

## SHORT COMMUNICATION

# Fluid and particle retention in the greater kudu (*Tragelaphus strepsiceros*)

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**ABSTRACT.** On the one hand, the greater kudu (*Tragelaphus strepsiceros*) is a strict browser and would therefore be expected to display a ‘moose-type’ digestive physiology with a comparatively low rumen fluid throughput, a low ratio of small particle to fluid mean retention time (MRT) in the reticulorumen (RR), and relatively unstratified RR contents. On the other hand, reports on relatively small salivary glands, susceptibility to negative effects of tannins, and a putative absence of tannin-binding salivary proteins would suggest the greater kudu to be an exceptional browser with a ‘cattle-type’ digestive physiology. We measured MRT in four zoo-kept greater kudu females, which resulted in a MRTparticleRR/MRTfluidRR ratio between 1.07–1.43, well within the range of ‘moose-type’ ruminants and similar to eland (*Taurotragus oryx*). In this regard, consistent morphophysiological studies on greater kudu are required to resolve the seemingly contradictory findings in this species.

## Introduction

Ruminant species differ distinctively in the way digesta phases are retained in the gastrointestinal tract (GIT), and, particularly, in the reticulorumen (RR) (Clauss et al., 2006; Przybyło et al., 2019). Whereas large particles of 10 and 20 mm are generally not retained in a discriminant manner (Schwarm et al., 2009), and the selective retention of large compared to small particles is a universal ruminant feature (Dittmann et al., 2015), the difference between fluid and small particle retention is not as distinct in ‘moose-type’ ruminants as it is in ‘cattle-type’ ruminants (Clauss et al., 2010). The ratio of the mean retention time (MRT) of small particles and fluids (the ‘selectivity factor’ SF; Lechner-Doll

et al., 1990) in the RR of ‘moose-type’ ruminants typically is below 1.80, whereas that of ‘cattle-type’ ruminants is higher than 1.80 and can reach values of up to 3.50 (Przybyło et al., 2019). This characteristic is also associated with a variety of other morphological and anatomical features of the ruminant digestive tract (Ehrlich et al., 2019). The association to diet appears to be indirect, with ‘moose-type’ ruminants apparently constrained to browse-dominated diets, whereas ‘cattle-type’ ruminants can ingest a large variety of diets – from large proportions of browse to grass-only diets (Przybyło et al., 2019). Thus, the original concept of a comparatively strict association between ruminant morphophysiology and diet (Hofmann, 1989) has in the meantime been softened to emphasize that while general trends are

evident, outliers as well as flexibility in the diet-morphophysiology relationship exist (Clauss and Hofmann, 2014; Przybyło et al., 2019; Hertaeg et al., 2021).

Members of the tribe of the ‘Tragelaphini’, the spiral-horned antelopes, have been at the core of the debate about the generalizability of the original concept (Hofmann, 1989): as a response to the original concept, Robbins et al. (1995) reported that the salivary gland mass of several Tragelaphini – the nyala (*Tragelaphus angasii*), the bushbuck (*T. scriptus*), and in particular the greater kudu (*T. strepsiceros*) – were lower than expected from the high proportion of browse these species typically include in their diet. A lack of expected correlation between the proportion of grass in the natural diet and salivary gland size or masseter mass was later confirmed for the Tragelaphini (Clauss et al., 2008; Hofmann et al., 2008). For greater kudu, a suspected susceptibility to tannin-induced digestive problems that would speak for comparatively low salivary tannin-binding proteins (Van Hoven, 1991), the reportedly small salivary glands (Robbins et al., 1995), a very low magnitude of salivary tannin binding (Ward et al., 2020), and a relatively distinct difference in the papillation of the dorsal as compared to the middle rumen (Clauss et al., 2009b) would all suggest that kudu saliva is not very protein-rich, hence not very viscous, and that therefore rumen contents might show a higher degree of stratification (as reflected in the papillation pattern). This would lead to the prediction of a ‘cattle-type’ physiology as observed in the *Tragelaphini* nyala, bongo (*T. eurycerus*) and sitatunga (*T. spekii*). By contrast, Codron and Clauss (2010) reported no stratification of free-ranging greater kudus’ rumen contents as quantified by the water content in the digesta of the dorsal and ventral rumen, which would suggest a ‘moose-type’ rumen physiology as observed in another large representative of the Tragelaphini, the eland (*Taurotragus oryx*) (Hejzmanová et al., 2020). This would also match the fact that greater kudus are strict browsers, both in their natural habitat, consistently reported across decades (Wilson et al., 1977; Owen-Smith and Cooper, 1989; Codron et al., 2007; Chinomona et al., 2018; Makhado et al., 2020), as well as in secondary habitats (Gray et al., 2006).

Greater kudu are notoriously nervous animals (Estes, 1991), which makes feeding experiments with frequent human contact comparatively challenging. Here, we used four calm animals at a zoological institution to perform standard measurements of

digesta retention, in order to elucidate whether greater kudu rather have a ‘moose-type’ or a ‘cattle-type’ digestive physiology.

## Material and methods

The experiments were performed at the Silesian Zoological Garden in December 2020, in accordance with Polish legislation on the protection of animals used for scientific purposes. Four adult female greater kudu (3 to 5 years of age, 90–148 kg) were used for experiments. The animals were kept individually (but with visual, acoustic and olfactory contact) for a period of 21 days, which included a 14-day adaptation and a 7-day collection period, in enclosures of 18 m<sup>2</sup> on a concrete floor with wood shavings (except for the collection period) during winter, when cold weather constrained access to the outside enclosure. The diet consisted of lucerne hay provided for *ad libitum* consumption, dried browse, carrots and a mixture of a browser pellet and chopped dried lucerne (proportions and crude nutrient composition of the ingested diet are presented in Table 1). Browse, carrots and the pellet mixture were offered in limited amounts (450, 150 and 550 g per animal and day, respectively, always completely eaten), but intake of lucerne hay was variable and recorded on a daily basis by weighing the amount offered and leftover. Water and salt lick were available for *ad libitum* consumption. One week after the experiment, the animals were weighed using a large animal scale placed in front of the hay rack (animals were standing on the scale during hay consumption). Representative samples of diet items were taken and analysed for dry matter, crude protein, neutral detergent fibre and acid detergent fibre using standard methods (Górka et al., 2016).

To assess digesta kinetics, four passage markers were fed to the animals simultaneously as a single dose with the pellet mixture: Co-EDTA as a solute marker representing the fluid digesta phase, and mordanted fibres of different particle size (chromium (Cr) < 2 mm, cerium (Ce) 10 mm, lanthanum (La) 20 mm), prepared as described in Lechner et al. (2010). Faecal samples were taken at 0, 4, 8, 12, 16, 20, 24, 28, 32, 36, 40, 44, 48, 54, 60, 66, 72, 78, 84, 90, 96, 104, 112, 120, 132, 144, 156 and 168 h after marker feeding. We referred to Przybyło et al. (2019) for the equations used to calculate the mean retention time (MRT), according to Thielemans et al. (1978) for the GIT and Lechner-Doll et al. (1990) for the RR.

## Results and discussion

All animals accepted the procedures well. At  $82 \pm 7 \text{ g kg}^{-0.75} \text{ day}^{-1}$  (Table 1), dry matter intake was high for zoo-kept greater kudus when compared to an estimated range of  $49\text{--}76 \text{ g kg}^{-0.75} \text{ day}^{-1}$  for greater kudus in UK zoos (Taylor et al., 2013), which was probably due to the high proportion of forage in the present study.

$33 \pm 2$  and  $33 \pm 3$  h, respectively. This resulted in a low SF of  $1.29 \pm 0.15$ , clearly in the range of the ‘moose-type’ ruminants (Przybyło et al., 2019).

While the number of animals was small in the present study, several studies have shown that digesta kinetics are species-specific, repeatable, and largely independent of the diet ingested by the experimental animals (Renecker and Hudson 1990; Lechner et al., 2010; Przybyło et al., 2019).

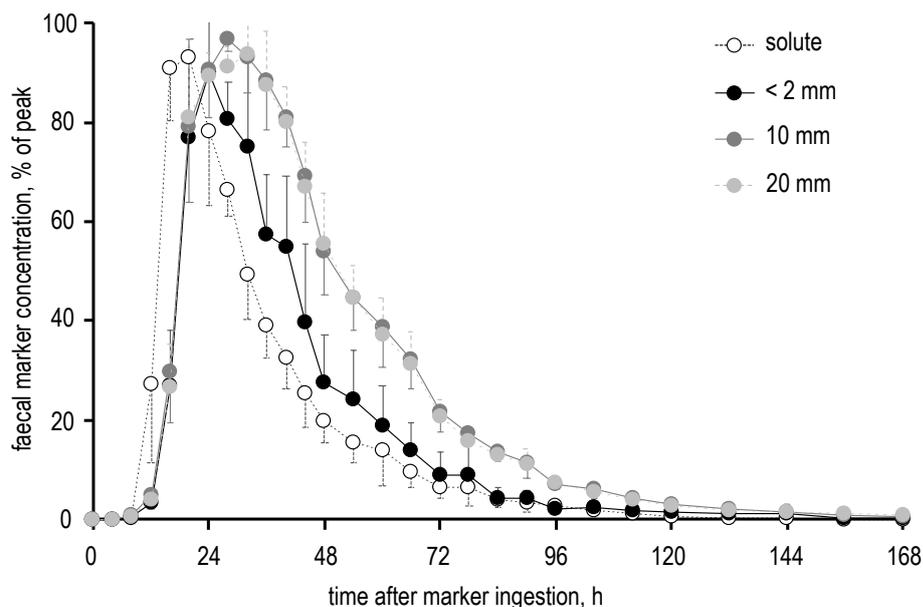
**Table 1.** Body mass, diet composition, dry matter intake and measures of digesta retention in four adult female greater kudu (*Tragelaphus strepsiceros*)

Indices	Animal <sup>1</sup>			
	1	2	3	4
Body mass <sup>2</sup> , kg	107	112	148	90
Diet composition, % dry matter (DM) intake				
lucerne hay	70	75	81	68
dried browse (various <i>Salix</i> spp.)	8	7	5	9
fresh, chopped carrot	1	1	1	1
concentrate mixture (pellets for browsers, dehydrated chopped lucerne)	21	17	13	22
CP/NDF/ADF <sup>3</sup> , % DM	15.1/52.0/43.0	15.0/52.6/43.8	14.9/53.3/44.7	15.1/51.7/42.7
DM intake, g/day	2447	2939	3781	2277
DM intake, $\text{g kg}^{-0.75} \text{ day}^{-1}$	74	85	89	78
MRT <sub>solute-Co</sub> GIT, h	30	33	28	34
MRT <sub>particle-Cr</sub> GIT, h	36	34	36	43
MRT <sub>particle-Ce</sub> GIT, h	44	43	42	44
MRT <sub>particle-La</sub> GIT, h	44	42	42	45
SF GIT <sub>Cr/Co</sub>	1.20	1.05	1.26	1.25
SF GIT <sub>Ce/Cr</sub>	1.24	1.25	1.16	1.04
SF GIT <sub>La/Cr</sub>	1.22	1.24	1.16	1.05
MRT <sub>solute-Co</sub> RR, h	19	21	18	26
MRT <sub>particle-Cr</sub> RR, h	24	23	25	34
MRT <sub>particle-Ce</sub> RR, h	33	31	31	36
MRT <sub>particle-La</sub> RR, h	32	31	31	37
SF RR <sub>Cr/Co</sub>	1.32	1.07	1.43	1.32
SF RR <sub>Ce/Cr</sub>	1.35	1.37	1.22	1.04
SF RR <sub>La/Cr</sub>	1.32	1.35	1.23	1.07

<sup>1</sup> each animal was kept in separate box (18 m<sup>2</sup>); <sup>2</sup> measured one week after the study; <sup>3</sup> average percentage of crude protein (CP)/neutral detergent fibre (NDF)/acid detergent fibre (ADF) in DM of the ingested diet; NDF analysed with amylase, NDF and ADF values include residual ash; MRT – mean retention time, GIT – gastrointestinal tract, SF – selectivity factor ( $=\text{MRT}_{\text{particle}}/\text{MRT}_{\text{solute}}$ ); RR – reticulorumen; Co – cobalt, Cr – chromium, Ce – cerium, La – lanthanum

The faecal marker excretion pattern was typical for ruminants: all markers showed the steep increase and the slower decrease indicative of a continuously stirred tank reactor (Jumars, 2000), the solute marker was excreted earlier than the small particle marker, the small particle marker was excreted earlier than the two large particle markers (Dittmann et al., 2015), and the two larger particle classes were excreted last, and together (Schwarm et al., 2009) (Figure 1). Mean retention times for the GIT were  $31 \pm 3$ ,  $37 \pm 4$ ,  $43 \pm 1$  and  $43 \pm 2$  h for the solute, 2, 10 and 20 mm particle marker, respectively. Corresponding values for the RR were  $21 \pm 4$ ,  $27 \pm 5$ ,

The range of diets for which this characteristic was found to be independent in these studies spans seasonal differences in browse structural and nutrient composition, which have been repeatedly noted for natural diets of greater kudu (Owen-Smith and Cooper 1989; Gray et al., 2006). Given the uniformity of the results for the SF across the four animals, the SF measured in the present study should therefore be representative for greater kudu. Notably, this does not mean that other seasonal changes in RR physiology do not occur; such seasonal changes have, for example, been suggested for the activity of kudu rumen fluid (Boomker, 1984).



**Figure 1.** Marker excretion pattern for a solute and three particle markers of different sizes; data represent averages (SD) of four female greater kudus (*Tragelaphus strepsiceros*)

The peak excretion did not occur in all animals at the same time point, so 100% value is not reached.

With a SF of  $1.29 \pm 0.15$ , greater kudu are similar to eland at 1.54 (Hejmanová et al., 2020), but different from sitatunga (1.81), nyala (1.95) and bongo (2.39) (Przybyło et al., 2019). Evidently, within the Tragelaphini, the whole range of SF are present. For greater kudu and eland, the ‘moose-type’ SF corresponds to their status as strict browsers, and they resemble giraffe (*Giraffa camelopardalis*) or moose (*Alces alces*) in that respect. As mentioned in the introduction, the low SF matches the observation of no distinct rumen content stratification in greater kudu (Codron and Clauss, 2010), as has been described for other species with a low SF such as giraffe or moose (Clauss et al., 2009a; Sauer et al., 2017). This is typically explained by the saliva characteristics of such species – and hence their rumen fluid being particularly viscous due to its proteinaceous content, which also constrains sheer saliva output (Hofmann et al., 2008). Salivary tannin-binding proteins are considered the reason for the high protein content of the saliva of such ruminants (Hofmann et al., 2008), and there is a certain relationship between salivary gland size and indicators of homogenous rumen contents (such as a low SF) (Ehrlich et al., 2019; Przybyło et al., 2019). However, as mentioned in the introduction, greater kudu are reported to have particularly small salivary glands (Robbins et al., 1995), to be susceptible to negative effects of tannins (Van Hoven, 1991), and do not have prominent salivary tannin-binding proteins (Ward et al., 2020). These findings are at odds with those of the

present study. A first step towards resolving the apparent discrepancy would be a systematic recording of morphological (macroanatomy, including salivary gland mass and intraruminal papillation) and physiological (including rumen contents stratification and salivary tannin-binding proteins) measures, in a larger number of greater kudu, for example in the course of game hunting (Hoffman et al., 2009; Magwedere et al., 2013) – possibly across several seasons. Ideally, yet-to-be-determined transcriptome markers applied to salivary gland cells could be found to quantify the expression of tannin-binding proteins in saliva.

## Conclusions

The results of this study represent greater kudu as ‘moose-type’ ruminants, which agrees with their dietary classification as strict browsers. However, these findings appear to conflict with other, previously reported characteristics of kudu. To resolve these contradictions, new morphophysiological investigations of the species would be required.

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## Data availability

All data generated or analysed during this study are included in this published article.

## Conflict of interest

The authors declare that there is no conflict of interest.

## Ethical approval

The study complies with all relevant national and regional laws and with all ethical standards.

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