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ORIGINAL ARTICLE

Retention of solute and particle markers in the digestive tract of captive Somali wild asses (*Equus africanus somaliensis*)

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Abstract In contrast to the domestic horse, whose digestive physiology has been thoroughly investigated, knowledge on the digestive physiology of wild equids is scarce. Comparisons between the domestic horse and the domestic donkey suggest that wild asses might achieve higher digestibilities. This could derive from longer retention times or a greater difference in the mean retention time (MRT) of particles vs. fluid (the selectivity factor (SF)). Here, we measured MRT of a solute (fluid; MRT_{solute}) and a particle (<2 mm; $MRT_{particle}$) marker in five captive male Somali wild asses (*Equus africanus somaliensis*) fed a diet of 95% grass hay. At a mean dry matter intake of 94 ± 3 g $kg^{-0.75}$ day^{-1}, MRT_{solute} was 33.3 ± 5.4 h and $MRT_{particle}$ 39.6 ± 3.9 h, resulting in a SF of 1.21 ± 0.14. For their food intake, Somali wild asses appeared to have slightly higher $MRT_{particle}$ than expected based on domestic equid data, in contrast to Grevy zebras (*Equus grevyi*), potentially indicating higher capacities of the digestive tract. However, considering data on domestic horses, donkeys, and zebra, there was no evident difference in the SF of wild equids compared to domestic ones. Together with an absence of reported anatomical differences in the digestive tract of wild and domestic equids, the data suggest a general similarity in the digestive physiology of equid species that contrasts with the diversity in the digestive physiology of ruminants, and that might be one contributing factor to a lack of sympatric, niche-differentiated equid species.

Keywords Hindgut fermenter · Passage · Digestion · Caecum · Colon · Gastrointestinal tract

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Introduction

While the digestive physiology of domestic horses is very well understood (e.g. Ellis and Hill 2005), knowledge on nondomestic equid species is limited. Conclusions made on the digestive physiology of nondomestic equids are mainly based on comparisons of domestic horses and domestic donkeys, or comparisons among old and more recent horse breeds. It is typically assumed that donkeys are better adapted to low-quality diets, due to both lower energy and nutrient requirements and a very distinct potential for urea recycling (Izraely et al. 1989; Pearson et al. 1992; Suhartanto et al. 1992), and that they achieve comparatively higher digestibilities than horses, possibly linked to longer digesta retention (Pearson and Merritt 1991; Tisserand et al. 1991; Cuddeford et al. 1995). Apart from a lower food intake (Meyer et al. 2010), this longer digesta retention could be achieved by a more voluminous large intestine, as demonstrated between an older and a more recent horse breed (Kobayashi et al. 2006). Comparisons between domestic horses and wild equids kept in zoos fed comparable roughages support the notion that

Table 1 Dry matter concentration and chemical composition of feeds (g/kg dry matter unless stated)

Item	Grass hay	Pelleted compound feed
Dry matter (g/kg as fed)	932	910
Ash	153	48
Crude protein	108	138
Crude lipids	35	49
Neutral detergent fibre	581	251
Acid detergent fibre	286	80
Acid detergent lignin	32	25

nondomestic equids achieve higher digestibility linked to slightly longer digesta retention times (Foose 1982).

A physiological feature of particular interest is the difference between the retention time of particles vs. that of a solute (fluid) marker (Müller et al. 2011). This ratio, called the selectivity factor (SF), is a major characteristic of different digestion types in ruminants (Dittmann et al. 2015) and distinguishes the white rhinoceros (*Ceratotherium simum*) from other perissodactyl hindgut fermenters (Clauss et al. 2010b; Steuer et al. 2010). A high SF means that particulate digesta is 'washed' by fluids, which has implications for the metabolic state of the microbes (Hummel et al. 2015); one would expect a high SF to select for fast-growing and hence particularly efficient microbes. Given that a study that compared the digestibility of standardized plant material in the caecum of fistulated ponies and donkeys found a more efficient digestion in donkeys (Juliand et al. 1997), it is tempting to speculate that a high SF is part of the digestive strategy of nondomestic equids. On the other hand, because the hindgut of donkeys serves as a fluid reservoir (Maloiy et al. 1978; Kasirer-Izraely et al. 1993), with increased fluid retention in the ventral colon during dehydration (Sneddon et al. 2006), some wild equids might have a low SF due to this pronounced fluid retention.

The digestive tract of domestic horses is characterized by an isthmus between the caecum and colon, and another isthmus that forms the transition from the proximal (large) colon to the *Colon transversum* (e.g. Nickel et al. 2004), and these structures have been proposed to serve to delay digesta passage (Drogoul et al. 2000). These anatomical traits are shared by wild equids (Clauss et al. 2008) and donkeys (Jerbi et al. 2014), so that based on the macroanatomical shape of the gastrointestinal tract, and in contrast to the considerations based on physiological comparisons, no differences in digesta retention characteristics are expected.

In this study, we measured the mean retention time (MRT) of a solute (fluid) and a particle marker in five captive Somali wild asses (*Equus africanus somaliensis*) fed a diet consisting mainly of grass hay. In doing so, we focussed especially on the SF and a comparison of our results with literature data on domestic horses and donkeys.

Methods

Five male Somali wild asses kept at Al Wabra Wildlife Preservation (AWWP), Qatar, were used for this study in 2009, in a management period when they were kept individually to facilitate the composition of new breeding groups. The experiment was approved by the acting director and the veterinary and curatorial departments of AWWP and was performed adhering to the NACLAR (2004) guidelines. Each animal had access to its own 20 m^2 indoor shelter as well as an outdoor enclosure of at least 100 m^2. Animals were fed two times daily with weighed amounts of grass hay and a commercial pelleted compound feed. Representative samples of these feeds were submitted to dry matter and nutrient composition (Table 1). Pellets were always consumed completely; hay leftovers were collected and weighed once daily to determine food intake. The resulting percentage of hay of the overall dry matter intake was 95.2 ± 0.6% (Table 2). Animals had access to drinking water ad libitum. They were weighed at the end of the experiment (Table 2).

Dissolved cobalt (Co)-EDTA and chromium (Cr)-mordanted fibre (<2 mm) prepared from grass hay (a different batch from the one fed to the animals) according to Udén et al. (1980) were used as markers for the fluid and the particle phase, respectively. A pulse dose of the markers (approximately 8 g Co-EDTA, dissolved in water, and 75 g Cr-mordanted fibre) was fed to each animal mixed into several handfuls of wheat bran. The latter was added to increase palatability and to guarantee the ingestion of the markers in a short time period. The marker was fed late in the evening and was well accepted. Prior to marker feeding, three faecal samples were taken to analyse Co and Cr background levels. After marker feeding, faecal samples were taken regularly for 7 days, with the most frequent faecal sampling during the first 2 days and increasing time intervals subsequently. Sampling only occurred during daylight hours. Thus, samples were

Table 2 Body mass, dry matter intake (DMI) and mean retention time (MRT) of a solute (Co-EDTA) and a particle (Cr-mordanted fibre <2 mm) marker and the selectivity factor (SF) in Somali wild ass (*Equus africanus somaliensis*)

Item	Unit	Animal				
		1	2	3	4	5
Age	years	4	7	9	2	3
Body mass (kg)	kg	234	269	260	205	208
DMI	kg d^{-1}	5.90	5.93	6.16	5.02	5.05
	g $kg^{-0.75}$ d^{-1}	99	89	95	93	92
Grass hay	% total DMI	95.4	95.7	95.7	94.4	95.0
MRT Co	h	36.1	37.1	35.9	24.0	33.3
MRT Cr	h	37.3	42.9	42.9	34.0	40.9
SF	–	1.03	1.16	1.19	1.42	1.23

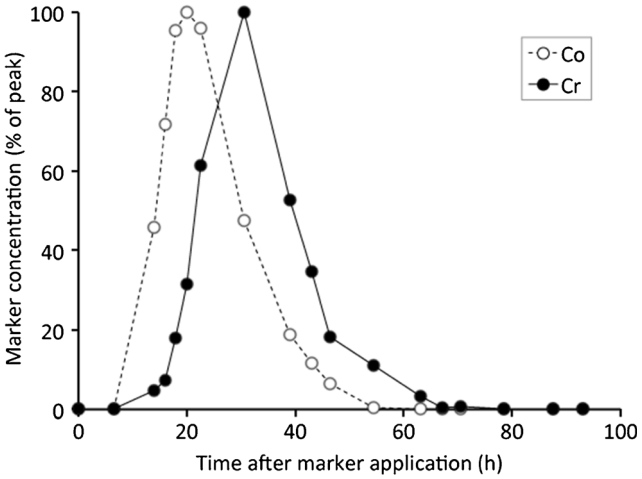

Fig. 1 Typical marker excretion curve in a Somali wild ass (*Equus africanus somaliensis*) for a solute (Co-EDTA) and a particle marker (Cr-mordanted fibre, <2 mm)

collected at 0, 13, 17, 19, 21, 24, 37, 41, 45, 48, 61, 65, 69, 72, 85, 90, 96, 109, 114, 120, 133, 144 and 157 h after marker application. Note that the equation used to determine mean retention times in this study is not affected by sampling interval (Van Weyenberg et al. 2006). Because the enclosure substrate was sand, total faecal collection was not deemed feasible. A representative subsample of all defecations was carefully picked to avoid sand contamination, dried at 60 °C and milled with a centrifuge mill (Retsch 2M1, 1-mm sieve; Retsch, Haan, Germany).

Marker analysis followed the procedure outlined by Hummel et al. (2005); a wet ashing with sulphuric acid (72%) was followed by atomic absorption spectroscopy. From the resulting faecal marker concentrations, mean retention time (MRT) for the fluid (MRT_{solute}) and the particle phase ($MRT_{particle}$) in the GIT was calculated according to Thielemans et al. (1978).

$$MRT = \sum(t_i^{*}\, dt^{*}\, c_i) \Big/ \sum(dt^{*}\, c_i)$$

with t_i = time after marker application (h), dt = time interval represented by marker concentration (calculated as $(((t_{i+1} - t_i) + (ti - t_{i-1}))$ / 2), and c_i = faecal marker concentration at time i (mg/kg DM)). The middle of the sampling intervals was used as t_i. The SF was calculated as the ratio of $MRT_{particle}$/ MRT_{solute}.

Results of this study were put into a comparative context by collecting MRT data for domestic horses, donkeys and Grevy zebras (*Equus grevyi*) from the literature.

Results

Daily dry matter intake was 5.61 ± 0.54 kg, consisting of 5.34 ± 0.54 kg grass hay and 0.26 ± 0.01 kg pelleted feed. The relative dry matter intake was 94 ± 3 g $kg^{-0.75}$ day^{-1}. The marker excretion pattern showed a distinct separation of the marker peaks in all animals (Fig. 1); differences in the calculated SF between individuals were due to variation in the descending part of the marker excretion curves. The mean retention time for the solute marker was 33.3 ± 5.4 h and for the particle marker 39.6 ± 3.9 h, resulting in a SF of 1.21 ± 0.14 (Table 2).

Discussion

The shape of the marker excretion curve is typical for horses, with a gradual increase in marker concentration that is

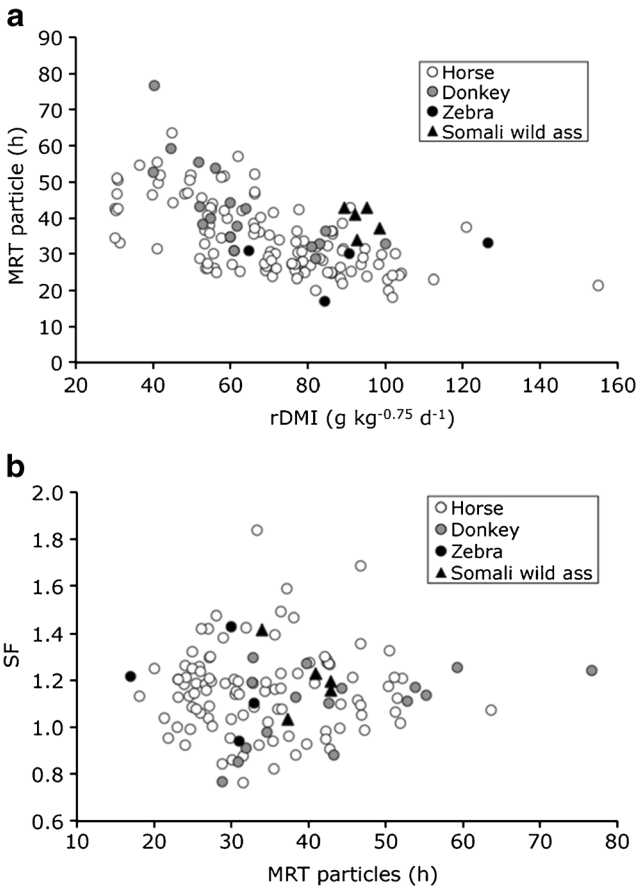

Fig. 2 Comparison of data for Somali wild ass (*Equus africanus somaliensis*) of the present study to data for domestic horses and donkeys and Grevy's zebra (*Equus grevyi*) of **a** the relative dry matter intake (rDMI) related to particle mean retention time (MRT) and **b** the particle MRT related to the selectivity factor (SF; the ratio of particle MRT to solute marker MRT) (Literature data from Wolter et al. 1976; Orton et al. 1985a, 1985b; Izraely et al. 1989; Suhartanto et al. 1992; Cuddeford et al. 1995; Todd et al. 1995; Yoder et al. 1997; Pagan et al. 1998; Drogoul et al. 2000; Drogoul et al. 2001; Pearson et al. 2001; de Araújo Oliveira et al. 2003; Moore-Colyer et al. 2003; Austbø and Volden 2006; Pearson et al. 2006; Rosenfeld et al. 2006; Moreira Pimentel et al. 2009; Goachet et al. 2010; Miyaji et al. 2011; Steuer et al. 2011; Earing et al. 2013; Clauss et al. 2014; Miyaji et al. 2014; Pimentel Silva et al. 2014)

matched by a very similar decrease. It indicates a digestive tract that does not consist of one large mixing chamber, but of a series of small mixing chambers (Jumars 2000). This corresponds to the equid large intestine with its comparatively distinct compartments, including the caecum and the ventral and dorsal proximal colon.

Literature data in general does not indicate a systematic difference in particle MRT between horses and donkeys (Fig. 2a); there is a distinct trend of decreasing MRT with increasing food intake, but horses and donkeys—and also the Grevy zebra (Steuer et al. 2011)—do not appear systematically different in this respect (Fig. 2a). However, the Somali wild asses of the present study appear to have, for their food intake level, comparatively long particle MRT, which would suggest a particularly voluminous digestive tract. When comparing the SF of domestic horses, donkeys, zebra and Somali wild ass, no systematic difference between the species is evident (Fig. 2b).

Rather than indicating differences between equid species, the results of this study suggest a comparatively uniform digestive physiology for this group. The Grevy zebra and the Somali wild ass—to our knowledge, the only two wild equids for which MRT for both a solute and a particle marker was measured with multiple faecal samples per day—do not suggest a consistent difference between domestic and nondomestic species. Even in the comparison between domestic horses and donkeys, differences are not consistently unidirectional (Tisserand et al. 1991; Pearson et al. 2006).

If we assume only very limited potential for intraguild differentiation in the digestive physiology of equids—in contrast to ruminants, in which a large variety of morphophysiological characteristics of the digestive tract have been described (Hofmann 1989; Clauss et al. 2010a; Dittmann et al. 2015)—then this may contribute to the fact that there are hardly any sympatric equid species (Kaczensky et al. 2008). Species differences among equids appear more expressed with respect to water use or behavioural characteristics (Zhang et al. 2015) than digestive physiology. Such an assumption would mean that in historic times of larger equid assemblages (Forsten 1989; Janis et al. 1994), the focus for niche differentiation was probably more on body mass variation (Alberdi et al. 1995), its link to habitat and resource availability (Clauss et al. 2013), and on dental features (Evans and Janis 2014) rather than on digestive physiology.

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