Solute and particle retention in the digestive tract of the Phillip's dikdik (*Madoqua saltiana phillipsi)*, a very small browsing ruminant: Biological and methodological implications

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ABSTRACT

Morphological characteristics of the forestomach, as well as reports of a natural diet that mostly excludes monocots, suggest that dikdiks (*Madoqua* spp.), among smallest extant ruminants, should have a 'moose-type' forestomach physiology characterised by a low degree of selective particle retention. We tested this assumption in a series of feeding experiments with 12 adult Phillip's dikdiks (*Madoqua saltiana phillipsi)* on three different intake levels per animal, using cobalt-EDTA as a solute marker and a 'conventional' chromium-mordanted fibre (<2 mm; mean particle size 0.63 mm) marker for the particle phase. Body mass had no influence on retention measurements, whereas food intake level clearly had. Drinking water intake was not related to the retention of the solute marker. In contrast to our expectations, the particle marker was retained distinctively longer than the solute marker. Comparisons with results in larger ruminants and with faecal particle sizes measured in dikdiks suggested that in these small animals, the chosen particle marker was above the critical size threshold, above which particle delay in the forestomach is not only due to selective particle retention (as compared to fluids), but additionally due to the ruminal particle sorting mechanism that retains particles above this threshold longer than particles below this threshold. A second study with a similar marker of a lower mean particle size (0.17 mm, which is below the faecal particle size reported for dikdiks) resulted in particle and fluid retention patterns similar to those documented in other 'moose-type' ruminants. Nevertheless, even this smaller particle marker yielded retention times that were longer than those predicted by allometric equations based on quarter-power scaling, providing further support for observations that small ruminants generally achieve longer retention times and higher digestive efficiencies than expected based on their body size.

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1. Introduction

Ruminants can be classified according to their natural diet (Talbot and Talbot, 1962; Hofmann and Stewart, 1972; Gagnon and Chew, 2000), and show a variety of convergent morphological and physiological adaptations to their diet niches (Hofmann, 1988; Hofmann, 1989; Clauss et al., 2008). The extent to which such morphophysiological characteristics and reports of the natural diet actually match varies between characteristics and datasets (Hofmann et al., 2008; Clauss et al., 2009; Clauss et al., 2010a). Such variation may be caused by differences in the evolutionary history of ruminant

species (Codron et al., 2008) and, most importantly, because different adaptations might allow different magnitudes of diet variation (Clauss et al., 2010b). Codron and Clauss (2010) recently demonstrated that a major characteristic of ruminant forestomach physiology – the degree to which forestomach contents are stratified, and fluid is passed through the forestomach quicker than particles – can constrain the diet niche of ruminants. Those species that show little evidence for stratification and have a low fluid throughput (the 'moose-type' ruminants, Clauss et al., 2010b) are constrained to a browse-only diet, not because of physiological limitations but because they cannot compete with 'cattle-type' ruminants in other diet niches. The one ruminant in that dataset with unstratified rumen contents, but with a natural diet in which a considerable proportion consisted of non-browse material, is the reindeer (*Rangifer tarandus*), which notably is not exposed to grazer competition in its natural habitat. On the other

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hand, the authors suggested that 'cattle-type' ruminants are constrained in that they cannot exist on browse-only diets, because their higher-fluid throughput strategy is incompatible with a high degree of salivary defences against secondary plant compounds in browse (such as tannins). However, in theory a 'cattle-type' ruminant could increase the proportion of browse in its diet if it could forage with a very high selectivity that ensures high levels of secondary plant compounds in its diet are avoided. Because feeding selectivity is size-dependent (Owen-Smith 1988; Codron et al. 2007), such an alternative strategy might be particularly found in small ruminants. Duikers, the smallest ruminants in which retention patterns of fluid and particles have been documented so far with markers that allow a comparison with other species, nevertheless showed a rather simultaneous excretion of the two digesta phases from their forestomach, in accord with reports on their rather homogenous intraruminal papillation pattern (Clauss et al., 2011a).

When performing passage measurements, the size of the particle marker is a crucial characteristic that will impact the results. The ruminant forestomach operates a density-dependent sorting mechanism in which large particles are retained selectively for rumination, whereas smaller ones can escape at a higher rate without being submitted to rumination (Lechner-Doll et al., 1991). In passage experiments, this is reflected in a delayed excretion of large particle markers as compared to small particle markers (Lechner-Doll et al., 1990; Schwarm et al., 2008; Lechner et al., 2010; Clauss et al., 2011b). In terms of particle size, this sorting mechanism appears to discriminate particles above and below a threshold (rather than being a continuous function of particle size), because different-sized large particles do not differ in their retention time (Schwarm et al., 2009a; Lechner et al., 2010). This threshold or 'critical' particle size is estimated to be about 1 mm in domestic sheep (Ulyatt et al., 1976; Sutherland, 1988). It has been suggested that the same critical particle size threshold can be applied when modelling the digesta kinetics of domestic sheep and cattle (Poppi et al., 1985), although empirical evidence suggests that this critical size threshold increases with increasing body mass (Udén and Van Soest, 1982; Poppi et al., 1985; Lechner-Doll and von Engelhardt, 1989; Clauss et al., 2002). When it is the aim to investigate the difference in the retention of fluid vs. particles in the forestomach (as a physiological measure that indicates fundamental differences between ruminants), without the confounding effect of a critical size threshold, i.e. without the influence of particle size discrimination and rumination, then the particle marker must be of a particle size that is *below the critical size*. So far, experiments using mordanted fibres ground to a size <2 mm yielded results that allowed differentiation of a large variety of ruminant species (reviewed in Clauss et al., 2006; Clauss et al., 2010b). A marker above the critical size threshold would lead to a distinct separation of fluid and particle passage pattern, because the particles would not only be retained by a general selective particle retention (as compared to fluids) – which represents the difference between 'moose-type' and 'cattle-type' ruminants – but also additionally because of the particle sorting mechanism. So far, markers ground simply to <2 mm did not produce this effect in ruminants as small as duikers (Clauss et al., 2011a).

Dikdiks are ideal test animals to challenge both concepts — those on rumen physiology, and those on methodological aspects of particle passage markers. They are among the smallest of extant ruminants and are strict browsers (Gagnon and Chew, 2000), but the papillation pattern in their rumen indicates a certain degree of content stratification. Actually, in the dataset presented by Clauss et al. (2009), dikdiks have a quite heterogeneous ruminal papillation pattern for their feeding behaviour (i.e., for a browse diet). Based on that papillation pattern and the relationship between this pattern and passage characteristics as demonstrated by Clauss et al. (2011a), we would expect particles below the critical size to be retained about 1.8 times longer than fluids in the dikdiks' forestomachs. This would be

within the range reported for other browsing ruminants (Hummel et al., 2005; Clauss et al., 2006). The digestive physiology of dikdiks is characterised by high fermentation rates, high amylolytic activity in the reticulorumen, and a high frequency of feeding and rumination bouts (Hoppe et al., 1983; Maloiy and Clemens, 1999). The digesta kinetics of dikdiks have been investigated previously, but the data are not readily available (Fig. 2 in Hoppe, 1977; Baer, 1987). The graphic representation of Hoppe (1977) suggests that small particles (dyed lucerne leaves) move more or less simultaneously with fluids (labelled by ^{14}C-PEG) through the dikdik's digestive tract, whereas larger particles (dyed lucerne stems) are retained for a longer time. Similarly, the data from Baer (1987) indicate that chromium-mordanted particles from pelleted feed move faster through the digestive tract than chromium-mordanted particles from alfalfa leaves. However, the results of these studies cannot be linked to food intake, and quantitative comparisons of solute and particle marker retention cannot be made.

Here, we report results of passage measurements in dikdiks for particle and solute markers. The size of the particle marker used was the same as in previous studies with various ruminants, including duikers, but turned out to be problematic with respect to the critical size threshold in this very small ruminant species, which made a second study necessary to determine the influence of marker particle size. Additionally, we recorded food and water intake to test for an effect of both on passage measurements.

2. Materials and methods

2.1. First study

The trials described in this study were carried out at the Al Wabra Wildlife Preservation (AWWP), Doha, Qatar. The general husbandry of the animals prior to the study is described by Hammer (2009). Twelve Phillip's dikdiks (*Madoqua saltiana phillipsi*; aged between 6 months and 5 years, 2.42 ± 0.25 kg), ten males and two females, were kept separately in individual pens (240 cm × 150 cm) on epoxide floor without litter and without visual contact to their neighbour animals. Each pen was furnished with a transport box for cats and 1 or 2 plywood plates as hiding area. A rubber mat with small holes with newspaper underneath was placed at the place of defecation to separate faeces from urine. Unrestricted access to drinking water was provided at all times. The animals were weighed on a daily basis.

The animals were divided into two groups, which received different pelleted feeds (for another study); Browser Maintenance (Mazuri Zoo Azuri Zoo Foods, Alwecka, Altrip, Germany) in group A and Altromin 0133 Breeding Maintenance Diet Small Ruminants (Altromin, Lage, Germany) in group B. In both groups the dikdiks received daily 45–60 g of fresh alfalfa (*Medicago sativa*) leaves, which were removed from their stalks by hand, and 14 g grated mix of carrots and apple mixed with 1 g wheat bran, and the respective pellets. The pelleted food was first provided ad libitum. The amount of food offered as well as left overs and the amount of water drunk were recorded each day (adjusting for evaporative water losses as determined by a separate bowl positioned next to the enclosures). Alfalfa and the vegetable mix were always consumed completely. There was a two-week adaptation period to this diet prior to the first trial. In a second and third trial, each animal received the same diet, but the pelleted food was offered as 85% and 70% of the ad libitum intake as determined in the first trial, respectively. For each of these trial periods, a nine-day adaptation period passed prior to the trials. Three animals per group received the 85% treatment prior to the 70% treatment; the other three animals first had the 70% treatment and then the 85% treatment.

Cobalt ethylene diaminetetracetic acid (Co-EDTA) was used as a solute marker and chromium (Cr)-mordanted fibre of <2 mm, prepared from grass hay, as the particle marker. Both markers were

prepared according to Udén et al. (1980). On the three days before the marker was fed, faeces of each animal were collected for a baseline measurement of Co- and Cr concentration. On the first day of each trial period, the animals were fed 0.5 g Cr-mordanted fibre and 0.05 g dissolved Co-EDTA at 10 am mixed into the carrots/apple/wheat bran mix to assure complete intake. The animals were given the alfalfa and pellets only after they had finished the vegetable mix with the marker. Animals that had not eaten the vegetable mix with the marker within the first 90 min were restrained manually, and the marker was applied by tube into the buccal cavity. The animals were observed to first chew on the material before swallowing it. As results between animals that ingested the marker voluntarily and by force-feeding did not differ, results are presented for all animals. Faeces were collected at 0, 4, 8, 12, 16, 20, 24, 28, 32, 36, 40, 46, 52, 58, 64, 72, 80, 88, 96, 104, 112, 120, 136, 148 and 160 h after marker feeding and were frozen immediately after sampling.

Samples of all feeds and faeces were dried at 103 °C to constant weight and dry matter content was recorded. 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 atomic absorption spectroscopy. Mean retention time (MRT) in the total gastrointestinal tract (GIT) was calculated according to Thiele-manns 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:

$$MRT = \sum (t_i * dt * c_i) / \sum (dt * c_i)$$

with t_i = time after marker application (h), dt = time interval represented by marker concentration (calculated as $((t_{i+1} - t_i) + (t_i - t_{i-1}))/2$), 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): $MRT_{solute}RR$ is determined by estimating the rate constant of the descending part of the marker excretion curve via an exponential equation:

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

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 characterised 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):

$$MRT_{particle}RR = MRT_{particle}GIT - (MRT_{solute}GIT - MRT_{solute}RR).$$

The "selectivity factor" – defined as the quotient of particle over solute MRT – was calculated for both the total GIT and the RR.

MRTs of solute and particle markers were compared by paired t-test. For one animal in one trial period, MRTs were not used because the marker excretion curves indicated that the animal had re-ingested a relevant amount of marker-containing faeces within the first days of the experiment. Body mass was determined as the mean body mass of an experimental period. Dry matter and drinking water intake were calculated as relative dry matter (rDMI) or drinking water (rDWI) intake using metabolic body weight as the basis. Relationships between various measurements were investigated by correlation analysis and linear regression. All statistical evaluations were performed in PASW 18.0 (SPSS Inc., Chicago, IL) with the significance level set at 0.05.

2.2. Second study

After analysing the results of the first study (see Results), we concluded that the particle marker had exceeded the critical size threshold of the species. The mean particle size of the marker was analysed by wet sieving, using the sieve set and calculations as described by Hummel et al. (2008a). For the second study, the particle marker was modified by grinding through a 0.5 mm sieve. A year after the first study, three additional animals were used, under identical conditions (using the Browser Maintenance diet), and the finer-ground version of the marker was applied together with the solute marker by tube into the buccal cavity. Sampling regimes and analytical procedures were identical to the ones used the year before. Two of these animals had already been used in the first study.

3. Results and discussion

In the first study, food intake was reduced as planned with the restriction of the pelleted diet (Table 1). There were generally no differences between the two pelleted diets. Animals drank more water as dry matter intake was restricted, with a significant negative correlation (rDMI vs. rDWI, r = −0.360, p = 0.031, n = 36), indicating that animals tried to compensate for a reduced gut fill; a similar behaviour has been reported in several domestic and pet animal species (Kamphues and Schulz, 2002). $MRT_{particle}GIT$ was, at 34–43 h, similar to the 41 h measured by Baer (1987) with mordanted lucerne fibre on a similar diet at 90% ad libitum intake in Kirk's dikdiks (*Madoqua kirki*). Marker excretion curves indicated a relevant difference between the solute and the particle marker (Fig. 1). The difference between MRT_{solute} and $MRT_{particle}$ was highly significant for both the GIT (MRT_{solute} 22.1 ± 5.6 h; $MRT_{particle}$ 43.2 ± h; paired t-test, t = −28.024, p < 0.001, n = 35) and the RR (MRT_{solute} 13.5 ± 4.0 h; $MRT_{particle}$ 34.8 ± 6.9 h; paired t-test, t = −27.202, p < 0.001, n = 35); this difference was expected based on results in other ruminants (Lechner et al., 2010; Clauss et al., 2011a). There was no correlation between body mass (BM) and solute or particle MRT (Fig. 2); however, rDMI was negatively correlated to both solute and particle MRT (Fig. 3). In a General Linear Model with $MRT_{particle}GIT$ as the dependent variable and both BM and rDMI as covariates, only rDMI

Table 1
Body mass, dry matter and drinking water intake, and retention parameters of 12 Philipp's dikdiks in the first study divided into two feeding groups with three intake levels per group.

Feeding group	Intake level	BM	DMI	DWI	$MRT_{sol}GIT$	$MRT_{part}GIT$	SF GIT	$MRT_{sol}RR$	$MRT_{part}RR$	SF RR
		g	g d^{-1}	g d^{-1}	h			h		
A	ad lib	2326 ± 198	83 ± 18	116 ± 105	16 ± 4	34 ± 8	2.16 ± 0.45	10 ± 2	28 ± 7	2.80 ± 0.68
	85%	2272 ± 221	67 ± 9	151 ± 140	21 ± 6	43 ± 8	2.16 ± 0.27	14 ± 5	36 ± 7	2.62 ± 0.66
	70%	2288 ± 213	58 ± 8	118 ± 50	22 ± 3	45 ± 6	2.06 ± 0.15	13 ± 3	36 ± 7	2.82 ± 0.25
B	ad lib	2422 ± 260	70 ± 17	57 ± 19	23 ± 5	43 ± 4	1.89 ± 0.25	14 ± 3	33 ± 5	2.50 ± 0.42
	85%	2345 ± 184	58 ± 6	239 ± 101	25 ± 4	49 ± 5	1.96 ± 0.20	16 ± 3	39 ± 5	2.56 ± 0.35
	70%	2345 ± 275	49 ± 5	254 ± 77	27 ± 5	48 ± 4	1.83 ± 0.29	16 ± 5	38 ± 5	2.40 ± 0.52

BM body mass, DMI dry matter intake, DWI drinking water intake, MRT mean retention time, GIT gastrointestinal tract, RR reticulorumen, sol solute marker, part particle marker (mean particle size 0.63 mm), SF selectivity factor (MRT_{part}/MRT_{sol}).
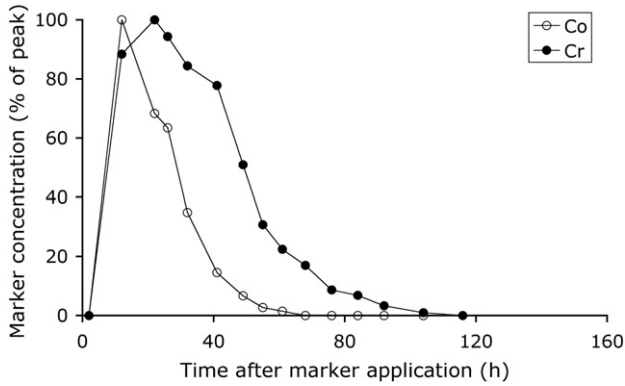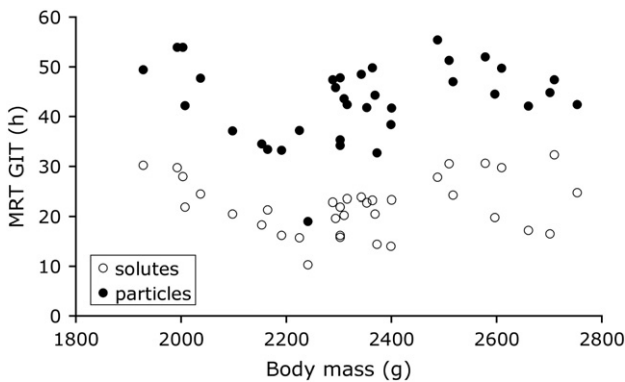
Fig. 1. Example for marker excretion curves of a solute marker (Co-EDTA) and a particle marker (Cr-mordanted fibre, <2 mm) in a Philipp's dikdik.
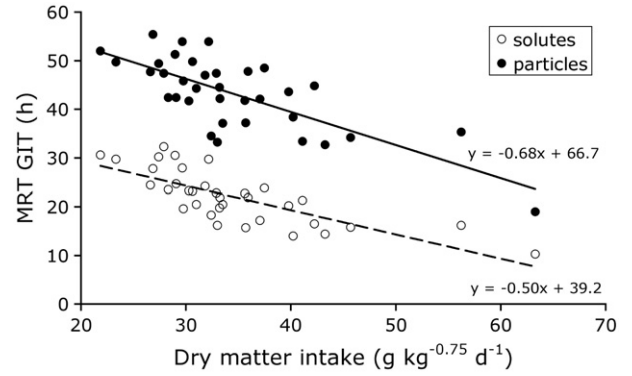

Fig. 3. Significant negative correlation between dry matter intake and mean retention time (MRT) in the gastrointestinal tract (GIT) for the particle and solute markers of the first study ($rDMI-MRT_{sol}GIT$: $r = -0.769$, $p<0.001$, $n = 35$; $rDMI-MRT_{part}GIT$: $r = -0.746$, $p<0.001$, $n = 35$).

($F = 39.601$, $p<0.001$) was significant but not BM ($F = 0.282$, $p = 0.599$). These results confirm the relevance of the food intake level on MRT measurements (Clauss et al., 2007). Neither the drinking water nor the total water intake was significantly correlated to solute MRT (Fig. 4), which underlines that the MRT of the solute marker does not reflect the passing of ingested fluid/water through the gastrointestinal tract but the combined mechanisms of fluid intake and secretion into, and absorption and re-absorption from, the gastrointestinal tract (Franz et al., 2011).

Although the relative dry matter intake was significantly positively correlated with the selectivity factor (SF, ratio between particle and solute MRT) in the GIT, it appeared to remain rather constant across the whole intake range; the correlation was not significant with the SF in the RR (Fig. 5). This finding is in accord with the hypothesis that the selective particle retention in the ruminant forestomach is maintained stable across a large range of food intake levels, and in particular does not decrease with increasing food intake as shown in some nonruminant foregut fermenters (Schwarm et al., 2009b; Lechner et al., 2010).

In contrast to these results, which basically confirmed existing concepts in a new species, the magnitude of the SF was surprising. At an average of 2.01 ± 0.30 for the GIT and 2.62 ± 0.49 for the RR across all treatments, the SF of the dikdiks in the original study was within the range found in grazing domestic ruminants (Hummel et al., 2005; Clauss et al., 2006) and was also much higher than expected from their intraruminal papillation pattern (see Introduction). Rather than suspecting that dikdiks might be extreme outliers in terms of their rumen physiology, with a much more distinct difference between fluid and particle passage than expected, we suspected that the particle marker used in the first study had exceeded the critical
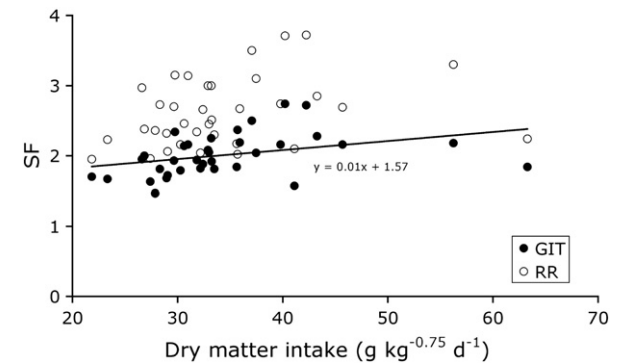
particle size threshold of the dikdik, due to its small body size. The SF would then not be representative of the selective retention of particles vs. fluids alone, but also include the additional delay caused by the rumen sorting mechanism. Actually, when plotting the MRTs in the RR for the solute and the particle marker of the first study with results for solute and particle markers from other studies in which particle markers exceeded the critical size threshold of the respective species (Fig. 6), it appeared that the dikdik results were in line with those of moose (*Alces alces*) and reindeer (*Rangifer tarandus*), two 'moose-type' ruminant species. The mean particle size of the marker in the
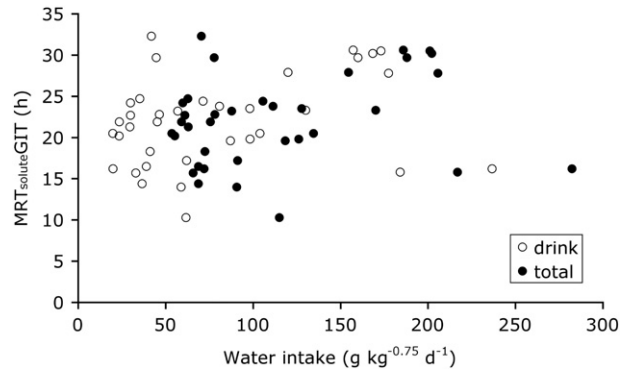
Fig. 4. Relationship between drinking and total water intake and mean retention time (MRT) in the gastrointestinal tract (GIT) for the solute marker of the first study. There was no significant correlation (drinking water-$MRT_{sol}GIT$: $r = 0.288$, $p = 0.094$, $n = 35$; total water-$MRT_{part}GIT$: $r = 0.235$, $p = 0.174$, $n = 35$).

Fig. 2. Relationship between body mass and mean retention time (MRT) in the gastrointestinal tract (GIT) for the particle and solute markers of the first study. There was no significant correlation ($BM-MRT_{sol}GIT$: $r = 0.077$, $p = 0.661$, $n = 35$; $BM-MRT_{part}GIT$: $r = 0.133$, $p = 0.448$, $n = 35$).

Fig. 5. Relationship between dry matter intake and the selectivity factor (SF, the ratio of particle vs. fluid retention) in the gastrointestinal tract (GIT; regression line) and the reticulorumen (RR) in the first study ($rDMI-SF_{GIT}$: $r = 0.358$, $p = 0.035$, $n = 35$; $rDMI-SF_{RR}$: $r = 0.305$, $p = 0.075$, $n = 35$).
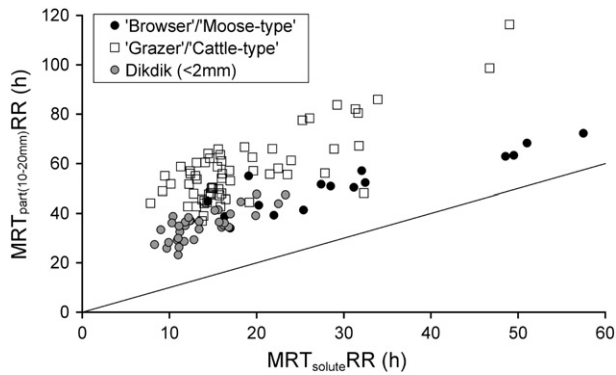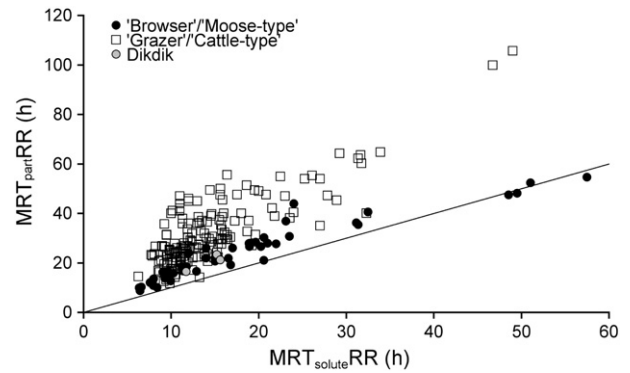
Fig. 6. Relationship between the mean retention time (MRT) of a solute and a particle marker in the reticulorumen (RR) of various ruminant species of two contrasting forestomach physiology types. Data on moose (*Alces alces*), reindeer (*Rangifer tarandus*) ('moose-type'), domestic cattle, sheep, goats, banteng (*Bos javanicus*) and muskoxen (*Ovibos moschatus*) ('cattle-type') from Lechner-Doll et al. (1990, pers. comm.), Schwarm et al. (2008) and Lechner et al. (2010) for 'large' particle markers (10–20 mm in length); data for dikdik from the first study for the original 'small' particle markers (<2 mm) which are usually below the critical size threshold for immediate RR escape in ruminants, but behave in the dikdik as particles above that threshold in other species. The line denotes y = x.

first study, as determined by wet sieving, was 0.63 mm and thus about 2.2 times higher than the mean particle size in dikdik faeces reported by Fritz et al. (2009) as 0.28 mm. Again, this supported the conclusion that the particle marker had exceeded the critical size threshold in this species. Because ingestive chewing usually does not obliterate the signal of a particle marker that exceeds the critical size threshold (Schwarm et al., 2008; Schwarm et al., 2009a), those dikdik that had ingested the marker voluntarily did not differ from those that had received the marker via buccal application.

The finer-ground marker had a mean particle size of 0.17 mm and was therefore below the faecal particle size of 0.28 mm. When this marker was applied to the three dikdiks in the second study, the resulting SF RR was 1.44 ± 0.09 (Table 2), and thus within the range reported for browsing ruminants (Hummel et al., 2005; Clauss et al., 2006), similar to the findings in 'moose-type' ruminant species (Fig. 7), and closer to the expectation based on intraruminal papillation (Fig. 8). The low degree of selective retention of particles below the critical threshold size in the dikdiks of the second study matches other characteristics of 'moose-type' ruminants, usually associated with a browsing feeding type, that have also been documented in dikdiks (Hofmann, 1973), such as comparatively large salivary glands (Hofmann et al. 2008) or comparatively shallow reticular crests (Clauss et al. 2010a). When plotting the marker excretion curves of the additional experiment for two of these three dikdiks together with the marker excretion curves of the same animals on a similar food intake level from the original study, the resulting patterns resemble those for other ruminants with particle markers above and below the critical size threshold (Fig. 9). When comparing the same results to the graph given by Hoppe (1977), the same pattern is evident (Fig. 10).

These findings demonstrate that choosing an appropriate particle size is important when assessing ruminant digesta passage charac-

Fig. 7. Relationship between the mean retention time (MRT) of solute and particle markers (the latter below the critical size threshold) in ruminants of contrasting forestomach physiology (from Clauss et al., 2011b with additional data from the three dikdiks from the second study). The line denotes y = x.
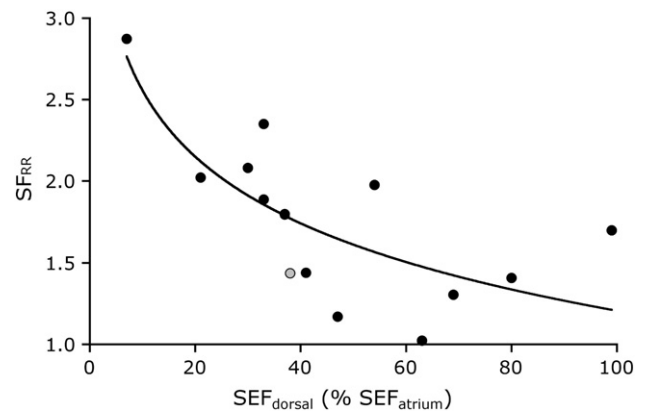
Fig. 8. Relationship between the dorsal surface enlargement factor (SEF, in % of the SEF of the Atrium ruminis; a measure of homogeneity of intraruminal papillation) and the selectivity factor (SF, the ratio of particle vs. fluid retention) in the reticulorumen (RR) of wild ruminant species (from Clauss et al., 2011b with the mean of the three dikdiks from the second study marked by the grey circle).

teristics; in terms of identifying patterns of selective particle retention related to the two major ruminant digestion types, findings of a distinct difference between the particle and solute marker excretion should be interpreted with the critical particle size threshold in mind. Rather than producing one marker with a consistent particle size (such as used by Behrend et al., 2004; Flores-Miyamoto et al., 2005; Hummel et al., 2005; Clauss et al., 2006; Hummel et al., 2008b; Schwarm et al., 2008; Lechner et al., 2010; Clauss et al., 2011a), it would be ideal to use fibres extracted from faecal material of the species under investigation as originally described by Udén et al. (1980). Using such species-specific particulate material as the basis for particle passage markers in ruminants would consistently guarantee that the marker is below the critical size threshold. Such markers could then additionally be combined with other, larger particle markers. Recently published results in duikers (Clauss et al.,

Table 2
Body mass, dry matter and drinking water intake, and retention parameters of three Philipp's dikdiks given the finer-ground particle marker in the second study.

Animal	BM	DMI	DWI	MRT$_{sol}$GIT	MRT$_{part}$GIT	SF GIT	MRT$_{sol}$RR	MRT$_{part}$RR	SF RR
	g	g d^{-1}	g d^{-1}	h			h		
I	2330	73	118	21	26	1.23	12	17	1.41
II	2356	49	92	21	29	1.39	15	23	1.54
III	2117	41	92	26	31	1.22	16	21	1.36

BM body mass, DMI dry matter intake, DWI drinking water intake, MRT mean retention time, GIT gastrointestinal tract, RR reticulorumen, sol solute marker, part particle marker (mean particle size 0.17 mm), SF selectivity factor (MRT$_{part}$/MRT$_{sol}$).
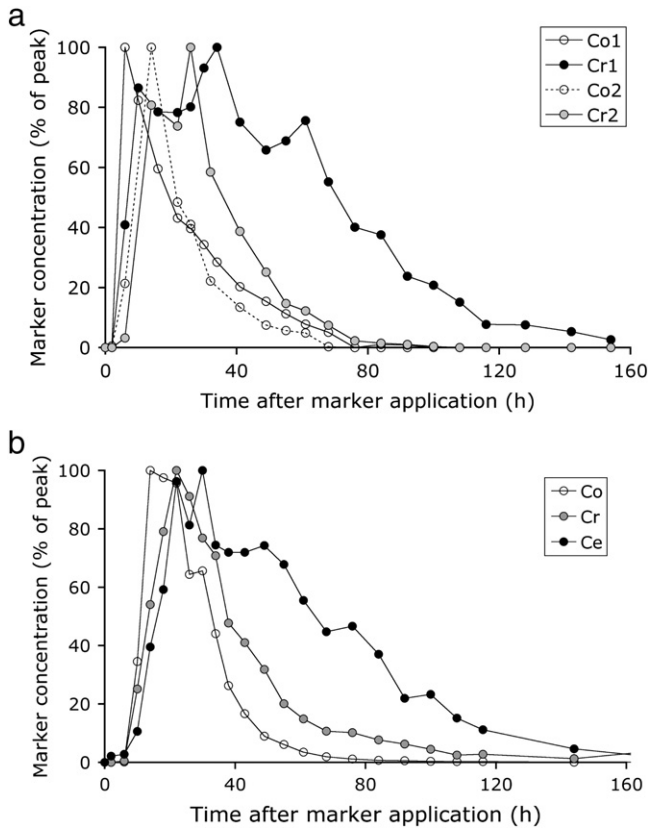
Fig. 9. Comparison of marker excretion patterns in a) a dikdik (data from the first (1) and the second (2) study combined in one graph (Co = solute marker cobalt EDTA; Cr = particle marker chromium-mordanted fibre, which was below the critical size threshold in study 1 and above that threshold in study 2) and b) a reindeer from Lechner et al. (2010); Co = solute marker cobalt EDTA; Cr = particle marker chromium-mordanted fibre below the critical size threshold; Ce = particle marker cerium-mordanted fibre above the critical size threshold.

2011a), however, do suggest that in ruminants from as little as 4 kg onwards, this precaution may not be necessary — at least if the animals ingest the markers by themselves.
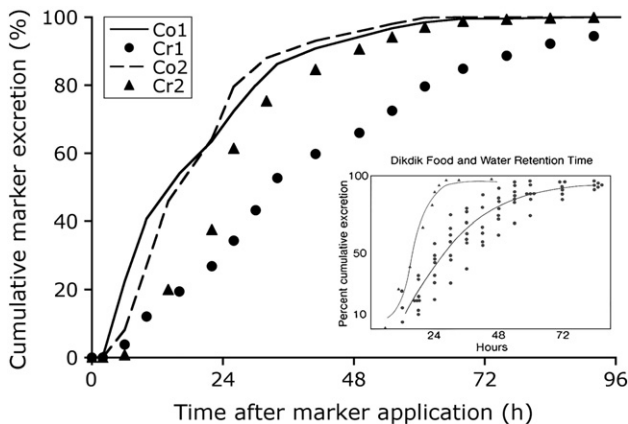
Fig. 10. Cumulative marker excretion in a dikdik (same data as Fig. 9) compared to a similar graph from Hoppe (1977)(inset). Note the similarity in the patterns with respect to the difference between large particle excretion (black circles; lucerne stems in Hoppe, 1977 and the marker in the first study) and small particle excretion (black triangles; lucerne leaves in Hoppe, 1977 and the marker in the second study). Full and hatched lines denote the solute markers in the first and second study; in the insert, the left line represents the solute marker. The general difference in the excretion time is most likely due to differences in food intake levels (which are not available from Hoppe, 1977).

The results of the second study support previous interpretations of ruminant digestive physiology. At an average of 2.27 kg body mass, a $MRT_{particle}GIT$ of 19 h would be expected in dikdiks based on the general allometric regression from Illius and Gordon (1992) of $MRT_{particle}GIT = 15.3 BM^{0.25}$. However, the average of the measured values (29 h) exceeded this prediction by 50%. This discrepancy suggests that the comparatively steep allometric scaling of the Illius-and-Gordon-equation does not adequately reflect empirical data on MRT measurements in ruminants across a wide body size range (Clauss et al. 2007). Actually, small ruminants generally appear to have comparatively long retention times (Wenninger and Shipley, 2000; Clauss et al., 2011a) and also to achieve unexpectedly high digestive efficiencies (Pérez-Barberìa et al. 2004), potentially due to these long retention times.

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