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Fluid and particle retention in captive okapi (*Okapia johnstoni*)

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Abstract

Retention time of food in the digestive tract is among the key variables that describe the digestive strategy of a herbivore. Mean retention time (MRT) was measured on 4 captive specimens of the okapi, a strictly browsing ruminant. Retention time was quantified on different diets, using Co-EDTA (fluid phase) and Cr-mordanted fibres (1–2 mm) (particle phase) as pulse-fed markers. Average food intake was 55–65 g DM/(kg $BW^{0.75}$*d). Fecal excretion of the markers was quantified over 10 days. Different models to calculate retention time and passage rate in the gastrointestinal tract (GIT) and the reticulorumen (RR) were applied. Average $MRT_{particle}$GIT was quantified to be 47 ± 8 h and MRT_{fluid}GIT 36 ± 5 h. Concerning estimation of retention times in the reticulorumen, $MRT_{particle}$RR was quantified to be 27 ± 7 h, while MRT_{fluid}RR was 17 ± 4 h. The quotients $MRT_{particle}/MRT_{fluid}$ were quantified to be 1.3 ± 0.1 for the GIT and 1.6 ± 0.2 for the RR. Compared to data established with comparable markers, the okapi has low coefficients of $MRT_{particle}/MRT_{fluid}$. A less well developed retention mechanism for fibres compared to species like cattle or sheep can be explained by a comparatively high fermentation rate and low digestibility of the natural food of the okapi—browse—in comparison to grass.

Keywords: Digestive strategy; Mean retention time; *Okapia johnstoni*; Passage rate; Browsing ruminant; Feeding type; Co-EDTA; Cr-mordanted fibres; Compartment models

1. Introduction

The extent of food retention in the digestive tract has important consequences for the digestive strategy of ruminants and other herbivorous animals. Since fibre digestion by symbiotic gut microbes is a time-dependent process, retention of food in the fermentation chamber of an animal largely determines the extent of fibre and, therefore, also of dry matter and energy digestion. In the ruminant forestomach, particles are generally retained substantially longer than fluid, supporting a thorough fermentation of slow fermenting fibres. On the other hand, this well developed food retention mechanism puts limits on the potential food intake of a species. Ruminants have been shown to be more intake-limited compared to hindgut fermenters like equids with their less developed retention mechanism (Duncan et al., 1992). While this difference in retention patterns is well established, differences in retention capacity between different ruminant species/feeding types are still debated, browsing species being regarded as having a lower capacity to retain food particles in their gastrointestinal tract (GIT) compared to grazing species (Kay et al., 1980; Hofmann, 1989; Clauss and Lechner-Doll, 2001).

When describing food excretion data of herbivores, mean retention time (MRT = the time after which 50% of a defined

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meal or marker dose have been excreted) is generally regarded as the best scale for comparisons (Hume, 1995). While calculations based on estimations of the area under the marker excretion curve may be accurate in quantifying the mean retention time, models regarding the GIT as composed by compartments of differing mechanistic principles (e.g., forestomach=continuous flow stirred-tank reactors; small intestine=plug flow reactor; see Caton and Hume, 2000) can give some additional information on the digestive system, although interpretation may differ (e.g., Grovum and Williams, 1973, Ellis et al., 1979, Pond et al., 1988, Van Soest, 1994). Therefore the pattern of marker excretion of a species also gives some information on the working of the digestive system of a herbivore.

This study aimed at evaluating retention times in the okapi (*Okapia johnstoni*), a mid- to large-sized strictly browsing ruminant (Hart and Hart, 1988; Cerling et al., 2004), using captive specimens. Different models to calculate retention time parameters were compared.

2. Materials and methods

Four okapis of the zoological gardens of Copenhagen (facility 1) and Cologne (facility 2) were included in this study (Table 1). Retention time measurements were done on one occasion at facility 1 (F 1-1, 5/2000) and on three occasions at facility 2 (F 2-1, 1/2001; F 2-2, 5/2001; F 2-3, 7/2001). Body weights of two of the animals were quantified by a scale. Animals had about 8 h per day access to the outside enclosures. During this time, some of the animals were kept together with other individuals. Titanium oxide was used as color marker to be able to distinguish the faeces of individuals. All animals were separated overnight. Feeding routines and feeding times were kept as constant as possible (concentrate separated on a morning and afternoon meal; ad lib. access to lucerne hay; in trials 2-2 and 2-3 additional access to larger volumes of fresh browse). The composition of the rations is presented in Table 2. In most cases, two animals had common access to alfalfa hay during the day. The amount consumed together was regarded to be equally distributed between both animals. Food intake was measured by weighing all items offered and re-weighing leftovers the next morning. Food samples were analysed for dry matter by drying at 103 °C to constant weight.

Cobalt (Co-EDTA) was used as a fluid and chromium (chromium-mordanted fibres—Cr-F) as a particle marker.

Table 1
Data and keeping of captive okapi (*O. johnstoni*) (F 1, 2=facility 1, 2)

	Animal	Sex	Birth	Enclosure size (m^2)	
				Night/inside	Day/outside
F 1	1	♂	5/86	42	~400+42
	2	♂	12/94	14/42	~400+28
F 2	3	♂	11/92	29	~1050+29
	4	♂	9/99	29	~1050+29

Both markers were prepared according to Udén et al. (1980). For the particle marker, lucerne hay was used that was ground in a feed mill (Retsch type 2M1) using a 2 mm pore size. During the washing process, a sieve with lateral dimension of holes of 1 mm was used. The particle marker, therefore, represents particles retained by sieve sizes between 1 and 2 mm. The Cr concentration of the Cr-F was determined as 4.5% Cr in dry matter.

The markers were applied as a pulse dose of 1.5 g Co-EDTA and 17 g Cr-F. The liquid Co-EDTA was applied to a pelleted feed, which was then mixed with the Cr-F and about 75 g of fresh banana pulp. This mixture was readily ingested by the animals within 15 min.

Fecal samples were taken during the first three days from each defecation, during the next four days every four hours, and during the subsequent three days every eight hours. Some samples were taken prior to marker application to establish the baseline of marker concentrations in the faeces. The samples were dried at 103 °C and ground (pore size 1 mm). The time of defecation or the representative time interval was noted. For the determination of defecation times at night, taped video-recordings in time-lapse mode and time code were used (Panasonic AG-6040 Time-Lapse). Red light was used as a light source not disturbing normal resting patterns of the animals. The different defecations were generally placed well apart so that individual defecations could be identified.

The markers were analysed according to Behrend et al. (in press). Approximately 0.3 g of a sample was mixed in test tubes with 5 ml 72% H_2SO_4 and placed on a shaker overnight. The next day, the samples were filtrated into new tubes; from these solutions, Co and Cr could be directly measured by atomic absorption spectroscopy (Perkin-Elmer 1100 B).

Mean retention time (MRT) of the total gastrointestinal tract (GIT) was calculated using three different models:

1. (*M1*) 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.

   $$\mathrm{MRT} = (t_i * dt * c_i)/(dt * c_i)$$

   with t_i=time after marker application (h), dt=time interval represented by marker concentration, c_i (calculated as $((t_{i+1}-t_i)+(t_i-t_{i-1}))/2$), and c_i=fecal marker concentration at time i (mg/kg DM) (for sampling intervals, the middle of the interval was used as t_i).
2. (*M2*) According to Grovum and Williams (1973): This model assumes 2 compartments (pools) in the gastrointestinal tract where mixing of ingesta occurs, which are both characterized by a constant outflow rate. The outflow probability is equal for all particles in both pools, independent of their previous retention in the pool. The transit time (TT,

Table 2
Body weight (BW), dry matter intake (DMI), roughage proportion of diets and number of defecations per day in captive okapi (*O. johnstoni*)

Sampling period	F 1-1		F 2-1		F 2-2		F 2-3	
Animal	1	2	3	4	3	4	3	4
BW (kg)	245[a]	205[a]	230	225	230	225	230	225
DMI (g/(kg $BW^{0.75}$ d))	64	65	55	61	60	58	64	56
Roughage proportion (%)[b]	30	49	46	71	44	65	46	52
Daily defecations	6.6	6.6	8.7	6.3	8.9	6.0	6.5	6.0

[a] Estimated body weights.
[b] F 1-1 and F 2-1: 100% lucerne hay; F 2-2: 79% lucerne hay, 14% browse leaves, 7% browse twigs; and F 2–3: 35% lucerne hay; 48% browse leaves, 17% browse twigs.

time of first marker appearance in the faeces after marker application, in h) represents those parts of the GIT where little or no mixing occurs. The rate-constants and TT are determined by non-linear regression using the model equation:

$$y = A^{*}\left(e^{k1^{*}(t-TT)} - e^{k2^{*}(t-TT)}\right)$$

with y=fecal marker concentration at time t (mg/kg DM), a constant A, the rate-constants k_1 and k_2 (h^{-1}), and t=time after marker application (h).The reciprocal of the rate-constants represents the MRT in the respective compartment according to Hungate (1966). Total tract MRT can be calculated as

$$\mathrm{MRT} = 1/k_1 + 1/k_2 + TT.$$

3. (*M3*) According to Pond et al. (1988): This model also assumes two mixing compartments, only one of which is characterized by a constant outflow rate. For the other pool, it is assumed that outflow probability increases with time retained in this pool. Here, a gamma-2 distribution was assumed for the retention in this pool. Again, segments of the GIT with no ingesta mixing are represented by TT. The rate constants and TT are determined by non-linear regression:

$$y = A^{*}\delta^{2}{*}e^{-k^{*}(t-TT)} - e^{-\lambda^{*}t}{*}\left(\delta^{2} + \delta^{*}\lambda^{*}(t-TT)\right)$$

with y=fecal marker concentration at time t (mg/kg DM), a constant A, the time-independent rate-constant k (h^{-1}), the time-dependent (assuming a gamma-2 distributed retention) rate-constant λ (h^{-1}), and t=time after marker application (h). δ is calculated as $\delta = \lambda^{*}(\lambda - k)$. Total tract GIT can be calculated as

$$\mathrm{MRT} = 1/k + n/\lambda + TT$$

with n characterising the kind of gamma-distribution assumed (here: n=2).

The MRT in the reticulorumen (RR) was estimated using two different models:

1. (*MA*) According to Ørskov (1992): The descending part of the marker excretion curve allows, by non-linear regression using the following equation, to calculate the rate-constant for the outflow of fluid and particles from the RR

$$y = A^{*}e^{-k^{*}t}$$

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

Again, according to Hungate (1966), the reciprocal of k represents the MRT within the compartment characterized by k.

2. (*MB*) According to Lechner-Doll et al. (1990): $\mathrm{MRT_{fluid}}$RR is determined as in method A. However, $\mathrm{MRT_{particle}}$RR is calculated differently, based on the assumption that fluid and particles do not differ in their passage characteristics distal to the RR (empirically confirmed by Grovum and Williams, 1973; Kaske and Groth, 1997 and Mambrini and Peyraud, 1997):

$$\mathrm{MRT_{particle}RR} = \mathrm{MRT_{particle}GIT} - \left(\mathrm{MRT_{fluid}GIT} - \mathrm{MRT_{fluid}RR}\right).$$

The results of *M2*, *M3* and *MA* are given including the R^2 and the standard deviation of the residuals $S_{y,x}$. Differences between the results from the different models were compared using the Wilcoxon test ($p<0.05$). As software, Graph Pad Prism 3.0 and SPSS 11.0 were used.

3. Results

Fig. 1 gives a typical example of a marker excretion curve in the okapis of this study. The first excretion of markers (transit time) occurs after app. 20 h. The excretion of particles is distinctively delayed as compared to fluids. After 4.5 days, the fluid marker and, after 5.5 days, the particle marker were completely excreted. The calculated retention parameters are given in Table 3. The average $\mathrm{MRT_{particle}}$GIT ranged between 47 and 50 h, the average $\mathrm{MRT_{fluid}}$GIT between 36 and 41 h. $\mathrm{MRT_{particle}}$GIT*M1* was shorter in all cases than $\mathrm{MRT_{particle}}$GIT*M2*. No according trend was observed for the fluid marker. In describing the particle excretion curve, the time-dependent model $\mathrm{MRT_{particle}}$GIT*M3* results in a better fit (lower $S_{y,x}$ values) than

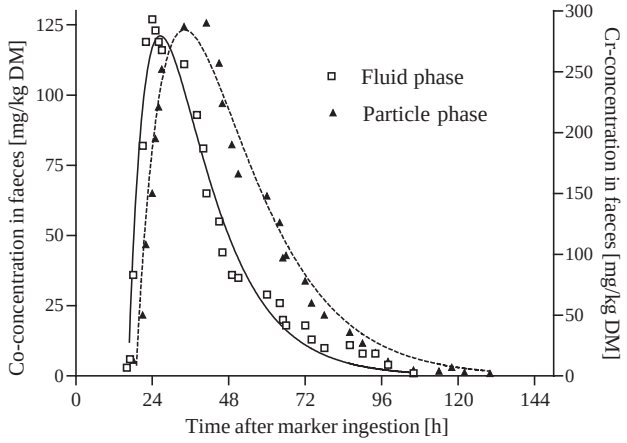

Fig. 1. Marker excretion pattern of okapi (F2-1; animal 3); particle marker=chromium-mordanted fibres (≤2 mm); and fluid marker=Co-EDTA.

$MRT_{particle}GIT$*M2*. The $MRT_{particle}GIT$*M3* results were shorter than those of $MRT_{particle}GIT$*M2* and thus were more similar to those of $MRT_{particle}GIT$*M1*. $MRT_{particle}GIT$*M2* were significantly longer than those of model 1 and 3 ($p<0.05$). In contrast, $MRT_{fluid}GIT$*M3* was significantly longer than those of model 1 and 2 ($p<0.05$). The quotient of $MRT_{particle}GIT/MRT_{fluid}GIT$ was relatively constant at 1.3. $MRT_{fluid}RR$ averaged at 17 h. Calculated averages for $MRT_{particle}RR$ (Table 4) varied between 19–27 h, with $MRT_{particle}RR$*MB* approximately 30% longer than $MRT_{particle}RR$*MA*. The quotient of $MRT_{particle}RR$*MA*/$MRT_{fluid}RR$*MA* was lower than the according value for the total GIT. In contrast, the quotient of $MRT_{particle}RR$*MB*/$MRT_{fluid}RR$*MA* was invariably larger than the according value for the total GIT.

4. Discussion

Several aspects need to be considered in performing ingesta retention measurements. Ideally, passage markers should be indigestible and should not influence the kinetics of the ingesta fraction they represent. Mordanting, as used in this study, results in a stable bond between the Cr and the fibre fraction (Udén et al., 1980). In contrast to normal fibre particles, Cr-mordanted fibres with a concentration of 8–10% Cr in DM are indigestible (Van Soest et al., 1988). However, the Cr changes the specific density of the fibre material which will influence the excretion patterns. With respect to particle density, the concentration of a particle marker should be 2% Cr in DM (Van Soest et al., 1988). The Cr-F used in this study with a concentration of 4.5% Cr in DM therefore is a compromise between these two extremes. Ideally, for inter-specific comparisons, markers of one batch should be used to avoid differences inherent in comparing data gained from markers of differing degrees of digestiblity and density.

Table 3
Retention parameters in the total gastrointestinal tract (GIT) in captive okapi (*O. johnstoni*)

Sampling period		F 1-1		F 2-1		F 2-2		F 2-3			
Animal		1	2	3	4	3	4	3	4		
	Model	MRT (h)								Ø	± SD
$MRT_{particle}$	M1	44	48	48	38	44	43	44	65	47	± 8
$MRT_{particle}$	M2	50	50	49	39	47	45	47	72	50	± 10
$CMRT_{1+2}$		29	33	31	22	29	29	33	47		
TT		21	18	19	17	18	17	14	25		
R^2		0.90	0.92	0.95	0.95	0.92	0.92	0.92	0.92		
S*y*,*x*		87.0	23.5	23.8	33.5	31.0	30.0	31.0	22.7		
$MRT_{particle}$	M3	48	50	49	37	45	41	45	70	48	± 10
$CMRT_{1+2}$		29	35	30	21	29	25	28	48		
TT		19	15	18	16	17	17	16	22		
R^2		0.94	0.92	0.99	0.98	0.94	0.97	0.98	0.97		
S*y*,*x*		69.0	24.5	13.5	21.5	27.0	17.9	16.3	15.3		
MRT_{fluid}	M1	33	39	41	30	36	36	32	44	36	± 5
MRT_{fluid}	M2	33	39	39	30	35	35	33	47	36	± 5
$CMRT_{1+2}$		15	21	22	14	20	19	22	34		
TT		19	19	16	16	15	16	11	13		
R^2		0.96	0.95	0.97	0.99	0.95	0.96	0.95	0.88		
S*y*,*x*		10.7	7.2	8.6	6.6	7.5	5.6	7.8	12.1		
MRT_{fluid}	M3	32	38	49	32	45	43	36	53	41	± 8
$CMRT_{1+2}$		15	21	33	17	30	28	19	40		
TT		17	17	16	16	15	15	17	13		
R^2		0.96	0.95	0.97	0.95	0.95	0.97	0.98	0.88		
S*y*,*x*		10.9	7.6	9.0	14.1	7.8	5.3	5.0	12.6		
$MRT_{particle}/MRT_{fluid}$	$part._{M1}/fl._{M1}$	1.3	1.2	1.2	1.3	1.2	1.2	1.4	1.5	1.3	± 0.1
	$part._{M3}/fl._{M2}$	1.4	1.3	1.3	1.2	1.3	1.2	1.4	1.5	1.3	± 0.1

MRT=mean retention time; $CMRT_{1+2}$=MRT in compartment 1 and 2; calculation according to different models (M1: Thielemans et al., 1978; M2: Grovum and Williams, 1973; and M3: Pond et al., 1988); and TT=transit time.

Table 4
Retention parameters in the reticulorumen (RR) in captive okapi (*O. johnstoni*)

Sampling period		F 1-1		F 2-1		F 2-2		F 2-3			
Animal		1	2	3	4	3	4	3	4		
		MRT (h)								Ø	± SD
$MRT_{particle}$	MA	17	25	22	19	20	17	16	24	19	± 3
R^2		0.98	0.95	0.99	0.95	0.90	0.96	0.98	0.98		
S*y*,*x*		31.3	15.8	11.3	27.0	25.0	16.4	13.2	9.5		
$MRT_{particle}$	MB	24	28	28	26	22	22	26	44	27	± 7
MRT_{fluid}	MA	12	19	21	17	14	15	14	24	17	± 4
R^2		0.93	0.89	0.95	0.98	0.95	0.93	0.97	0.96		
S*y*,*x*		11.8	7.4	7.8	6.5	4.7	5.2	5.4	5.6		
$MRT_{particle}RR/MRT_{fluid}RR$	$part._{MA}/fl._{MA}$	1.4	1.3	1.0	1.1	1.4	1.2	1.1	1.0	1.2	± 0.2
	$part._{MB}/fl._{MA}$	1.9	1.5	1.3	1.5	1.6	1.5	1.8	1.9	1.6	± 0.2

MRT=mean retention time; calculation according to different models (MA: Ørskov, 1992; MB: Lechner-Doll et al., 1990).

Number of defecations per day (Table 2) was relatively low in the study okapis (~6–9/day) compared to values of 28/day reported for captive axis deer (*Axis axis*) on a diet including considerable proportions of concentrates (Dinerstein and Dublin, 1982) and for sheep fed concentrates and hay (13.3/day) or fresh grass (15.5/day) reported by Longhurst (1954). Nevertheless, the fecal output frequency was sufficient to get enough data points for calculations.

In this study, different calculation models for the MRT parameters were used. According to Rothfuβ (1996), the calculation according to Thielemans et al. (1978) (*M1*) yields reliable MRT estimates for the total GIT. Quiroz et al. (1988) found that the two-compartment model of Grovum and Williams (1973) (*M2*) yields good estimates for the fluid ingesta phase, whereas the particle phase is better modelled using a time-dependent model as the one by Pond et al. (1988) (*M3*). The results of this study confirm these evaluations of the respective models, if the results of the calculation according to Thielemans et al. (1978) are accepted as a calibrating standard. They support the use of time-dependent compartment models for particle data and the use of exponential compartment models for the data on the fluid phase. Of the two methods used for the calculation of $MRT_{particle}RR$, the one by Lechner-Doll et al. (1990) invariably results in longer estimates. Given that particles and fluids do not differ in kinetics distal to the RR (Grovum and Williams, 1973; Kaske and Groth, 1997; Mambrini and Peyraud, 1997), the quotient $MRT_{particle}RR/MRT_{fluid}RR$ must, by necessity, be greater than $MRT_{particle}GIT/MRT_{fluid}GIT$ (Hummel and Kolter, 2003). Therefore, the estimates based on the method of Lechner-Doll et al. (1990) (*MB*) appear more realistic and should be the preferred method used in further investigations.

According to Lechner-Doll et al. (1991), the quotient of $MRT_{particle}/MRT_{fluid}$—the so-called selectivity coefficient—represents a good measure for the comparative selective particle retention that is independent of other influence factors such as food intake level or ratio of concentrates and roughage in the diet. However, in studies of Shaver et al. (1988) and Cherney et al. (1991), the selectivity coefficients for different particle classes increased at low food intake levels. Therefore, a certain influence of feeding level on this parameter cannot be excluded. Nevertheless, this coefficient is a practical measure for the comparison of results from different studies.

The diets used in this study differed in their roughage composition. In a study including ruminant species of different feeding types, Renecker and Hudson (1990) found considerably shorter MRTs for diets high in browse leaves compared to pure lucerne or lucerne/grass diets. Clauss et al. (2002b) speculate about a decreasing influence of browse leaves on MRT in comparison to other forages due to differences in particle size and shape. For captive okapi, a clear effect of the different diets cannot be established. The by far longest $MRT_{particle}GIT$ (65 h) was measured for an animal on the high browse diet and the lowest for the same animal on the diet without browse (38 h), while all other measurements were in the range of 43–48 h.

Comparative data on retention parameters in the total GIT and the RR are listed in Tables 5 and 6, respectively. Although Tables 5 and 6 only comprise data where similar markers were used as in this study, comparisons should only be made bearing in mind that differences in food intake, food type and digestibility can also influence the results and cannot be standardized when collating literature data. Calculated by model 1, $MRT_{fluid}GIT$ and $MRT_{particle}GIT$ in this study averaged at 36 and 47 h. The latter value compares well with the 46 h reported by Clauss and Lechner-Doll (2001) in captive okapi. The MRTs measured for okapis are longer than those reported for smaller ruminants such as roe deer (*Capreolus capreolus*) and mouflon (*Ovis ammon musimon*, Behrend et al., 2004) and also slightly exceed values measured in captive giraffe (*Giraffa camelopardalis*, Clauss et al., 1998). In contrast, values measured in sheep are either of similar scope as those of the okapis, or notably longer, and those measured in cattle distinctively exceed those measured in the okapi for particles but tend to be shorter for fluids. The quotient of $MRT_{particle}GIT/MRT_{fluid}GIT$ is generally low in okapi (as in roe deer and giraffe), especially as compared to values in cattle (Table 5).

Table 5
Overview on retention times in the GIT of studies on different ruminant species

Species	BW (kg)	MRT_{fluid} (h)	Marker fluid	$MRT_{particle}$ (h)	Marker particle	$MRT_{part.}/MRT_{fl.}$	DM intake (g/(kg $BW^{0.75}$*d))	Roughage proportion (% DM)	Food	
Roe deer	21	18	EDTA	24	Cr-F. (2 mm)	1.3	–	100	Ad lib. natural forage	[1]
Okapi	–	–	–	46	Cr-F. (2 mm)	–	–	–	Zoo diet	[2]
Okapi	225	36	EDTA	47	Cr-F. (2 mm)	1.3	61	50	Zoo diet	[3]
Moose	353	38	EDTA	–	–	–	80	0	Pellet	[4]
Moose	347	38	EDTA	–	–	–	52	40	Pellet / browse	[4]
Giraffe	350	31	EDTA	–	–	–	–	–	Zoo diet	[5]
Giraffe	860	34	EDTA	40	Cr-F. (2 mm)	1.2	66*	44*	Zoo diet	[6]
Goat	48	26	EDTA	28	Cr-glumes (1.5 mm)	1.1	101	40	Grass hay/ concentrate	[7]
Goat	30	33	EDTA	43	Ce-F. (< 2 mm)	1.3	–	100	Ad lib. veg. (dry season)	[8]
Goat	30	29	EDTA	36	Ce-F. (< 2 mm)	1.2	–	100	Ad lib. veg. (rainy season)	[8]
Goat	29	39	EDTA	52	Cr-F. (< 6 mm)	1.3	56	100	Grass hay	[9]
Goat	42	23–28	EDTA	46–56	Cr-F. (0.03–0.50 mm)	1.6–2.4	48–53	100	Grass hay/ lucerne hay	[10]
Ibex ♀	23	23	EDTA	35	Cr-F. (long)	1.5	50–59	100	Grass hay/ lucerne hay	[11]
Ibex ♂	60	28–32	EDTA	44–54	Cr-F. (long)	1.6–1.7	67–71	100	Grass hay/ lucerne hay	[11]
Mouflon	32	23	EDTA	36	Cr-F. (2 mm)	1.6	–	100	Ad lib. natural forage	[1]
Sheep	30	38	EDTA	70	Cr-F. (< 6 mm)	1.8	51	100	Grass hay	[9]
Sheep	45	–	–	54	Cr-F. (1.2–2.4 mm)	–	40	59	Hay/molasses	[12]
Sheep	67	37	EDTA	43	Cr-F. (fecal part.)	1.2	–	100	Ad lib. roughage	[13]
Sheep	67	39	EDTA	47	Cr-F. (fecal part.)	1.2	52	100	1.8% BW roughage	[13]
Sheep	89	–	–	75	Cr-F. (1–2 mm)	–	50	25	Grass hay / maize and soymeal	[14]
Sheep	71	30	EDTA	58	Cr-F. (long)	1.9	50	50–88	Lucerne hay / maize sil./conc.	[15]
Sheep	30–45	46	PEG	63–73	Cr-F. (< 1 mm)	1.4–1.6	–	–	Straw ad lib.+conc.	[16]
Sheep	50	33	PEG	56–58	Cr-F. (< 1 mm)	1.7–1.8	–	–	Straw ad lib.+conc.	[16]
Sheep	39	37	EDTA	49	Ce-F. (< 2 mm)	1.3	–	100	Ad lib. natural forage	[8]
Sheep	39	32	EDTA	38	Ce-F. (< 2 mm)	1.2	–	100	Ad lib. natural forage	[8]
Water buffalo	417	29	EDTA	58	Cr-F. (long)	2.0	50	50–88	Lucerne hay/maize sil./conc.	[15]
Cattle	555	28	EDTA	78	Cr-F. (rumen part.)	2.8	68	100	Grass hay	[9]
Cattle	243	30	EDTA	62	Cr-F. (rumen part.)	2.1	55	100	Grass hay	[9]
Cattle	509	32	EDTA	65	Cr-F. (long)	2.0	50	50–88	Lucerne hay/maize sil./conc.	[15]
Cattle	Adult	–	–	61	Cr-F. (fecal part.)	–	–	75	Grass silage+3 kg concentrate	[17]
Cattle	Adult	–	–	65	Cr-F. (fecal part.)	–	–	45	Grass silage+9 kg concentrate	[17]

EDTA=Cr- or Co-ethylene diamine tetraacetate; PEG=polyethylene glycol; Cr-F./Ce-F.=chromium-/cerium-mordanted fibres; rumen part.=rumen particles; fecal part.=fecal particles; sil.=silage; and conc.=concentrates.
[1]Behrend (1999); [2]Clauss and Lechner-Doll (2001); [3]this study; [4]Schwartz et al. (1988); [5]Hatt et al. (1998); [6]Clauss (1998); [7]Lindberg (1988); [8]Rutagwenda (1989); [9]Udén et al. (1982); [10]Quiroz et al. (1988); [11]Gross et al. (1996); [12]Udén and Van Soest (1982) [13]Cherney et al. (1991); [14]Ramanzini et al. (1991); [15]Bartocci et al. (1997); [16]Weyreter et al. (1986); and [17]Gasa et al. (1991). *Food intake and diet composition was quantified directly after the trial on retention times.

Differences in particle and fluid retention in the GIT are mainly due to differences in retention in the RR (Lechner-Doll et al., 1990). If MRTs for the RR are compared calculated by method A, moose (*Alces alces*) have comparable particle and fluid MRTs as the okapi of this study, albeit on higher food intakes (Renecker and Hudson, 1990, summer feeding). In spite of their lesser body weight, mouflons have $MRT_{particle}RR$ values similar to those of the okapi (Behrend et al., 2004). Even on distinctively higher dry matter intake levels, cattle have longer $MRT_{particle}RR$ than the okapi but shorter $MRT_{fluid}RR$. Therefore, as already noted by Clauss and Lechner-Doll (2001), cattle have particularly high selectivity factors ($MRT_{particle}RR/MRT_{fluid}RR$) of 1.7–4.6. In contrast, browsing ruminants

Table 6
Overview of rumen retention times of studies on different ruminant species

Species	BW [kg]	$MRT_{fl.}$ [h]	Marker fluid	$MRT_{part.}$ [h]	Marker particle	$MRT_{part.}/MRT_{fl.}$	DM intake [g/kg $BW^{0.75}$*d]	Roughage Proportion [% DM]	Food	
Roe deer	21	8	EDTA	14[b]	Cr-F. (< 2 mm)	1.8	–	100	Ad lib. natural forage	1
Okapi	225	17	EDTA	19[a]/27[b]	Cr-F. (1–2 mm)	1.6[c]	61	50	Zoo diet	2
Moose (wi)	265–271	19–24	EDTA	28–37[a]	Cr-F. (1–2 mm)	1.3–1.6	59–65	100	Lucerne hay/ grass hay/ browse	3
Moose (su)	294	10–17	EDTA	16–19[a]	Cr-F. (1–2 mm)	1.1–1.7	83–93	100	Lucerne hay/ grass hay/ browse	3
Moose	270	25	EDTA	–	–	–	42–71	100	Meadow hay	4
Moose	252	28	EDTA	–	–	–	46–58	100	Twigs	4
Giraffe	350	16	EDTA	–	–	–	–	–	Zoo diet	5
Giraffe	860	16	EDTA	23[b]	Cr-F. (< 2 mm)	1.4	66*	44*	Zoo diet	6
Elk (wi)	302–340	9–12	EDTA	18–26[a]	Cr-F. (1–2 mm)	1.6–2.4	48–61	100	Lucerne hay/ grass hay/ browse	3
Elk (su)	317–347	10–11	EDTA	20–27[a]	Cr-F. (1–2 mm)	1.9–2.6	79–92	100	Lucerne hay/ grass hay/ browse	3
Goat	23–47	14	EDTA	30[b]	Cr-F. (< 2 mm)	2.1	–	100	Ad lib. Natural forage	7
Ibex ♀	23	12–14	EDTA	21–22[b]	Cr-F (long)	1.7	50–59	100	Grass hay	9
Ibex ♂	60	19–21	EDTA	32–42[b]	Cr-F. (long)	1.7–2.0	67–71	100	Grass hay	9
Mouflon	32	12	EDTA	25[b]	Cr-F. (<2 mm)	2.1	–	100	Ad lib. natural forage	1
Sheep	19–55	19	EDTA	38[b]	Cr-F. (<2 mm)	1.9	–	100	Ad lib. natural forage	7
Sheep	45	–	–	23[a]	Cr-F. (1.2-2.4 mm)	–	ca. 40	59	Hay+molasses	8
Cattle (wi)	611–650	8–16	EDTA	24–36[a]	Cr-F. (1–2 mm)	2.3–3.3	46–112	100	Lucerne hay/ grass hay/ browse	3
Cattle (su)	686–738	10–13	EDTA	20–28[a]	Cr-F. (1–2 mm)	1.7–2.7	91–124	100	Lucerne hay/ grass hay/ browse	3
Cattle	702	12	EDTA	50[a]	Cr-F. (0.6–1.0 mm)	4.2	100	95	Grass silage+ concentrates	10
Cattle	606	12	EDTA	48[a]	Cr-F. (0.6–1.0 mm)	4.0	147	66	Grass silage+ concentrates	10
Cattle	550–650	7	PEG	32[a]	Cr-F. (< 5 mm)	4.6	75–146	30+70	Straw/concentrate mixture	11
Cattle	550–580	8	EDTA	32[a]	Cr-F. (2.9 mm)	3.9	153	80	Chopped hay (2.9 mm)	12
Cattle	185–375	13	EDTA	35[b]	Cr-F. (< 2 mm)	2.8	–	100	Ad lib. natural forage	7

wi=winter; su=summer; EDTA=Cr- or Co-ethylene diamine tetraacetate; PEG=polyethylene glycol; and Cr-F./Ce-F=chromium-/cerium-mordanted fibres.
[1]Behrend (1999); [2]this study; [3]Renecker and Hudson (1990); [4]Hjeljord et al. (1982); [5]Hatt et al. (1998); [6]Clauss (1998); [7]Lechner-Doll et al. (1990); [8]Udén and Van Soest (1982); [9]Gross et al. (1996); [10]Bruining and Bosch (1992); [11]Ørskov et al. (1988); and [12]Tafaj et al. (2001) *Food intake and diet composition was quantified directly after the trial on retention times.
[a]Estimated according to MA.
[b]estimated according to MB. and
[c]calculated according to $MRT_{Particle}RRMB/MRT_{Fluid}RR$.

(okapi, giraffe, roe deer, moose) have lower selectivity factors of 1.1–1.8. Wapiti (*Cervus elaphus*), goats, ibex, mouflon and sheep display values between 1.7–2.6 (Table 6). This comparison seems to indicate a trend of a more distinct dissociation of fluid and particle ingesta phase in the RR in mixed feeders and grazers as compared to browsing ruminants; however, due to unequal experimental conditions this conclusion needs to be regarded with caution.

Differences in the digestive physiology between ruminant feeding types have been postulated repeatedly (Hofmann, 1989, Clauss and Lechner-Doll, 2001, Peréz-Barbeira et al., 2004). According to Hofmann (1973, 1989), the digestive

anatomy of ruminants correlates with feeding habits. This interpretation has both been challenged (Peréz-Barbeira et al., 2001) or supported (Jiang and Takatshuki, 1999, Clauss et al., 2003) in recent publications. Investigations on the morphology of the digestive tract of okapi (Burne, 1917, Neuville and Derscheid, 1928, Burne, 1939, Scheidegger, 1950, Langer, 1988, Clauss et al., 2002a) indicate that the okapi forestomach has many features considered characteristic for browsing ruminants by Hofmann (1989), such as a comparatively low capacity, thin ruminal pillars, low reticular crests, a small omasum and a complete papillation including the dorsal rumen wall.

As conclusion of the comparison with literature data, the results of this study support the hypothesis that the okapi and other browsing ruminants are characterized by shorter $MRT_{particle}RR$, especially of lower selectivity factors. It has been suggested that browsing ruminants should benefit from shorter $MRT_{particle}RR$ due to the fermentation characteristics of their preferred forage, browse (Short et al., 1974), which generally reaches a maximum of energy release sooner than grass material. While data of this study point in the direction of a shorter $MRT_{particle}GIT$ in browsing ruminants, this question should ideally be tested in a large number of species, using markers from one batch, and under conditions of comparable food choices. Although a lesser degree of RR contents stratification has been suggested as the mechanism responsible for shorter $MRT_{particle}RR$ and a lesser dissociation of fluid and particles in browsing ruminants (Clauss et al., 2003), differences in RR contents stratification, and potentially influential factors, remain to be investigated.

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