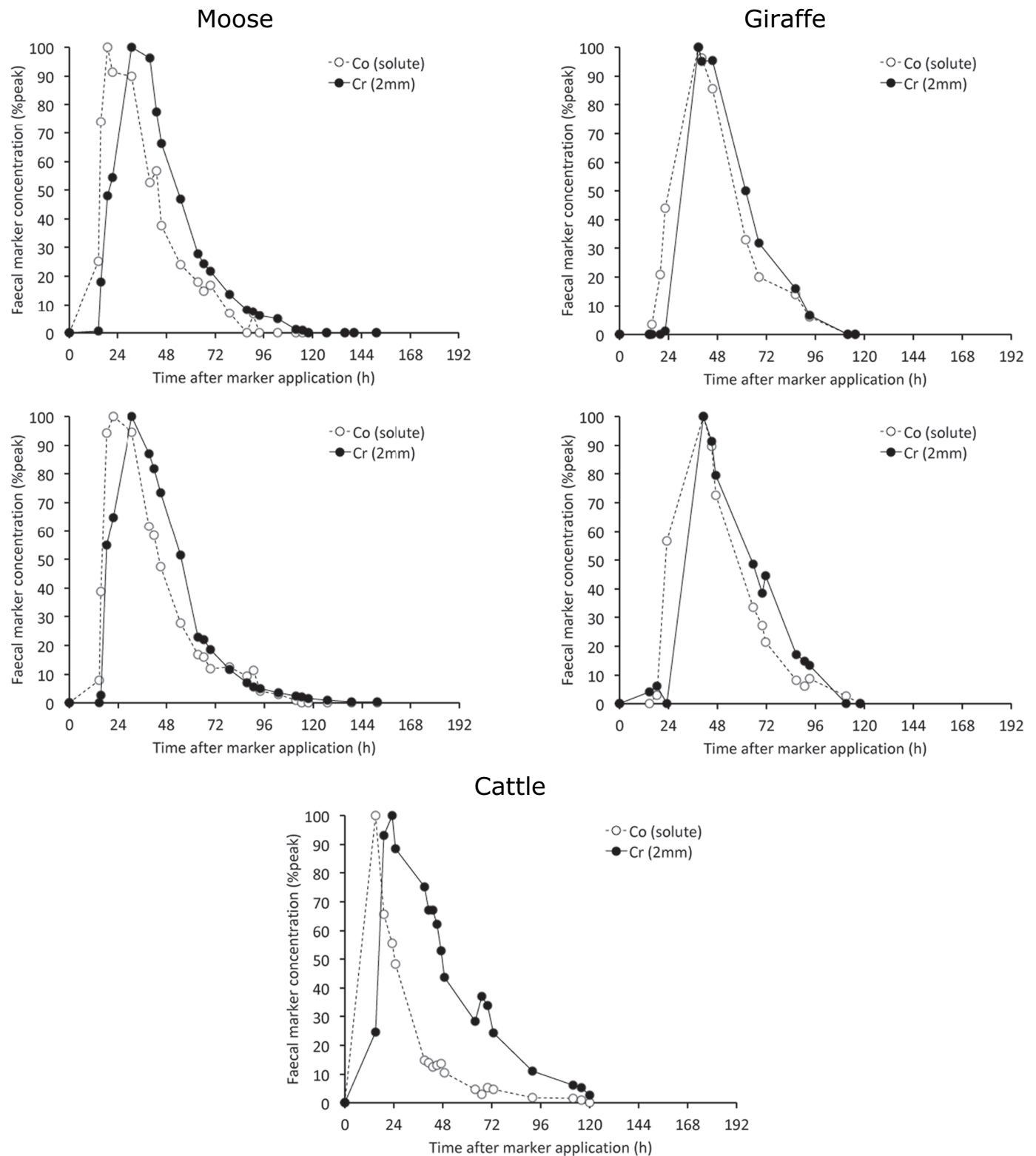


Fig. 1. Excretion patterns of a solute (Co-EDTA) and a particle (Cr-mordanted fibre, < 2 mm) marker in faeces of moose (*Alces alces*) and giraffe (*Giraffa camelopardalis*) as examples of ‘moose-type’ ruminants, and of domestic cattle (*Bos taurus*) as an example of a ‘cattle-type’ ruminant. Note the nearly simultaneous excretion of both markers in moose and giraffe, and the delayed excretion of the particles in cattle.

2014; Dittmann et al., 2015). In a large feeding experiment with 42 cattle, there was also no significant effect of relative feed intake on SF RR (Grandl et al., 2018). However, the SF tended to decrease with increasing relative intake level in a dataset of nonruminant foregut fermenters (Schwarm et al., 2009). These findings emphasize the

apparent, particular relevance of maintaining a certain SF, and the putatively associated effects such as microbial harvest, in ruminants.

Across 42 cattle, ranging in age from 199 days to 10 years of age, there was no age effect on the SF RR (Grandl et al., 2018), leading the authors to conclude that the high SF RR typical for cattle most likely

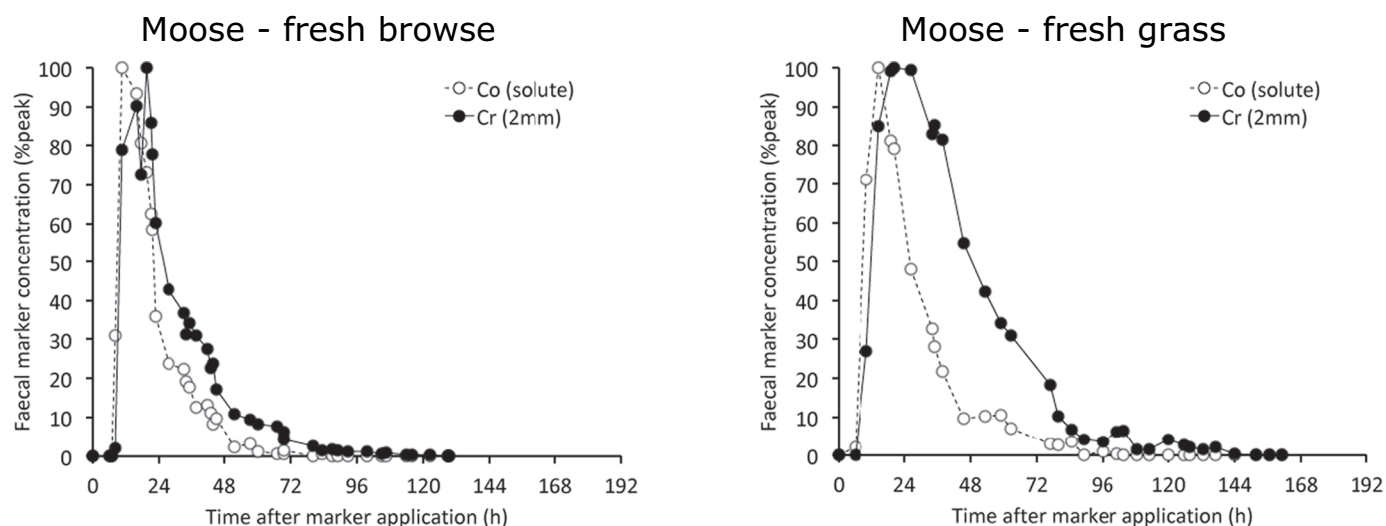


Fig. 2. Excretion patterns of a solute (Co-EDTA) and a particle (Cr-mordanted fibre, < 2 mm) marker in faeces of two different moose (*Alces alces*) fed exclusively on fresh browse or freshly cut grass. Note the nearly simultaneous excretion of both markers in the browse-fed animal, and the delayed excretion of the particles in the grass-fed animal.

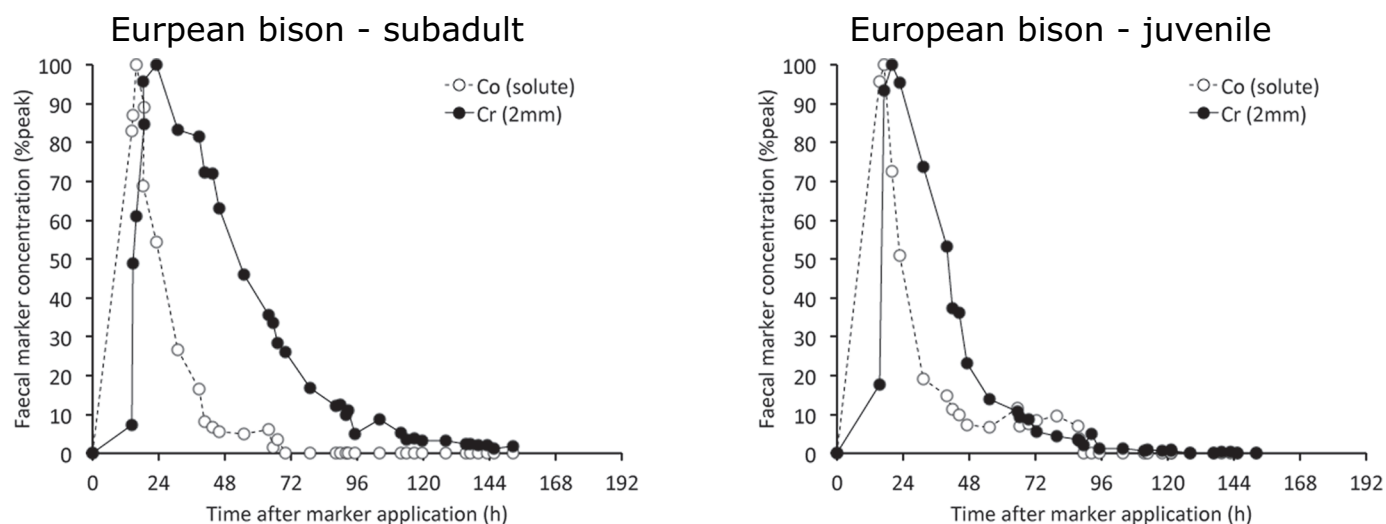


Fig. 3. Excretion patterns of a solute (Co-EDTA) and a particle (Cr-mordanted fibre, < 2 mm) marker in faeces of a subadult and a juvenile European bison (*Bison bonasus*) fed exclusively on grass hay. Note the difference in patterns that allow the interpretation that a marked difference between the excretion of the solute and the particle marker develops over ontogeny.

develops at a very early age. By contrast, the comparison of the single juvenile and the subadult European bison of the present study (Fig. 3) appears to suggest that high SF RR may not necessarily be a characteristic of cattle-type ruminants from the moment of weaning onwards, but may develop during early ontogeny. Further studies investigating the SF, for example in cattle during the first year of life, would be required to clarify this question.

Generally, the SF RR appears to be relatively constant across diets (e.g., Grandt et al., 2018). Certain differences between diets can be observed, especially when comparing diets with and without the inclusion of grass. This was suggested for moose in Lechner et al. (2010) and again for moose in the present study (Fig. 2), even though the difference in the resulting SF RR was small (Table 3). Similar findings were made for Soemmerring's gazelles (*Nanger soemmerringii*) in Dittmann et al. (2015). However, these differences between diets are mainly smaller than those between species. Therefore, even though it would be preferable to either compare all ruminant species on a common diet, or each species on its natural diet, the results of experiments in captivity, with varied diets as in the present study, will most

likely nevertheless indicate relevant differences between ruminant species.

4.4. Variation in ruminant digestive physiology

The different measurements in ruminant species have been put together to yield a cohesive picture of 'cattle-type' and 'moose-type' ruminants (Codron et al., 2019; Ehrlich et al., 2019), and the additional data gained in the present study match the overall pattern and narrative: ruminants with larger salivary glands have a lower SF RR (Fig. 6A), possibly because they produce less, but more protein-rich and hence viscous, saliva (Hofmann et al., 2008). This lower amount of more viscous saliva prevents the development of a distinct stratification of RR contents (Clauss et al., 2009a, 2009b; Sauer et al., 2017), and hence also prevents the development of a distinct stratification of the intraruminal papillation (Clauss et al., 2009c). Therefore, lower SF RR are linked to a more homogenous intraruminal papillation (Fig. 6B). Finally, as a lower SF RR is linked, in this scenario, to a lower saliva production and hence fluid throughput through the RR, it makes sense

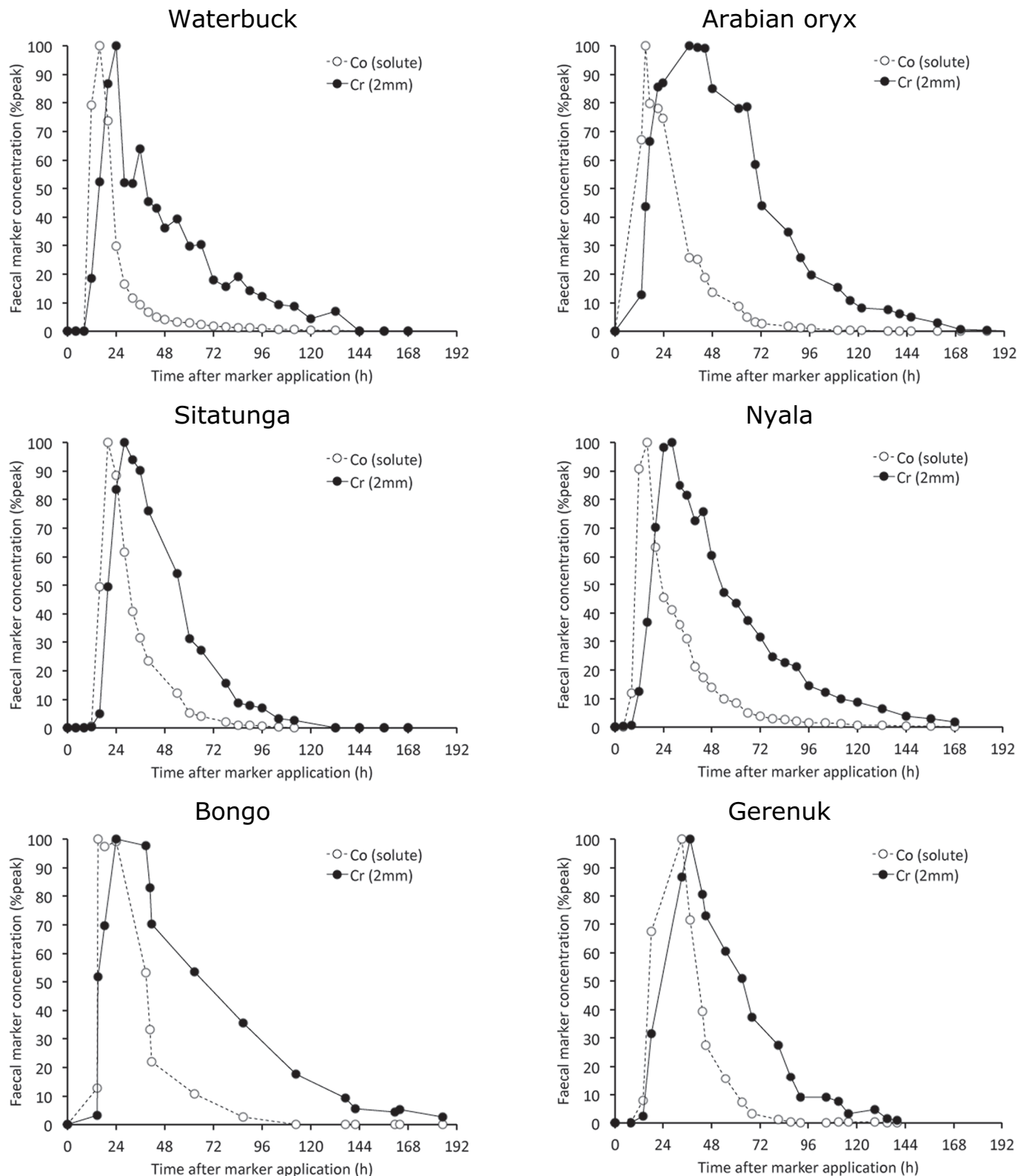


Fig. 4. Excretion patterns of a solute (Co-EDTA) and a particle (Cr-mordanted fibre, < 2 mm) marker in faeces of waterbuck (*Kobus ellipsiprymnus*), Arabian oryx (*Oryx leucoryx*), sitatunga (*Tragelaphus spekei*), nyala (*Tragelaphus angasii*), bongo (*Tragelaphus eurycerus*) and gerenuk (*Litocranius walleri*). Note that all species show a pattern of ‘cattle-type’ ruminants.

that it should also be linked to smaller omasa, as less fluid resorption is required (Fig. 6C). Although these general associations appear evident, there is not only a large amount of data scatter, but also specific outliers, such as the blackbuck (*Antilope cervicapra*) (Hummel et al., 2015;

Sauer et al., 2016), indicating that while the above description may explain some of the variation observed across ruminant species, it only describes a *frequent* but not an *obligatory* pattern. Theories explaining the scatter in these relationships beyond variation inherent in the

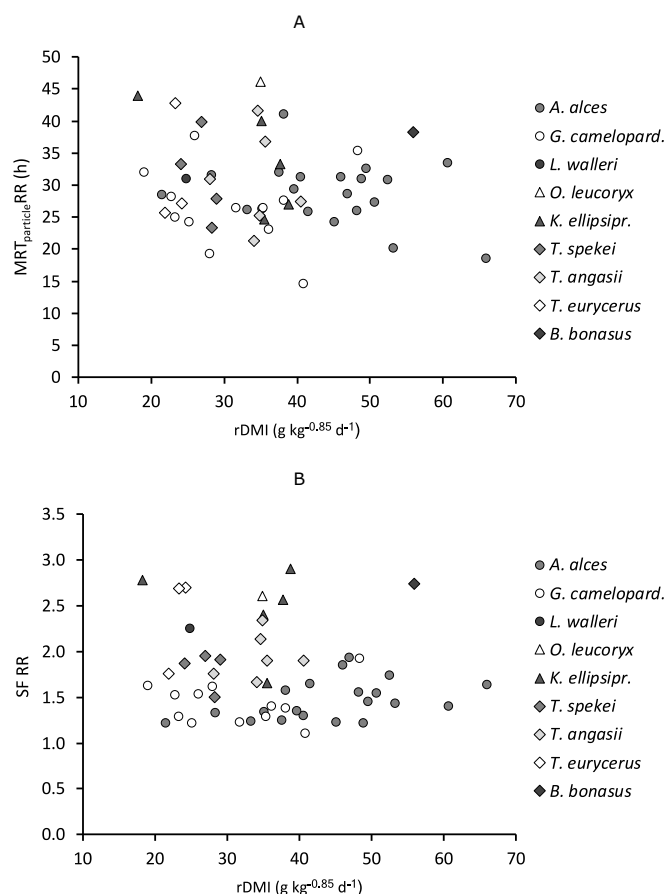


Fig. 5. Relationship of the relative dry matter intake (rDMI, in $\text{g kg}^{-0.85} \text{d}^{-1}$) and (A) the mean retention time (MRT) of particles ($< 2 \text{ mm}$) in the gastrointestinal tract (GIT), with shorter MRT at increasing intake levels, and (B) the selectivity factor of the reticulorumen (SF RR, the ratio of $\text{MRT}_{\text{particles}}/\text{MRT}_{\text{solute}}$), which is basically stable across intake levels, but at species-specific magnitudes.

measurement techniques have not been presented or tested, to our knowledge. Possibly, a convergent evolution towards a ‘cattle-type’ and ‘moose-type’ physiology among ruminant species has led to different degrees of adaptation, with a high fluid throughput at a very small omasum size in blackbuck as the one, and a high fluid throughput with very large omasa in Bovini as the other extreme.

4.5. Ruminant feeding niches and digestive physiology

Previously, it was suggested that ‘moose-type’ ruminants with low SF RR are limited to natural diet niches of $< 15\%$ of grass, whereas ‘cattle-type’ ruminants with higher SF RR should not choose diets of $< 20\text{--}30\%$ grass (Codron and Clauss, 2010; Dittmann et al., 2015). Several findings of the present study do not match these predictions (Fig. 7A), including the single specimens of gerenuk and European bison, but also two tragelaphine species (bongo, nyala) assessed in larger samples sizes. Considering the relationship between fluid and particle passage, our new results place some clearly browsing species among the intermediate-feeding or grazing species (Fig. 7B).

Possibly, the case of the European bison should be discussed separately from that of the African species. European bison appear very flexible in their natural diet, with a large variation in the proportion of grasses eaten (Krasińska and Krasiński, 2007). Whereas cattle and buffalo relatives – the Bovini – have been traditionally interpreted as showcase examples of grazing ruminants (Hofmann, 1989), this group comprises a variety of species or subspecies that include high

proportions of non-grass material in their natural diets, as reviewed by Clauss and Hofmann (2014): the wood bison (*Bison bison athabascæ*), the forest buffalo (*Syncerus caffer nanus*), the gaur (*Bos gaurus*), water buffalo (*Bubalus arnee*), banteng (*Bos javanicus*; cf. the position of banteng in Fig. 7A), or the anoa (*Anoa* spp.), as well as fossil forms. Additionally, in some historical husbandry systems, domestic cattle have been maintained on diets with a high proportion of tree leaves. In the case of the European bison, a large proportion of the non-grass diet items consists of herbs (Kowalczyk et al., 2011), but whether such herbs differ from tree leaves with respect to tannin levels remains to be investigated in detail.

Anyhow, whether a lower tannin content in the non-grass diet components of the Bovini named above can really be assumed remains doubtful. Even if it has been claimed that African browse species may contain higher amounts of active tannins than browse from other regions (Makkar and Becker, 1998), the global distribution of ‘moose-type’ and ‘cattle-type’ ruminants that ingest high proportions of browse apparently does not follow an Africa/Non-Africa distinction. Rather, some ruminant groups, such as the tragulids, giraffids, new world cervids (Capreolinae), and among the bovids the Cephalophinae and some Antilopini and Neotragini species display a ‘moose-type’ strategy and are predominantly browsers (reviewed in Dittmann et al., 2015). By contrast, some ‘cattle-type’ bovid species consume significant proportions of browse. Examples exist among the two Bovinae tribes, the Bovini and the Tragelaphini (Clauss and Hofmann, 2014 and the present study). Among the Caprinae, the muskoxen (*Ovibos moschatus*) during summer feeding on browse (Lechner et al., 2010) represents another example. Finally, among the Antilopini, if the gerenuk result of the present study is accepted as representative, this species would constitute yet another example.

Thus, it appears that other strategies to cope with tannin-rich browse forage than the ‘moose-type’ strategy are possible. Whether these alternative strategies occur only among the bovids, or also among cervids, would have to be tested by measuring the SF RR in a larger range of browsing cervids, not only among the Caprolinae (e.g., brocket *Mazama* spp. or *Pudu pudu puda*), but also among the Cervinae (in particular, Muntiacini). Among the bovids, differences within the Antilopini – the gerenuk of the present study, and the *Madoqua*, *Gazella* and *Nanger* spp. from previous studies (Hebel et al., 2011; Dittmann et al., 2015) apparently indicate a high degree of SF flexibility within a closely related group.

Salivary defences against tannins are clearly not an obligatory feature of the digestive strategy of ruminants (Hanovice-Ziony et al., 2010; Salem et al., 2013). Although tannins have negative effects on measures of digestibility (Robbins et al., 1987a; Robbins et al., 1987b), positive effects in ruminants at low dosages have been reported, and linked to the protection of dietary proteins against microbial degradation in the rumen due to a (reversible) binding with tannins (Clauss et al., 2003a; Makkar, 2003). Alternative strategies to the primary defence against tannins by a high-viscosity, proteinaceous saliva have been reviewed repeatedly (Makkar, 2003; Mlambo et al., 2015) and comprise behavioural diet selection strategies, most importantly adaptations of the rumen microbiome, and detoxification in the liver. To what extent these mechanisms occur in different ruminant species, and whether they occur at different intensities depending on whether a ruminant has a ‘moose-type’ or a ‘cattle-type’ digestive physiology, is unknown to date. Recently, the hypothesis that browsing ruminants generally have larger livers than grazing ones (Hofmann, 1989; Duncan et al., 1998) was generally rejected based on a larger dataset (Codron et al., 2019), but the digestive strategy was notably not a covariable in the analysis. The costs and benefits of being a ruminant species with a dietary niche that includes a high amount of browse with either a ‘moose-type’ or a ‘cattle-type’ strategy cannot be assessed to date.

Possibly, being a browser with a ‘cattle-type’ strategy might mean that the animal is more susceptible to the detrimental effects of tannins if it has little opportunity to select various diet items; this might have

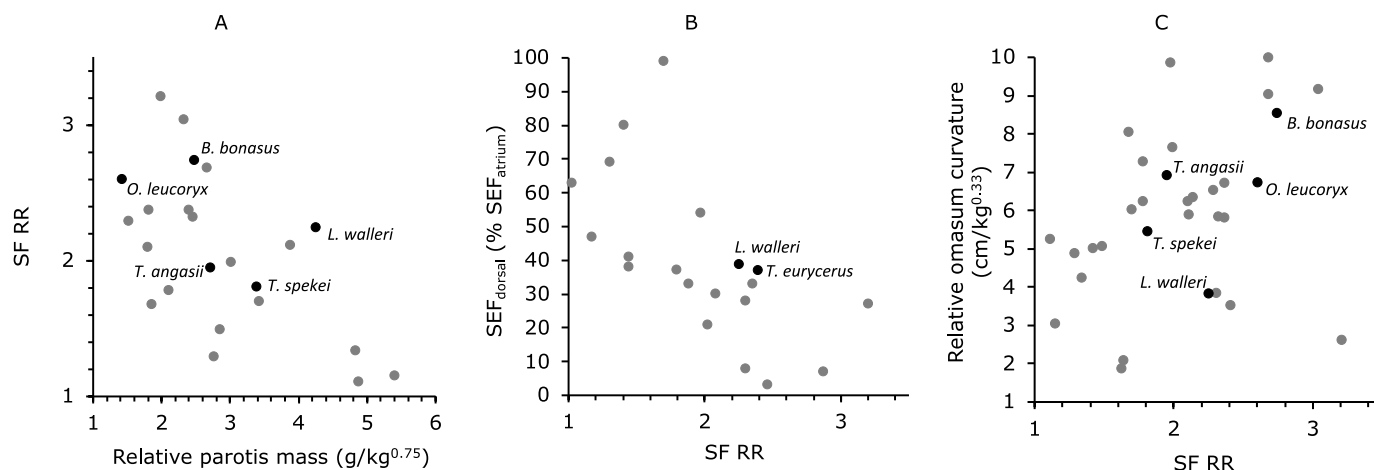


Fig. 6. Interrelationships of different morphophysiological measurements in ruminant species with the selectivity factor (SF, the ratio of small particle/solute marker retention) in the reticulorumen (RR): (A) a larger relative salivary gland size (measured as parotis mass) is linked to lower SF RR; (B) a lower SF RR is linked to a more homogenous intraruminal papillation pattern (measured as the surface enlargement factor [SEF] of the dorsal rumen in % of the SEF in the Atrium ruminis); (C) a lower SF RR is linked to a smaller relative omasum size (measured as the curvature). Data on salivary gland size, intraruminal papillation and omasum size from Hofmann et al. (2008), Clauss et al. (2009c) and Ehrlich et al. (2019), respectively. Data on SF RR from Dittmann et al. (2015), and from the present study (black dots). The outlier with the highest SF RR and the smallest omasum is the blackbuck (*Antelope cervicapra*).

been the reason behind the die-off of a tragelaphine species, the greater kudu (*Tragelaphus strepsiceros*), in a potentially overbrowsed reserve (Van Hoven, 1991). On the other hand, other factors than the presence of secondary plant compounds in the natural diet might play a role – in particular, the load of external abrasives on the natural diet items. Recent evidence indicates that the processing of ingesta in the reticulorumen washes off external abrasives prior to regurgitation and rumination, so that the main chewing load in ruminants occurs on ‘washed’ material that likely causes less wear (Hatt et al., 2019). Arguably, a higher SF might lead to a more thorough washing, and hence browsers exposed to high dust loads on their diets might benefit from a high SF in this way. This hypothesis requires further investigation.

The observation of two different strategies to cope with secondary compounds in browse leads to the hypothesis that browsers with a ‘cattle-type’ physiology might be obliged to use a larger variety of food sources to avoid the accumulation of any one particular toxin to a larger extent (Freeland and Janzen, 1974; Westoby, 1974). However, because this does not mean that ‘moose-type’ browsers should *not* use a large variety of plants when they are available, this hypothesis may be difficult to test in natural habitats. In theory, the ‘cattle-type’ strategy should facilitate a more intensive use of the foregut microbiota by an increased harvest of microbes via fluid throughput (Clauss and Hummel, 2017), but the ecological success of extant ‘moose-type’ species such as moose and roe deer (*Capreolus capreolus*) (e.g., Andersen et al., 1998) indicate that ruminant species can occupy large geographical areas without this feature. The diversification of ruminant digestive strategies may well be an example of the evolution of different, equally valuable solutions to an ecological challenge.

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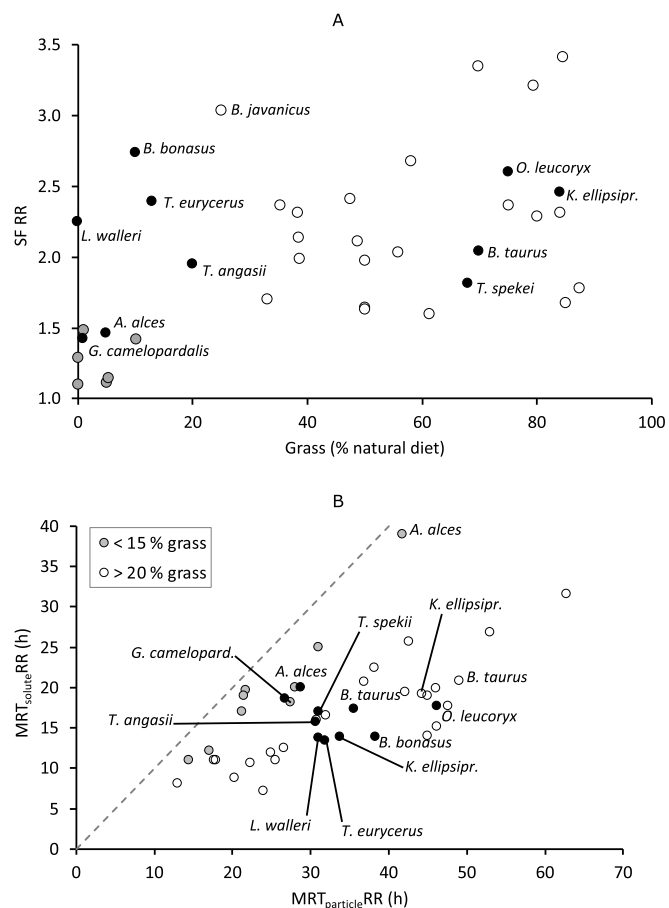


Fig. 7. Relationship between species-specific averages of adult animals for (A) the percentage of grass in the natural diet and the selectivity factor (SF, the ratio of small particle/solute marker retention) in the reticulorumen (RR); (B) the mean retention time (MRT) of a solute and a small particle marker in the reticulorumen (RR) in ruminants of different natural diets (from Dittmann et al., 2015). The species measured in the present study are marked in black, and their previous measures from the literature are noted in (B). Note the nearly identical placement of the data point for giraffe (*Giraffa camelopardalis*). Note that European bison (*Bison bonasus*), bongo (*Tragelaphus eurycerus*) and gerenuk (*Litocranius walleri*) are positioned among ruminant species (of the ‘cattle-type’) whose natural diet typically contains less browse than these three species.

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