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Fluid and particle retention in the digestive tract of the addax antelope (*Addax nasomaculatus*)—Adaptations of a grazing desert ruminant

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Keywords: Ingesta passage; Mean retention time; Grazer; Browser; Digestive physiology; Food intake; Selectivity factor

1. Introduction

Natural pastures grazed by wild ruminants differ in their chemical composition (Dougall et al., 1964; Owen-Smith, 1982; Hummel et al., 2006; Codron et al., 2007), in fermentation patterns (Short et al., 1974; Holechek et al., 2004; Hummel et al., 2006), and in physical characteristics (Clauss et al., 2003). Wild ruminants also differ in several morphological (Hofmann, 1988, 1989; Clauss et al., 2003, 2006a; Hofmann et al., in press) and physiological (Clauss et al., 2001, 2002; Pérez-Barbería et al.,

2004) features of their digestive tract. For a long time, it has been speculated that the differences in the morphophysiological design observed across different phylogenetic subgroups (such as the bovids and the cervids) represent a case of consistent, convergent evolutionary adaptation to particular feeding niches (Hofmann, 1973, 1989); these niches are usually defined along a browser-grazer continuum but may include frugivores as well. The large variety of wild ruminant species, covering a broad range of feeding types, offers an ideal object for the study of convergent evolution. Whereas large datasets exist for cranio-dental and other skeletal parameters (Solounias and Dawson-Saunders, 1988; Spencer, 1995; Pérez-Barbería and Gordon, 1999; Mendoza et al., 2002) that await comparative analyses (using phylogenetically controlled statistics for the discovery of

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convergent traits), comparative data on the digestive physiology is still scarce. With the exception of digestibility coefficients for fibre (Pérez-Barbería et al., 2004), no comprehensive database exists yet that allows to address the question of a systematic, convergent trend in digestive physiology.

An important characteristic of herbivore animals is how long the ingesta is retained in the digestive tract (Stevens and Hume, 1998). Long retention times are the prerequisite for efficient bacterial degradation and fermentation of the ingested plant material. Given differences in the fermentation characteristics between browse (lower amount of slowly fermenting constituents like cellulose) and grass (high amount of slowly fermenting constituents) material, it has been hypothesized that browsing ruminants should have shorter ingesta retention times than grazing ruminants (Hummel et al., 2005, 2006). Actually, this claim has been made repeatedly for a long time (Kay, 1987; Hofmann, 1989; Clauss and Lechner-Doll, 2001). However, the existing data on mean retention times that has been generated by comparable methods (using similar marker systems) is still too limited to yield any but tentative insights (Clauss et al., 2006b). Therefore, more studies on ingesta retention characteristics of wild ruminant species (using marker systems that are comparable to the existing data set) are warranted. Especially data on non-domestic, grazing species seem to be scarce.

As other members of the Hippotraginae, the addax shows a predominantly grazing feeding habit and has been described to feed on coarse, bulky roughage, although it may also take some minor amounts of browse (acacia) or herbs (Newby, 1984; Estes, 1991; Kingdon, 2001). According to Kingdon (2001), the food consists of coarse desert grasses like *Stipagrostis vulneras*, *Panicum sp.*, *Tribulus sp.* or *Aristida pungens*, and only includes some browse in its diet in times of absence of these grasses. Gagnon and Chew (2000) estimated a content of 80% monocots in the diet of the addax. Today, only relict ranges of addax populations may exist in Mali and Chad, while their range used to include the whole Saharan region (Kingdon, 2001). Besides the camel, it is the ungulate penetrating most deeply into the Saharan desert, presumably showing the adaptations in water metabolism described for other desert ungulates, including using the rumen as a voluminous water reservoir (Silanikove, 1994).

Here, we report data on the mean retention time (MRT) of fluids and particles in the gastrointestinal tract (GIT) and the reticulo-rumen (RR) of the addax antelope. Given the classification of the addax as a grazer or intermediate feeder with a tendency towards grazing, we expected, in comparison to other ruminant species, long particle MRT, short fluid MRT, and hence a distinct difference in the retention time of the two ingesta phases.

2. Materials and methods

Eight adult addax antelope were used for the trials described in this study. The animals were kept individually at the Al Wabra Wildlife Preservation (AWWP), Qatar, and had been adapted to a diet of 100% grass hay (Rhodes Grass, *Chloris gayana*) for at least a month. Due to the splitting of the study in two different time periods, the use of two batches of hay became

necessary. Animals A and B were given *ad libitum* access to hay 1 and animals C–H were given *ad libitum* access to hay 2 (Table 1). The enclosures approximated 200 m² in size, and each was equipped with a roofed and walled area for protection against direct sunlight and wind. Unrestricted access to drinking water was provided at all times. Within the week following the passage trial, each animal was weighed (Table 2).

During 2 days preceding the passage trial and the seven trial days, the food intake of the animals was quantified by weighing the amount of hay offered and the amount of hay left over on a daily basis. Dry matter, ash, crude protein (6.25 × N) and ether extracts of the trial hays were determined according to Bassler (1988, 1993). Detergent fibre fractions (neutral detergent fibre, acid detergent fibre and acid detergent lignin (ADL)) were analysed according to Van Soest et al. (1991). The detergent fibre analyses were performed without the use of decalin. Sodium sulfite was omitted and triethylene glycol was used instead of 2-ethoxyethanol in the neutral detergent fibre procedure. Fibre values are reported including residual ash. In vitro degradability was determined using the Hohenheim gas test (Menke et al., 1979).

Similar to earlier trials (Behrend et al., 2004; Flores-Miyamoto et al., 2005; Hummel et al., 2005) dissolved cobalt (Co)-EDTA and chromium(Cr)-mordanted fibre (<2 mm) prepared from grass hay according to Udén et al. (1980) were used as markers for the fluid and the particle phase, respectively. A pulse-dose of the markers was fed to each animal mixed into a handful of a rye/wheatbran mixture. 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 afternoon. It was accepted well, each animal ingested approximately 0.7 g of Co-EDTA and 10 g of Cr-mordanted fibre. Prior to marker feeding, three faecal samples were taken to analyse Co and Cr background levels. After marker feeding, faeces were sampled during daylight hours (6 am–6 pm) in four 2 h plus one 3 h interval for the first 2 days, in two 4 h plus one 3 h interval for the third day and in one 5 h plus one 6 h interval for the following 4 days. In addition to these samples, faeces defecated at night were collected and treated as one defecation unit. A representative subsample of all defecations was taken and stored frozen until drying at 60 °C and milling with a centrifuge mill (Retsch 2 M1, 1 mm sieve; Retsch, Haan, Germany).

Table 1

Chemical composition and energy concentration of the grass hay used in the passage trials

Grass hay	DM g/kg	Ash g/kg DM	CP	NDF	ADF	ADL	EE	ME MJ/kg DM
1	927	130	116	713	347	43	12.1	7.2
2	930	98.3	102	709	303	41	9.73	7.1

¹ME [MJ/kg DM] = 136 × 24 h Gp [mL/200 mg DM] + 5.7 × CP [g/kg DM] + 0.286 × EE² [g/kg DM] + 2200.

(DM = dry matter; CP = crude protein; NDF = neutral detergent fibre = hemicellulose, cellulose and lignin; ADF = acid detergent fibre = cellulose and lignin; ADL = acid detergent lignin; EE = ether extract; ME = metabolizable energy, calculated from nutrient composition and gas production (Gp) in the Hohenheim gas test according to Menke and Huss (1987)).¹

Table 2
Body weight (BW), dry matter intake, food retention parameters for the gastrointestinal tract (GIT) and the reticulo-rumen (RR) measured in addax antelopes

Animal	A	B	C	D	E	F	G	H	Mean	SD
Body weight [kg]	95	89	85	89	80	93	81	87	87	5.3
Daily dry matter intake [kg/d]	1.48	1.50	1.94	1.63	1.72	2.08	1.80	1.53	1.71	0.22
[g/kg BW ^{0.75}]	49	52	69	56	64	69	67	54	60	8.3
MRT _{fluid} GIT [h]	41	35	33	40	28	35	35	39	36	4.2
MRT _{particle} GIT [h]	65	59	63	67	51	43	57	63	59	8.1
SF GIT	1.6	1.7	1.9	1.7	1.8	1.2	1.6	1.6	1.6	0.2
MRT _{fluid} RR [h]	16	12	20	27	13	27	18	23	20	5.8
MRT _{particle} RR [h]	40	36	49	54	36	35	40	47	42	7.0
SF RR	2.5	3.0	2.5	2.0	2.8	1.3	2.2	2.0	2.3	0.5

(MRT = mean retention time; SF = selectivity factor = MRT_{particle}/MRT_{fluid}) of the addax antelopes used in this study.

Marker analysis followed the procedure outlined by Behrend et al. (2004) and Hummel et al. (2005); a wet ashing with sulfuric acid was followed by atom absorption spectroscopy. Mean retention time in the total gastrointestinal tract (GIT) was calculated according to Thielemans et al. (1978): This method calculates the area under the excretion curve and defines MRT as the time that separates the total area under the excretion curve in two equal parts:

$$\text{MRT} = \sum (t_i \times dt \times c_i) / \sum (dt \times c_i)$$

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

MRT in the reticulo-rumen (RR) was estimated according to Lechner-Doll et al. (1990): MRT_{fluid}RR is determined by estimating the rate constant of the descending part of the marker excretion curve via an exponential equation:

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

with y = faecal marker concentration at time t (mg/kg DM), A = a constant, rate-constant k (h^{-1}) and t = time after marker

dosing (h). According to Hungate (1966), the reciprocal of k represents the MRT within the compartment characterized by k . MRT_{particle}RR is calculated as follows, based on the assumption that fluid and particles do not differ in passage characteristics distal to the RR (empirically confirmed by Grovum and Williams, 1973; Kaske and Groth, 1997; Mambrini and Peyraud, 1997):

$$\text{MRT}_{\text{particle}}\text{RR} = \text{MRT}_{\text{particle}}\text{GIT} - (\text{MRT}_{\text{fluid}}\text{GIT} - \text{MRT}_{\text{fluid}}\text{RR}).$$

The “selectivity factor”—defined as the quotient of particle over fluid MRT—was calculated for both the total GIT and the RR.

The t -test was used for the comparison of fluid and particle MRT of addax. Linear regression analysis served to evaluate potential relationships between DMI and MRT-parameters. Since differences in retention time of the fluid and particle phase in the GIT of ruminants basically result from selective retention of particles in the reticulo-rumen, all further comparisons were done using data on estimations of these parameters. MRT RR data generated in the addax antelope was compared to existing

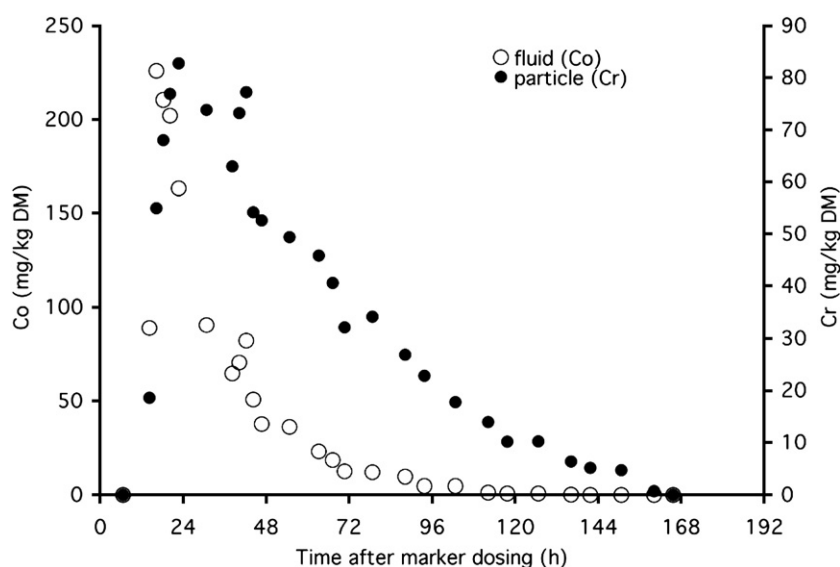


Fig. 1. Faecal marker excretion pattern in addax antelope (*Addax nasomaculatus*) G. Note the differences between fluid and particle excretion.

Table 3

Results of the contrast test for the comparison of mean retention times in the reticulo-rumen (MRT_{RR}) of addax to different ruminant species

	MRT _{fluid} RR	MRT _{particle} RR
	p-values	
<i>Capreolus capreolus</i>	<0.001	<0.001
<i>Alces alces</i>	0.482	<0.001
<i>Okapia johnstoni</i>	0.344	<0.001
<i>Giraffe camelopardalis</i>	0.336	<0.001
<i>Capra hircus f. dom.</i>	0.001	<0.001
<i>Capra ibex</i>	<0.001	<0.001*
<i>Bubalus depressicornis</i>	0.009	0.002
<i>Cervus elaphus</i>	0.001*	<0.001
<i>Bos taurus f. dom.</i>	<0.001	0.006
<i>Ovis aries f. dom.</i>	0.008	<0.001*
<i>Ovis ammon musimon</i>	<0.001	<0.001

Samples marked with an asterisk had to be excluded from the contrast test due to non-uniform variances and were compared with a *t*-test.

literature data for cattle, sheep, mouflon (*Ovis ammon musimon*), goat, red deer (*Cervus elaphus*), ibex (*Capra ibex*), anoa (*Bubalus depressicornis*), giraffe (*Giraffa camelopardalis*), okapi (*Okapia johnstoni*), moose (*Alces alces*) and roe deer (*Capreolus capreolus*), using the data collection from Clauss et al. (2006b) and Flores-Miyamoto et al. (2005). ANCOVA was used to test for differences between the MRT_{fluid}RR–MRT_{particle}RR regression lines of feeding types based on the data from the same collection (dependent variable = MRT_{particle}RR, fixed factor = feeding type, covariate = MRT_{fluid}RR). Comparisons for ruminal retention times between addax and other species were done using ANOVA and contrast tests. To meet the ANOVA requirements, logarithmic values of the parameters were used. If taxa had to be excluded from the contrast test, (MRT_{fluid}RR: red deer, due to very small variance; MRT_{particle}RR: sheep and Nubian ibex, due to very large variances), these were compared

with addax using a *t*-test for non-uniform variances. All statistical calculations were performed with the SPSS 12.0 software (SPSS, Chicago, IL).

3. Results

The body weights and the food intake of the animals are given in Table 2. On average, the animals consumed an amount of 1.71 ± 0.22 kg DM of the hay per day, corresponding to 60 ± 8.3 g DM/kg BW^{0.75}. First occurrence of the markers in the faeces was after 16 ± 3 and 17 ± 6 h for the fluid and particle marker, respectively. A typical marker excretion pattern is displayed in Fig. 1; the difference in the excretion patterns between the fluid and the particle phase is clearly visible.

The individual retention time measurements are given in Table 2. Average MRT_{fluid}GIT was 36 ± 4.2 h and significantly shorter than the average MRT_{particle}GIT of 59 ± 8.1 h ($p < 0.001$). Estimations for the reticulo-rumen (RR) (Table 2) were 20 ± 5.8 h for MRT_{fluid}RR and 42 ± 7.0 h for MRT_{particle}RR ($p < 0.001$). No significant correlation between DMI and retention time was found in the data. Compared to the other 11 taxa for which comparable data was available, the addax in this study had significantly longer MRT_{particle}RR than all other species; MRT_{fluid}RR of addax was similar to that of the browsing taxa giraffe, moose or okapi, and was significantly longer than all other taxa (Table 3).

The selectivity factor in the total GIT was with 1.6 ± 0.2 within the range of grazing ruminants (1.5–2.3; compared to 1.2–1.3 for the browsing and 1.4–1.6 for the intermediate feeding type) described by Hummel et al. (2005). In the RR, the selectivity factor was 2.3 ± 0.5 , again within the range of 1.9–3.5 described for grazing ruminants by Hummel et al. (2005), in comparison to 1.8–2.2 for intermediate and 1.4–1.8 for browsing ruminants. When average data for MRT_{fluid}RR and

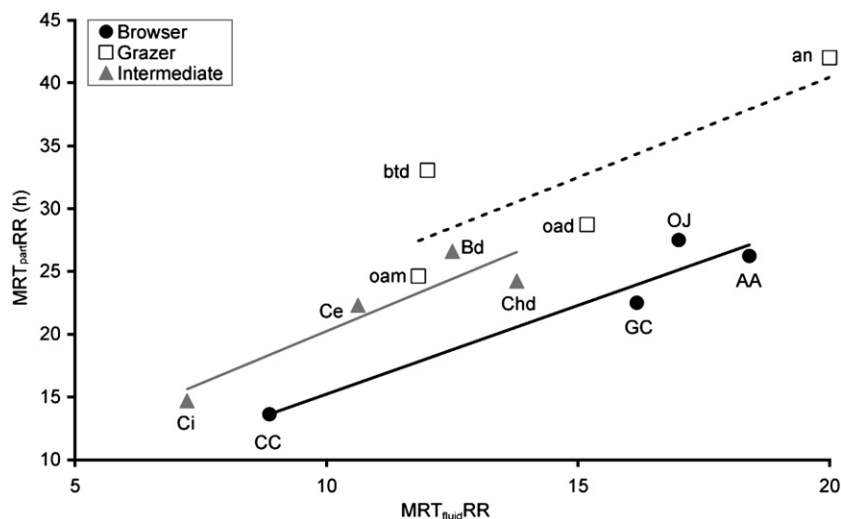


Fig. 2. Relation of mean retention time of fluid and of particles in the reticulo-rumen (MRT_{fluid}RR and MRT_{particle}RR) for different feeding types. The difference between intercepts is significant ($p = 0.012$). Data collection from Clauss et al. (2006b) plus Flores-Miyamoto et al. (2005) and this study. ANCOVA: $p(\text{slopes}) = 0.921$, $p(\text{MRT}_{\text{fluid}}\text{RR}) = 0.002$, $p(\text{intercepts}) = 0.012$. Browsers: AA *Alces alces*, CC *Capreolus capreolus*, GC *Giraffa camelopardalis*, OJ *Okapia johnstoni*; Intermediate feeders: Bd *Bubalus depressicornis*, Ce *Cervus elaphus*, Chd *Capra hircus f. dom.*, Ci *Capra ibex*; Grazers: btd *Bos taurus f. dom.*, oad *Ovis aries f. dom.*, oam *Ovis ammon musimon*, an *Addax nasomaculatus*.

MRT_{particle}RR were plotted for each species, and species groups were compared according to the three feeding types (grazer, intermediate, browser) (Fig. 2), there was a significant difference in the intercept between the feeding types ($p=0.012$).

4. Discussion

In the debate on morphophysiological differences in the digestive tract of browsing and grazing ruminants, two major differences in ingesta retention variables have been suggested: a) due to the slower and longer lasting fermentation of grass as compared to browse, grazers should have longer particle retention times (Hummel et al., 2006), and b) this particular long particle retention is achieved by the mechanism of rumen contents stratification, which is indicated by a particularly high “selectivity factor”, i. e. a distinct difference in the excretion of particulate versus fluid ingesta (Clauss and Lechner-Doll, 2001; Hummel et al., 2005; Clauss et al., 2006b). In the grazers investigated so far, this high selectivity factor is achieved by both—a long particle, but also a short fluid retention time. When compared to other ruminants (Fig. 2), the dominantly grazing addax shows an as yet unusual combination of characteristics. It has a long fluid retention in the RR, similar to that measured in strictly browsing ruminants, but has drastically high particle retention in the RR, which means that in terms of the relative, selective particle retention (the “selectivity factor”), it resembles other grazing ruminants. Evidently, the addax is an example for another solution to the question of how to achieve high selective particle retention when fast fluid throughput is not an option.

To clarify the levels of argumentation in this discussion, a terminology and concept traditionally used in ethology appears to be useful in the context of digestive physiology, too: Tinbergen (1989) asked four questions regarding the understanding of behaviour as a whole, on the one hand “Why” or ultimate questions, dealing with the evolutionary advantage of a trait like 1.) What is the evolutionary history of a trait? 2.) What selective advantage does this trait convey to its bearer?, and on the other hand “how” or proximate questions, dealing with the realisation of the trait: 3.) What are the underlying mechanisms (behaviour, physiology)? 4.) How does the trait develop in ontogeny? It is the distinction between the second and third of the questions above that is relevant for the following discussion. In terms of digestive physiology, the ultimate question would be about the selective advantage of long or short retention times (maximisation of energy and nutrient gain), while the proximate question would deal with the morphophysiological mechanisms at work in the GIT to realise them. Such a distinction between the development of a trait in evolution and its morphological and physiological background has been considered as important to avoid confusion in argumentation (Alcock and Sherman, 1994).

Significantly longer MRT_{particle}RR than for all other ruminant taxa have been found for the addax in this study. The animals have a large proportion of coarse forage of grass genera of the C₄-type in their natural diet, which are known for their especially slow fermentation (Casewell et al., 1973; Wilson et al., 1989). Therefore, very long retention times for particles can be expected from an ultimate point of view since a slow, but

continuous fermentation rate of a food source makes a long retention time for particles an evolutionary advantage.

On a proximate level this leads us to the question how and by which physiological/morphological traits such long retention times are finally realised. As ingesta retention generally can also be considered a function of the relative food intake (Clauss et al., 2007), any particularly long retention times would most conveniently be explained by a low food intake as compared to other species, even if no significant correlation between DMI and MRT was evident in the data of the addax of this study. However, the average intake level of 60 g/(kg BW^{0.75}*d) recorded for the study animals was within the standard range of ruminants on maintenance requirements. E.g. a mean of 67±16 g/kg BW^{0.75}*d was found for non-performing animals in the data collection on 7 ruminant taxa of Hummel et al. (2005). Differences in intake level therefore cannot explain the long MRTs measured in the addax. Additionally, the addax in our study were fed a coarse forage only diet (CP: 10.9% DM; 7 MJ ME/kg DM) which reflects the diets of addax in the wild to some extent; therefore, the long MRTs measured can also not be explained by the use of an extraordinarily highly digestible food.

One of the most obvious adaptations that will allow long MRTs at average levels of food intake is a particularly capacious gastrointestinal tract; as MRTs calculated for the RR are especially high, it can be predicted that addax should have particularly capacious forestomachs. Such an adaptation has been described for another ruminant that has to feed on forage of particularly low digestibility, an indigenous breed of sheep (Heidschnucken) (Weyreter et al., 1987). Newby (1984) actually commented upon the bulky body of the addax, which he interpreted as an adaptation to the need to harbor a large water tank at the negligible expense of low mobility in a practically predator-free environment. To date, it can only be speculated that addax have other anatomical properties associated with a rumen contents stratification that is considered the prerequisite for a distinct difference in fluid and particle passage from the rumen. Such adaptations could be strong rumen pillars (Clauss et al., 2003) or particularly well-developed reticular honeycomb cells (Hofmann, 1989).

For a ruminant adapted to desert habitats, a capacious forestomach might be advantageous also in another context. Water sparing and storing mechanisms are very important under desert conditions. Such mechanisms are obviously at work in the addax, and their faecal water content was found to be among the lowest (46.4%) in a study investigating a range of 81 captive wild ruminant species (Clauss et al., 2004). While this is basically realised by efficient water re-absorption in the large intestine, an additional adaptation of the digestive tract in desert-adapted ruminants and camelids has been described: The use of the forestomachs as a large water storage organ (Adolph and Dill, 1938; Brosh et al., 1988; see Silanikove, 1994 for a review). Such a strategy should move along with a long retention time for fluids in the reticulo-rumen. Considering the low overall water requirement and the correspondingly low water intake of desert ruminants in addition (Wilson, 1989), their MRT_{fluid}RR could therefore be hypothesized to be longer than that of a comparable non-desert species. Indeed, the

MRT_{fluid}RR of addax was found to be surprisingly long, being significantly longer compared to all other grazers. However, it remains to be tested if extraordinary long retention times of fluid are found in other desert-adapted ruminants, too. For camelids, this hypothesis does not seem to hold true: Heller et al. (1986a) and Lechner-Doll et al. (1990) found a rather short MRT_{fluid} in the forestomach of dromedaries (*Camelus dromedarius*) of about 10–14 h; and data on Bactrian camels as well as hybrid animals are, with 12–16 h, in the same order (Cahill and McBride, 1995; von Engelhardt et al., 2006). Only when *Camelus sp.* were deprived of water for 8–11 days did their MRT_{fluid} in the forestomach increase to similar values (22–23 h) as the mean MRT_{fluid}RR of the addax of this study. However, this increase in MRT in the camelids was associated with a drastic decrease in daily food DM intake to 6 g/kg BW^{0.75}. If the forestomach is considered a water storage organ for desert ruminants and camelids (Silanikove, 1994), a short MRT_{fluid} in the forestomach would mean a high rate of water recycling via passage from the RR, re-absorption (in the omasum and the large intestine), and re-secretion into the RR via saliva. The differences in measurements between camelids and addax would suggest that this recycling occurs at a distinctively lower rate in the addax; in other words, fluid stasis in the RR is more pronounced in the addax. Actually, data on salivary secretion in camels appear to indicate that camelids do maintain a higher salivary flow rate than cattle during dehydration (reviewed by Silanikove, 1994). Differences in strategy might actually be related to the capacity of the red blood cells to withstand the osmotic challenge of rapid dehydration; in this respect, camelids have been shown to differ from ruminants (reviewed by Silanikove, 1994). Water ingested during rapid rehydration might be more quickly absorbed from the GIT by camels but remains to a higher proportion in the ruminant RR (reviewed by Cain et al., 2006, but note that this does not correspond to the review of Silanikove, 1994). In a comparison between another member of the hippotraginae ruminants, the oryx (*Oryx leucoryx*), and the dromedary, it was found that the ruminant had a mass-specific water-influx rate that is only 32% of that of the camelid (Ostrowski et al., 2002), at an estimated DMI of 98 g/kg^{0.75}/d. The authors noted that the ruminant appeared to be even more adapted to water shortage than the camelid, and listed several behavioural adaptations as possible explanations. The result of our study, when compared to camelids, add the physiological mechanism of particularly long MRT_{fluid}RR to these potential adaptations of desert ruminants. A more detailed review is beyond the scope of this contribution. While the very long MRT_{fluid}RR estimated for addax in this study suggest that the forestomach plays an important role for the increase in water retention, further MRT data on other desert-adapted ruminants are warranted to substantiate this seeming fundamental physiological difference in desert-adapted ruminants and camelids.

Clauss et al. (2006b) speculated that a high fluid throughput would guarantee the presence of a stratification of rumen contents in cattle, providing the rumen with a constant supply of low-viscosity fluid that facilitates the separation of particles according to their flotation and sedimentation behaviour. A large volume of a low-viscosity-fluid that has a lesser turnover,

as suggested for the addax of this study, should be equally suited to allow such a separation by buoyancy characteristics to occur. This gives rise to the question for the adaptive advantages of either solution—especially the value of the strategy evidently adopted by cattle and possibly also by other bovini (Clauss et al., 2006b), and by camelids (Heller et al., 1986a,b; Lechner-Doll et al., 1990; von Engelhardt et al., 2006). Several authors have commented on the influence of rumen dilution rates on fermentation characteristics (e. g. Harrison et al., 1975; Isaacson et al., 1975; Meng et al., 1999) (reviewed by Owens and Goetsch 1986; Van Soest 1994), the overall conclusion being that efficiency of microbial growth and supply of valuable microbial protein to the small intestine, the absorption site of the host, is positively correlated to the fluid passage rate from the forestomach. Following this argument, desert ruminants would sacrifice maximisation of microbial protein supply to the small intestine for the sake of water storage and probably some improvement in DM digestibility, while ruminants with a comparatively high fluid passage from the rumen like cattle may maximise protein supply at the expense of a higher water requirement.

Food retention times in the gut describe an important aspect of the digestive strategy of herbivores. While the data on addax start to close a gap in information on retention times in ruminants, further data on more non-domesticated, not-desert-adapted ruminants like e.g. the roan antelope also belonging to the Hippotraginae, but inhabiting savannah biotopes, gained with comparable methods, would be highly desirable. On the other hand, additional studies in retention times in desert ruminants will provide further insight in the role of the rumen as a water storing organ in these animals.

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