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ORIGINAL PAPER

Fluid and particle passage in three duiker species

Marcus Clauss · Nicola Lunt · Sylvia Ortmann ·
Amy Plowman · Daryl Codron · Jürgen Hummel

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Abstract Ruminants are characterised by two different types of reticulorumen (RR) physiology. ‘Cattle-type’ ruminants have, amongst other features such as RR contents stratification and a heterogenous intraruminal papillation, a distinct difference between the mean retention time (MRT) of small particles and fluids (the ratio is called the selectivity factor, SF). ‘Moose-type’ ruminants have RR contents that are less stratified, a more homogenous intraruminal papillation and low SFs, indicating less difference in the MRT of small particles and fluids. To date, physiological data indicating a ‘moose-type’ physiology have only been measured in giraffids and Odocoilean cervids, raising the

question whether it is limited to these taxonomic groups only. Here, we measured MRTs of fluids and particles in five duikers (Bovidae, Cephalophinae) from three species (*Sylvicapra grimmia*, *Cephalophus monticola* and *Cephalophus sylvicultor*) and found SFs in the RR of 1.27 ± 0.18 —well within the range of these other browsers. These results are the first physiological indication that a ‘moose-type’ physiology may also occur in bovid species and thus might represent a true convergent adaptation.

Keywords Stratification · Rumen physiology · Particle retention · Browser · Grazer

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M. Clauss (✉) · D. Codron
Clinic for Zoo Animals, Exotic Pets and Wildlife,
Vetsuisse Faculty, University of Zurich,
Winterthurerstr. 260,
8057 Zurich, Switzerland
e-mail: mclauss@vetclinics.uzh.ch

N. Lunt
Antelope Project, Marwell Zimbabwe Trust,
Box 3863, Bulawayo, Zimbabwe

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

A. Plowman
Whitley Wildlife Conservation Trust,
Paignton Zoo, Totnes Road, Paignton,
Devon TQ4 7EU, UK

J. Hummel
Institute of Animal Science, University of Bonn,
Endenicher Allee 15,
53115 Bonn, Germany

Introduction

One of the most prominent differences in rumen physiology between different ruminant species is the pattern of fluid vs. particle passage. In many ruminants, fluids pass from the rumen well before small particles, whereas in other species, fluids and particles move almost together. It has been suggested that this difference reflects feeding habits of species, with grazers having a very distinct difference between fluid and particle passage and browsers with a lesser difference (Clauss and Lechner-Doll 2001; Clauss et al. 2006b). More recently, we suggested that ruminants of different physiology should not be defined in terms of their natural diet but in terms of their physiology, so that conceptually, physiology and diet are separated and can thus be compared against each other. Thus, the term ‘cattle-type’ ruminant was suggested for ruminants characterised by a distinct difference in fluid and particle passage and the term ‘moose-type’ ruminant for species characterised by a very slight difference between fluid and particle passage (Clauss et al. 2010c).

The ‘cattle-type’ physiology has been observed in ruminants as taxonomically variable as cervids (*Cervus elaphus*; Renecker and Hudson 1990); domestic and wild cattle, goat and sheep (Lechner-Doll et al. 1990; Gross et al. 1996; Behrend et al. 2004; Flores-Miyamoto et al. 2005; Clauss et al. 2006b; Schwarm et al. 2008); antelope (*Addax nasomaculatus*; Hummel et al. 2008); and muskox (*Ovibos moschatus*; Lechner et al. 2010). A ‘moose-type’ physiology has, so far, only been demonstrated in giraffids (*Giraffa camelopardalis* and *Okapia johnstoni*; Clauss et al. 1998; Hummel et al. 2005) and in the Odocoilean cervids moose (*Alces alces*) and roe deer (*Capreolus capreolus*; Renecker and Hudson 1990; Behrend et al. 2004; Lechner et al. 2010), which raises the question if this physiology is limited to these taxonomic groups only.

Duikers consume browse and fruits in the wild (Gagnon and Chew 2000; Wilson 2005). Contrary to common intuition, the wild fruits that are part of the duikers’ diets have very high fibre content and also contain significant levels of secondary plant compounds (Dierenfeld et al. 2002; Molloy and Hart 2002). Duikers are nonetheless well-adapted to digest high-fibre and tannin-containing diets (Shipley and Felicetti 2002). The anatomy of the forestomach of duikers has been described in detail by Hofmann (1973). When compared to other ruminant species, duikers have relatively large salivary glands (Hofmann et al. 2008), a small rumen with thin ruminal pillars (Clauss et al. 2003) and an even papillation (Faurie and Perrin 1995; Clauss et al. 2009), shallow reticular crests (Clauss et al. 2010b) and a small omasum (Clauss et al. 2006a). As these anatomical features are typical for browsing species and also characterise those species in which a ‘moose-type’ physiology has been observed, we hypothesised that fluids and particles would pass without much difference through the digestive tract of duikers.

Ingesta passage has so far been measured in blue duiker (*Cephalophus monticola*; Luginbuhl et al. 1990; Wenninger and Shipley 2000) and Maxwell’s duiker (*Cephalophus maxwellii*; Conklin-Brittain and Dierenfeld 1996). Although the standard set of passage markers (cobalt–ethylenediaminetetraacetic acid (Co–EDTA) for fluids and chromium-mordanted fibres for particles) used to investigate wild ruminants in the studies listed above was applied in blue duiker (Luginbuhl et al. 1990; Wenninger and Shipley 2000), the pattern of fluid vs. particle retention was not the focus of, and was not discussed in, these previous studies.

Materials and methods

We used five duikers from three species—grey duiker (*Sylvicapra grimmia*), blue duiker (*C. monticola*) and yellow-backed duiker (*Cephalophus sylvicultor*; Table 1)—

kept at the Dambari Field Station of the Marwell Zimbabwe trust. Animals were kept individually in vegetated enclosures that they had inhabited for more than 1 year. The husbandry and diets of the animals at Dambari Field Station were described by Plowman (2002). In short, duikers received a diet of mixed domestic vegetables (gem squash, butternut, carrot, pumpkin and green banana; 100, 250 and 500 g fresh weight per blue, grey and yellow-backed duiker, respectively), game cubes (National Foods, Harare, Zimbabwe; 150, 450 and 1,000 g as fed) and a variety of browse species indigenous to the area at approximately 1600 hours daily; water was available ad libitum. Uneaten feed was removed by 0800 hours the following morning. Food intake was not recorded throughout the study, as measuring consumption of vegetation growing in enclosures was logistically impractical.

The markers cobalt–EDTA and chromium(Cr)-mordanted fibre (<2 mm) were prepared according to Udén et al. (1980). Animals were fed the markers with a small quantity of vegetables or molasses; the mixture was removed 1 h later and the usual diet was provided. Pens were checked regularly at hourly intervals for the first 48 h and at increasing intervals until approximately 130 h after marker application, and faeces defecated within the respective intervals were sampled and dried at 100°C to constant mass. A faecal sample taken from the animals prior to marker dosage was used as baseline value. Samples were treated and analysed as described by Behrend et al. (2004).

The mean retention time for the whole gastrointestinal tract (MRT GIT) was calculated according to Thielemans et al. (1978) as

$$\text{MRT GIT} = \frac{\sum t_i C_i dt_i}{\sum C_i dt_i}$$

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

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

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

$$C_i = a e^{-kt_i} \text{ or } \ln C_i = -k t_i + b$$

$\text{MRT}_{\text{fluidRR}}$ then is k^{-1} . Because markers can be assumed to move in parallel in the distal gastrointestinal tract of ruminants (empirically confirmed by Grovum and Williams 1973a; Kaske and Groth 1997; Mambrini and Peyraud 1997; Wylie et al. 2000), $\text{MRT}_{\text{particlesRR}}$ was calculated according to Lechner-Doll et al. (1990) by

Table 1 Animals used in this study, estimated body mass (BM, kg), age (years), mean retention times (MRT, h) in the whole gastrointestinal tract (GIT) and the reticulorumen (RR) for fluids and particles (<2 mm) and selectivity factors (SF; ratio of particle–fluid MRT)

Species	Sex	BM	Age	MRT _{GIT}		SF _{GIT}	MRT _{RR}		SF _{RR}
				Fluid	Particles		Fluid	Particles	
<i>S. grimmia</i>	m	13	1	27	27	1.02	21	21	1.02
	f	13	13	23	28	1.24	17	22	1.32
<i>C. monticola</i>	f	4	7	26	35	1.33	20	28	1.44
<i>C. sylvicultor</i>	m	65	12	39	43	1.10	31	35	1.13
	f	65	11	30	38	1.26	19	27	1.41

assuming that $MRT_{fluid}^{distal} = MRT_{fluid}^{GIT} - MRT_{fluid}^{RR}$ and $MRT_{particle}^{distal} = MRT_{fluid}^{distal}$; hence, $MRT_{particles}^{RR} = MRT_{particles}^{GIT} - MRT_{particles}^{distal}$. Selectivity factors (SFs) according to Lechner-Doll et al. (1990) were calculated for GIT or RR as $MRT_{particles} / MRT_{fluid}$.

Because digesta passage patterns probably correlate with intraruminal papillation patterns (Clauss et al. 2009), the results of this study were added to a corresponding data collection. The intraruminal papillation pattern is expressed as the proportion of surface enlargement at the site of the smallest surface enlargement factor (SEF)—the dorsal rumen—of the surface enlargement at the site of the highest SEF—the atrium.

Comparisons were made with literature data, and statistical evaluations were performed by regression analysis using PASW 18.0 (SPSS Inc., Chicago, IL, USA).

Results

Marker excretion curves in the duiker showed very similar patterns for fluids and particles (Fig. 1). MRT_{fluid}^{GIT} and $MRT_{particle}^{GIT}$ ranged from 23 to 39 h and from 27 to 43 h, respectively, with a mean SF_{GIT} of 1.19 ± 0.13 h. MRT_{fluid}^{RR} and $MRT_{particle}^{RR}$ ranged from 17 to 31 h and from 21 to 35 h, respectively, with a mean SF_{RR} of 1.27 ± 0.18 h. When combining data of body mass (BM) and $MRT_{particle}^{GIT}$ from this study with literature data, there was no significant allometric relationship between the two parameters (Fig. 2).

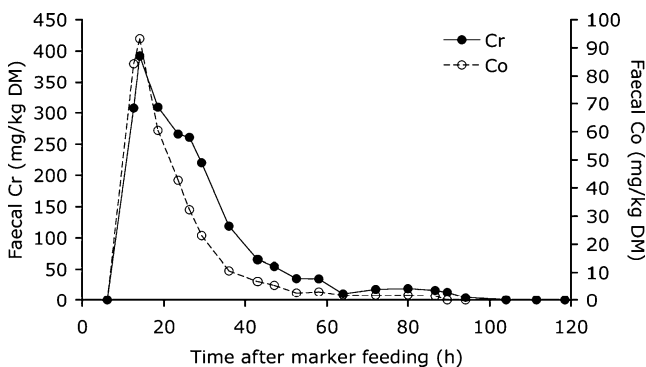


Fig. 1 Marker excretion patterns for fluids (Co) and particles (Cr) in a grey duiker (*S. grimmia*)

Compared to results on fluid and particle retention in the RR of other ruminants, duikers fit the pattern of other ‘moose-type’ ruminants (Fig. 3). When combining data on rumen papillation and the SF_{RR} for different species (Fig. 4), there was a significant negative linear correlation ($R = -0.645$, $p = 0.017$, $n = 13$; $SF_{RR} = 2.39 - 0.013 SEF$), indicating that larger differences in papillation within the rumen are related to larger differences between fluid and particle passage from the rumen; a better fit to the data was achieved using a logarithmic regression ($R = 0.781$, $p = 0.002$, $n = 13$; $SF_{RR} = 3.94 - 0.589 \ln(SEF)$).

Discussion

To our knowledge, the results of this study represent the first physiological indication of a ‘moose-type’ physiology in bovid species. So far, bovid species investigated had always had a distinct difference between fluid and particle passage, i.e. they belonged to the ‘cattle-type’ physiology (anoa *Bubalus depressicornis*, Flores-Miyamoto et al. 2005; domestic cattle, sheep and goats, ibex *Capra ibex* and mouflon *Ovis ammon musimon*, reviewed in Clauss et al. 2006b; addax *Addax nasomaculatus*, Hummel et al. 2008; banteng *Bos javanicus*, Schwarm et al. 2008 and muskoxen *Ovibos moschatus*, Lechner et al. 2010).

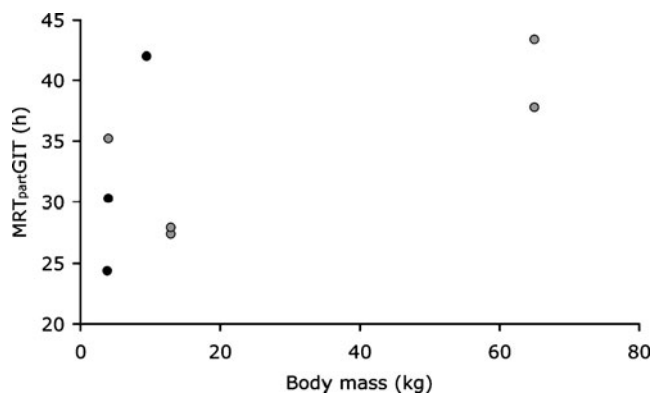


Fig. 2 Body mass and the mean retention time (MRT) of particles in the gastrointestinal tract (GIT) of different duiker species; data from this study (grey circles) and the literature (black circles; Luginbuhl et al. 1990; Conklin-Brittain and Dierenfeld 1996; Wenninger and Shipley 2000)

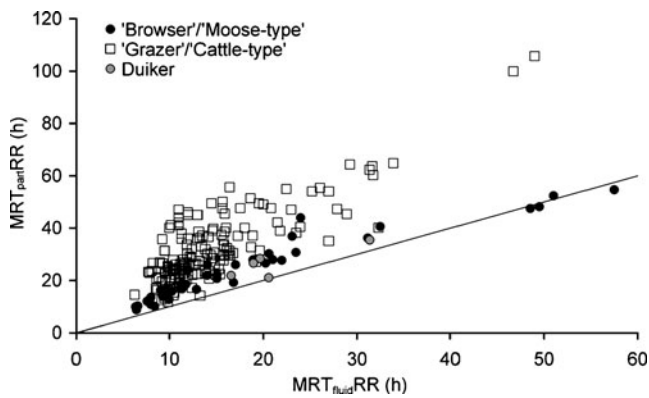


Fig. 3 Relationship of the mean retention time (*MRT*) of fluids and small particles in the reticulorumen (*RR*) of various ruminant species classified as ‘cattle-type’ or ‘moose-type’ (from Clauss et al. 2010c) with data for duikers added from this study

The duikers had very low SF_{GIT} (1.19 ± 0.13) and SF_{RR} (1.27 ± 0.18) within the typical ‘browser’ range of SF_{GIT} 1.2–1.3 and SF_{RR} 1.1–1.8, respectively (Hummel et al. 2005). Our findings are in accord with a SF_{GIT} of 1.29 calculated from data for Co–EDTA and Cr-mordanted fibres in blue duikers from Wenninger and Shipley (2000; in that study, however, these two markers were not fed simultaneously); they do not match the SF_{GIT} of 1.52–1.81 calculated from data for Co–EDTA and Cr-mordanted fibres in blue duikers from Luginbuhl et al. (1990; no particle size given for mordanted fibres, method of calculation of *MRT* not explained). Our study indicates that a strategy of little differentiation between fluid and particle passage from the *RR* is not restricted to giraffids and Odocoilean cervids, can be adopted by bovid species as well and might therefore represent a true convergent adaptation (Fig. 3).

Some limitations of this study need to be mentioned. Apart from the small sample size, the food intake of the duikers could not be recorded for logistic reasons. Food intake is one of the major factors influencing *MRT* (Clauss et al. 2007) and has been shown to also influence *MRT* in duikers; however, in ruminants, food intake does not appear to notably influence *SF*, i.e. the ratio of $MRT_{particle}/MRT_{fluid}$ (Schwarm et al. 2009), which was the main target of this study. Similarly, diet does not appear to have a major influence on *SF* (cf. Renecker and Hudson 1990); results from this study must therefore be considered meaningful even if not measured on the natural diet of the species.

Wenninger and Shipley (2000) collated literature data that showed that within ruminants of a body mass below 100 kg, there was no indication for an increase in $MRT_{part,GIT}$ with body mass. Combining literature data and data from this study, there was no significant correlation between *BM* and $MRT_{part,GIT}$, either (Fig. 2). Clauss et al. (2007) had already refuted such a relationship based on empirical data, although

theoretical considerations support it (Demment and Van Soest 1985). As in the larger dataset in Clauss et al. (2007), this is mainly due to the fact that even in small species, like the smaller duikers, comparatively long *MRT*s are achieved. Other authors have commented before on the high-fibre digestibilities achieved by duikers (Hart 1986; Conklin-Brittain and Dierenfeld 1996; Wenninger and Shipley 2000; Pérez-Barbería et al. 2004), most likely due to the long *MRT*s in these species. The capacity for long *MRT*s may well be an adaptation to the high level of fibre in the natural diet of duikers as described in the ‘Introduction’.

Anatomical characteristics are often used to differentiate functional guilds of ruminants (Hofmann 1989; Mendoza and Palmqvist 2006). With respect to *RR* physiology and *RR* contents stratification, the intraruminal papillation pattern is an important proxy (Clauss et al. 2009), distinguishing ‘moose-type’ from ‘cattle-type’ species (Codron and Clauss, *subm.*). However, such interpretations will often have to be tempered by the fact that the relationship between form (an anatomical proxy, such as the papillation pattern) and function (a physiological proxy, such as the *SF*) is nonlinear. In the comparison of the intraruminal papillation pattern with *SF* measurements in Fig. 4, there is no clear correlation above or below the thresholds of an SF_{RR} of 2.0 and a dorsal surface enlargement factor of 30% of the *SEF* in the *Atrium ruminis*. A similar trend was observed in the correlation of

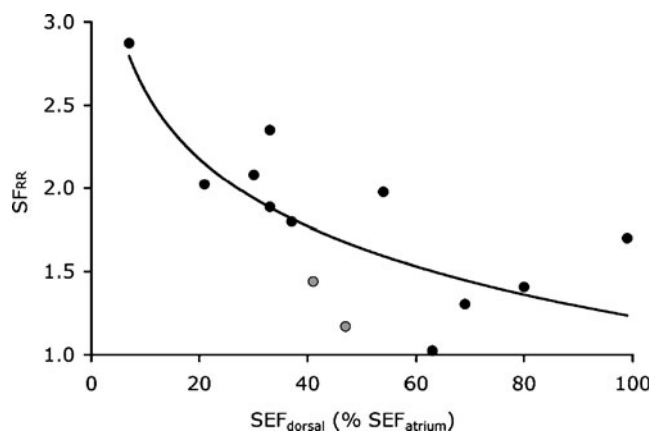


Fig. 4 Relationship between the selectivity factor (*SF*; ratio of the mean retention time of particles in the reticulorumen (*RR*) to that of fluids—a physiological indicator of *RR* contents stratification) and the intraruminal papillation pattern (an anatomical indicator of *RR* contents stratification). The intraruminal papillation pattern is expressed as the proportion of surface enlargement at the site of the smallest surface enlargement factor [*SEF*]—the dorsal rumen—of the surface enlargement at the site of the highest *SEF*—the atrium. Original data collection from Clauss et al. (2009), with additional results from recent studies on muskoxen (*O. moschatus*) and reindeer (*Rangifer tarandus*; Clauss et al. 2010a; Lechner et al. 2010) and with data on duiker from this study (*grey circles*; *MRT* data from this study for *S. grimmia* and *C. monticola*, linked to papillation data from Clauss et al. 2009 on *S. grimmia* and *Cephalophus harveyi*). Logarithmic regression is described in ‘Results’

intraruminal papillation with another measure of RR contents stratification—the difference in dry matter concentration between the dorsal and the ventral RR content (Codron and Clauss, *subm.*). Similar nonlinear or threshold-dependent effects could be expected for different morphological measurements.

To conclude, the results of our trials indicate that similar to other ruminants depending on diets with consistent amounts of tannins, duikers are characterised by a low difference in the MRT of small particles and fluids, which indicates a low degree of RR content stratification and thus fits the observed intraruminal papillation patterns. Such a physiology is probably linked to other features common to these and similar animals, for example large salivary glands that potentially produce tannin-binding proteins and hence a more viscous saliva (Hofmann et al. 2008). While proximate causes for the observed variation in particle and fluid retention remain to be investigated, comparative retention measurements are an important addition to our understanding of ruminant physiology.

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