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Increasing feed intake in domestic goats (*Capra hircus*): Measured effects on chewing intensity are probably driven by escape of few, large particles from the forestomach

Eva Findeisen^{a,1}, Karl-Heinz Südekum^a, Jürgen Hummel^b, Marcus Clauss^{c,*}

^a Institute of Animal Science, University of Bonn, Endenicher Allee 15, 53115 Bonn, Germany

^b Ruminant Nutrition, Department of Animal Sciences, University of Goettingen, Kellnerweg 6, 37077 Goettingen, Germany

^c Clinic für Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland

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ABSTRACT

On the one hand, oral processing – mastication – is considered a relatively inflexible component of mammalian feed acquisition that constrains instantaneous intake rates. On the other hand, experimental data shows that the level of feed intake affects faecal particle size and hence net chewing efficiency in ruminants, with larger particles occurring in the faeces at higher intakes. Here, we report the effect of an increased feed intake during maintenance (L1), late (200% of L1) and peak lactation (300% of L1) of a consistent diet (hay:concentrates 50:50) in eight domestic goats on various measures of digestive physiology including faecal mean particle size (MPS). Increasing intake led to an increased gut fill, a reduction in digesta retention times, and an increase in faecal MPS (from 0.57 to 0.72 mm). However, this was an effect of the large particle fraction (>2 mm) being disproportionately excreted at higher intakes; if MPS was assessed on the basis of particles below the typical escape threshold (≤ 1 mm), there was no difference between intake levels. These findings suggest that the effect of intake on the calculated net chewing efficiency in ruminants may rather be an effect of increased large particle escape from the forestomach than a reduced chewing intensity per bolus during ingestion or rumination.

1. Introduction

Chewing efficiency is an important characteristic of mammals, due to the effect of particle size on microbial digestion and fermentation (Bjorndal et al., 1990; Hummel et al., 2020). Animals adjust their chewing intensity to the feed they ingest (Janis et al., 2010; Jalali et al., 2012a; Jalali et al., 2012b) and to the chewing surface available to them in the course of dental eruption during ontogeny (Grandl et al., 2018). Nevertheless, different feeds are ultimately comminuted to different particle sizes (Renecker and Hudson, 1990; Hummel et al., 2008; Clauss et al., 2014; Jalali et al., 2015; Kljak et al., 2019), indicating an influence of feed characteristics on chewing efficiency.

Whether time constraints on mastication can have an effect on chewing efficiency remains an open question, and literature evidence is equivocal. Note that in terrestrial mammals, faecal particle size is considered a useful proxy for chewing efficiency (Hummel et al., 2020). On the one hand, there are reports that higher intake levels lead to

higher mean particle size in the faeces of domestic ruminants (*Bos primigenius taurus*, *Ovis aries*) (Shaver et al., 1986; Luginbuhl et al., 1990; Okine and Mathison, 1991; Kaske and Groth, 1997; Kovács et al., 1997a). But on the other hand, this was not detected in experiments with domestic horses (*Equus caballus*) or rabbits (*Oryctolagus cuniculus*) (Clauss et al., 2014; Findeisen et al., 2021). Maybe even more important, experiments testing the ‘functional response’, i.e. how increased feed density (or increased bite size volumes) influences instantaneous intake rates, show that intake rate does not increase continuously but reaches a plateau at a certain feed density (Spalinger et al., 1988; Shipley and Spalinger, 1992; Gross et al., 1993; Laca et al., 1994; Ginnett and Demment, 1995; Bergman et al., 2000; Illius et al., 2002; Searle et al., 2005; Fleurance et al., 2009). In these studies, this is generally interpreted as the constraining effect of mastication, which cannot be sped up. This interpretation speaks against the assumption that animals might sacrifice chewing efficiency for increased intake. However, these experiments measure instantaneous intake, and typically with animals at

* Corresponding author.

E-mail addresses: ksue@itw.uni-bonn.de (K.-H. Südekum), jhummel@gwdg.de (J. Hummel), mclauss@vetclinics.uzh.ch (M. Clauss).

¹ Current address: Hostertsweg 18, 53501 Grafshaft, Germany

maintenance, and the hypothetical scenario that particularly hungry or time-limited animals might reduce their chewing efficiency in order to achieve a higher feed, and thus energy and nutrient intake, cannot be excluded. Additionally, detailed observations indicated that animals may change their chewing intensity over the course of a feeding event (Searle et al., 2005). Together with the mentioned report of increasing faecal particle size in domestic ruminants at higher intakes, these observations justify further investigations into ruminant chewing efficiency.

When challenging animals in terms of their feed intake, two different options are available. Feed intake can be reduced below the maintenance level to achieve variation in intake (Bae et al., 1981). With respect to intake behaviour, this method bears the risk of deprived animals feeding in a particularly greedy manner, which could lead to the result that at very low intake, chewing efficiency is not increased but actually reduced. When intake variation was achieved in this manner in horses, this effect appeared numerically but was not significant (Clauss et al., 2014). In cattle, animals maintained on very restricted intake had faster eating rates (Santana et al., 2020) and a higher proportion of very large particles in swallowed feed boli (Luginbuhl et al., 1989), corroborating this methodological constraint. Possibly, achieving intake variation by investigating animals in different metabolic states, such as females during maintenance and during lactation, is the biologically more meaningful approach.

Thus, the aim of the present study was to test whether different levels of intake of a consistent diet in a domestic ruminant, the goat (*Capra hircus*), at maintenance as well as during peak and moderate milk production, lead not only to marked variation in digesta retention, gut fill and digestibility, but also in chewing efficiency measured as faecal particle size.

2. Methods

Experiments were performed under Animal Experiment Licence 56–2 of the Official Veterinary Office, Bonn, Germany. Eight adult female Saanen-type goats (German Improved White Goat breed; initial live weight 60 kg) were used at three different time points – at peak lactation, in late lactation, and at maintenance (dry) – for the assessment of the effect of intake on digesta retention, digestibility, gut fill and faecal particle size. All animals were without obvious dental problems. They were fed a diet with a constant proportion of 50% chopped grass hay and 50% concentrate (Table 1) at three feed intake levels representative for maintenance (DMI L1), late lactation (DMI L2) and peak lactation (DMI L3). Measurements were performed at day 42–50 (peak

Table 1
Feeds used in the present study (means \pm standard deviation; $n = 3$).

		Grass hay	Pelleted concentrate*	Total diet
Total ash	g kg ⁻¹ DM	98 \pm 27	90 \pm 1	94 \pm 13
Crude protein	g kg ⁻¹ DM	112 \pm 27	170 \pm 5	141 \pm 16
Ether extracts	g kg ⁻¹ DM	26 \pm 5	44 \pm 1	35 \pm 2
Neutral detergent fibre	g kg ⁻¹ DM	479 \pm 49	315 \pm 6	397 \pm 27
Acid detergent fibre	g kg ⁻¹ DM	305 \pm 30	188 \pm 3	247 \pm 16
Acid detergent lignin	g kg ⁻¹ DM	52 \pm 4	47 \pm 4	50 \pm 3
24 h gas production	ml 200 mg ⁻¹ DM	45.1 \pm 1.7	49.0 \pm 1.4	47.1 \pm 0.9
Metabolizable energy	MJ kg ⁻¹ DM	9.4 \pm 0.4	11.2 \pm 0.0	10.3 \pm 0.2
Mean particle size	mm	21.13	0.96	11.04

* Ingredients in % as fed: lucerne meal (32.9), wheat middlings (13.9), oat grain (10.7), wheat grain (9.3), soybeans (8.7), barley grain (5.9), sunflower expeller (5.9), beet pulp (5.2), oats huskmeal (3.0), molasses (0.9), mineral-vitamin-premix (3.6).

lactation), day 159–167 (late lactation), and after lactation (before a new pregnancy). Animals were fed twice daily at 07:30 and 14:30 and had *ad libitum* access to water. During the collection periods, they were kept in metabolism crates allowing total collection of faeces. Milking occurred twice daily.

The length of the experimental period at maintenance requirements was 22 days, consisting of a 14-day period for adaptation and an 8-day period for collecting samples. Samples of feedstuffs were taken regularly during the trial and were pooled. Faeces were collected quantitatively at intervals necessary for determination of digesta mean retention time (MRT). Two different markers were ingested by the animals on day 15 with a small proportion of morning concentrate. The animals were dosed with 15 g chromium(Cr)-mordanted fibre (1–2 mm particles) and 1.1 g cobalt(III)ethylene diamine tetraacetate (Co-EDTA; solutes) (Udén et al., 1980). To ensure total consumption, Co-EDTA was dissolved in water, mixed with the concentrate and the Cr-mordanted fibre, and dried again before feeding (60 °C, 6 h). The faecal samples were collected at time intervals of increasing length (day 1–2: 4 h; day 3–5: 6 h; day 6–7: 8 h; day 8: 12 h). One part was dried at 60 °C for 24 h and after that at 100 °C for another 24 h, and then milled and stored for marker analysis; another part was pooled over the sampling period and stored frozen for wet-sieving and chemical analysis.

Chemical analysis was done according to VDLUFA (2012) for dry matter (DM) (method 3.1), ash (method 8.1), crude protein (CP) (method 4.1.2; Dumas method; instrument FP-328, LecoEnterprise, St. Joseph, MI, USA) and starch (enzymatically; method 7.2.3). Ether extract (EE) was analyzed after acid hydrolysis using an ANKOM Extractor (Ankom Technology, Macedon, NY, USA) according to AOCS (2009) (Am 5–04 official method). Neutral detergent fibre (NDFom; not assayed with a heat stable amylase), and, in feeds, acid detergent fibre (ADFom) and acid detergent lignin (ADL) were analyzed following Van Soest and Robertson (1985); all values are given without residual ash.

Analysis of faecal samples for retention markers followed the procedure of Behrend et al. (2004) and Hummel et al. (2005). The calculation of mean retention times (MRT) from faecal marker concentrations was done according to Thielemans et al. (1978). Mean retention time of reticulorumen (MRT_{RR}) was quantified by first estimating solute passage rate from the rumen from the exponential decay of the decreasing part of the marker excretion curve, then subtracting the calculated MRT_{soluteRR} from total MRT_{solute} and then finally subtracting the resulting residual MRT from MRT_{particle} to arrive at MRT_{particleRR} (Lechner-Doll et al., 1990).

The faeces and feeds were also subjected to a wet-sieving procedure (sieves of 16, 8, 4, 2, 1, 0.5, 0.25, 0.125, and 0.063 mm mesh size). Known amounts of samples were soaked in water before sieving to separate all cohering particles (hay for 10 min, concentrate for 30 min, faeces overnight in a refrigerator). Wet sieving was done for 10 min with a water flow of 2 l/min sprayed on the top sieve using a Vibrotronic Type VE 1 (Retsch Technology, Haan, Germany). The amplitude of the sieve shaker was adjusted at 2 mm. The difference between the amount of dry matter subjected to sieve analysis (as calculated from the amount of sample and the respective dry matter concentration) and the dry matter retained on all sieves was calculated to represent the very fine particle (<0.063 mm) fraction. Mean particle size (MPS) of material retained on the sieves was calculated as dMean following Fritz et al. (2012). These calculations were done including all sieves (MPS_{0.063-8mm}), but were also repeated by successively omitting the material retained on the larger sieves (MPS_{0.063-4mm}, MPS_{0.063-2mm}, MPS_{0.063-1mm}, MPS_{0.063-0.5mm}, MPS_{0.063-0.25mm}).

Relative dry matter intake was expressed per unit of body mass (BM)^{0.85} as suggested for large herbivores (Müller et al., 2013; Riaz et al., 2014). Digestibility was calculated as the amount (of nutrient) not eliminated as faeces in percent of the amount ingested. Dry matter gut fill was estimated from dry matter intake, particle MRT, and dry matter digestibility using the linear equation of Holleman and White (1989).

Statistical analyses were performed in R (R Core Team, 2017).

Differences between the intake levels were assessed by mixed effects linear models including individual as a random factor to account for repeated measurements, using the packages ‘lmerTest’, ‘MuMIn’ and ‘car’ with multiple post hoc comparisons using least square mean differences. The allometric relationship between MRT particles in the GIT and the relative DMI was assessed using a mixed effects linear model with individual as random factor and log-transformed data. The significance level was set to 0.05.

3. Results

As planned, the goats had a significantly higher feed intake during lactation, both in absolute and relative terms (Table 2). Daily milk production, determined during milking, corresponded to a typical lactation curve, with a drop at 120 days when feed was reduced to DMI

Table 2
Mean (\pm standard deviation) body mass and measures of digestive physiology in eight goats (*Capra hircus*) fed at three different intake levels.

Measure	Unit	Maintenance	Late lactation	Peak lactation	P*
Body mass	kg	60.4 \pm 4.8 ^A	56.3 \pm 3.4 ^B	49.0 \pm 3.2 ^C	<0.001
Dry matter intake	g d ⁻¹	911	1822	2733	–
Relative dry matter intake	g kg ^{-0.85} d ⁻¹	28 \pm 2 ^C	59 \pm 3 ^B	100 \pm 5 ^A	<0.001
Mean retention time GIT	h				
MRT _{solute}		46 \pm 5 ^A	30 \pm 2 ^B	27 \pm 2 ^C	<0.001
MRT _{particle}		67 \pm 7 ^A	44 \pm 4 ^B	37 \pm 3 ^C	<0.001
MRT _{particle} /MRT _{solute}		1.44 \pm 0.12	1.47 \pm 0.11	1.39 \pm 0.13	0.409
Mean retention time RR	h				
MRT _{solute}		27 \pm 4 ^A	14 \pm 2 ^B	14 \pm 2 ^B	<0.001
MRT _{particle}		47 \pm 7 ^A	28 \pm 4 ^B	24 \pm 3 ^C	<0.001
MRT _{particle} /MRT _{solute}		1.77 \pm 0.21 ^{AB}	2.00 \pm 0.26 ^A	1.71 \pm 0.28 ^B	0.046
Faecal excretion	g DM d ⁻¹	347 \pm 20 ^C	722 \pm 21 ^B	1137 \pm 58 ^A	<0.001
Dry matter GIT fill	kg	1.7 \pm 0.2 ^C	2.3 \pm 0.2 ^B	3.0 \pm 0.3 ^A	<0.001
	% BM	2.9 \pm 0.3 ^C	4.1 \pm 0.3 ^B	6.1 \pm 0.6 ^A	<0.001
Apparent digestibility	%				
Dry matter		62 \pm 2 ^A	60 \pm 1 ^A	58 \pm 2 ^B	<0.001
Organic matter		63 \pm 2	62 \pm 1	61 \pm 2	0.133
Neutral detergent fibre		41 \pm 4	40 \pm 3	39 \pm 3	0.518
Relative digestible dry matter intake	g kg ^{-0.85} d ⁻¹	17 \pm 1 ^C	36 \pm 2 ^B	59 \pm 4 ^A	<0.001
Very fine faecal particles	% all particles	23.8 \pm 2.3 ^A	22.8 \pm 1.4 ^{AB}	22.0 \pm 1.6 ^B	0.038
MPS _{0.063-8mm}	mm	0.57 \pm 0.03 ^C	0.65 \pm 0.02 ^B	0.72 \pm 0.05 ^A	<0.001
MPS _{0.063-4mm}	mm	0.57 \pm 0.03 ^C	0.65 \pm 0.02 ^B	0.71 \pm 0.05 ^A	<0.001
MPS _{0.063-2mm}	mm	0.56 \pm 0.03 ^B	0.62 \pm 0.01 ^A	0.63 \pm 0.02 ^A	<0.001
MPS _{0.063-1mm}	mm	0.45 \pm 0.03	0.45 \pm 0.02	0.47 \pm 0.03	0.177
MPS _{0.063-0.5mm}	mm	0.36 \pm 0.02	0.35 \pm 0.02	0.35 \pm 0.01	0.218
MPS _{0.063-0.25mm}	mm	0.25 \pm 0.01 ^A	0.24 \pm 0.01 ^{AB}	0.24 \pm 0.00 ^B	0.026

MRT mean retention time, GIT gastrointestinal tract, RR reticulorumen, MPS mean particle size.

*linear mixed effects model (with individual as random factor); ^{ABC}different superscripts within columns denote significant differences between intake levels.

L2 (Fig. 1). Maximal milk yield ranged between 4.2 and 4.6 kg/d, with the peak occurring between the 19th and the 22nd day of lactation in six animals, and at day 36 and 63 in the other two animals.

Retention marker excretion curves resembled those reported earlier for small ruminants (Fig. 2A), with a steeper increase than decrease of the concentration of both markers. At the higher intake, MRT_{solute} (Fig. 2B) and MRT_{particle} (Fig. 2C) were significantly shorter; their ratio, however, remained basically unchanged (Table 2). MRT of particles in the GIT scaled to the relative DMI (rDMI) at [95% confidence interval] MRT_{partGIT} = 317 [263,383] rDMI^{-0.47}[-0.52,-0.43].

With increasing intake, the goats also had a higher faecal output, a higher dry matter gut fill, and a lower dry matter digestibility (Table 2). The apparent digestibility for other nutrients, though numerically decreasing with intake for organic matter and NDF, generally did not differ significantly between the intake levels (Table 2). The overall digestible dry matter intake was higher at the increased intake (Table 2).

There was an increase in MPS_{0.063-8mm} and a decrease in the percentage of very fine particles in the faeces with increasing intake level (Fig. 3A, Table 2). However, when expressing the amount of particles of a specific size excreted per day in percent of the amount of the respective particle size excreted at DMI L1, it became evident that particles \leq 0.5 mm were excreted at the respective 200% and 300% level that corresponded to the overall difference in dry matter excretion between the intake levels (Fig. 3B). The excretion of 1–2 mm particles was slightly above these proportionate thresholds, but especially particles of 4–8 mm were excreted at much higher proportions than expected based on differences in faecal amounts alone. Correspondingly, MPS using a maximum sieve size of 8 or 4 mm (MPS_{0.063-8mm} and MPS_{0.063-4mm}) differed significantly between the three intake levels; at a maximum of 2 mm sieve size, the two higher intake levels differed in MPS_{0.063-2mm} from the maintenance conditions; but at a maximum sieve size of 1 mm (MPS_{0.063-1mm}) and below, generally no effect of intake level was evident (Fig. 3C, Table 2).

4. Discussion

Compared to other studies that assessed both intake and faecal mean particle size (MPS) in ruminants, the present study achieved comparatively high variation in intake levels (Fig. 4). This variation in intake had previously well-documented and hence expected effects on gut fill and retention time, and also led to the expected increase in faecal MPS. At the same time, the results question whether this can be really ascribed to a reduction of chewing efficiency, rather than to increased large particle escape from the reticulorumen. The main limitation of the present study was that it had not been possible to record chewing behaviour, so that

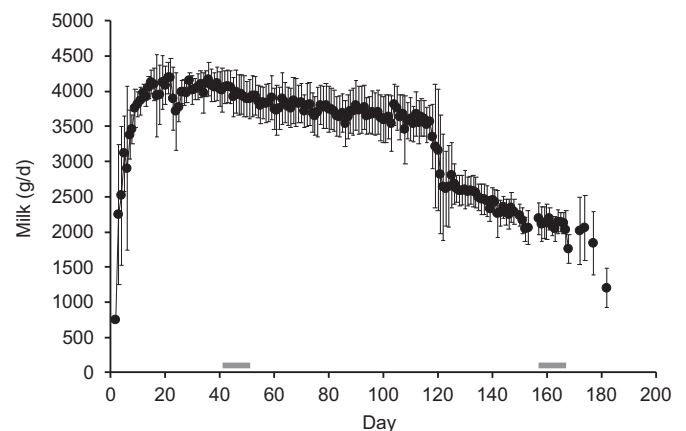


Fig. 1. Mean (\pm standard deviation) daily milk production in the eight goats (*Capra hircus*) of the present study; the grey bars represent experimental periods DMI L3 (peak lactation) and DMI L2 (late lactation), respectively.

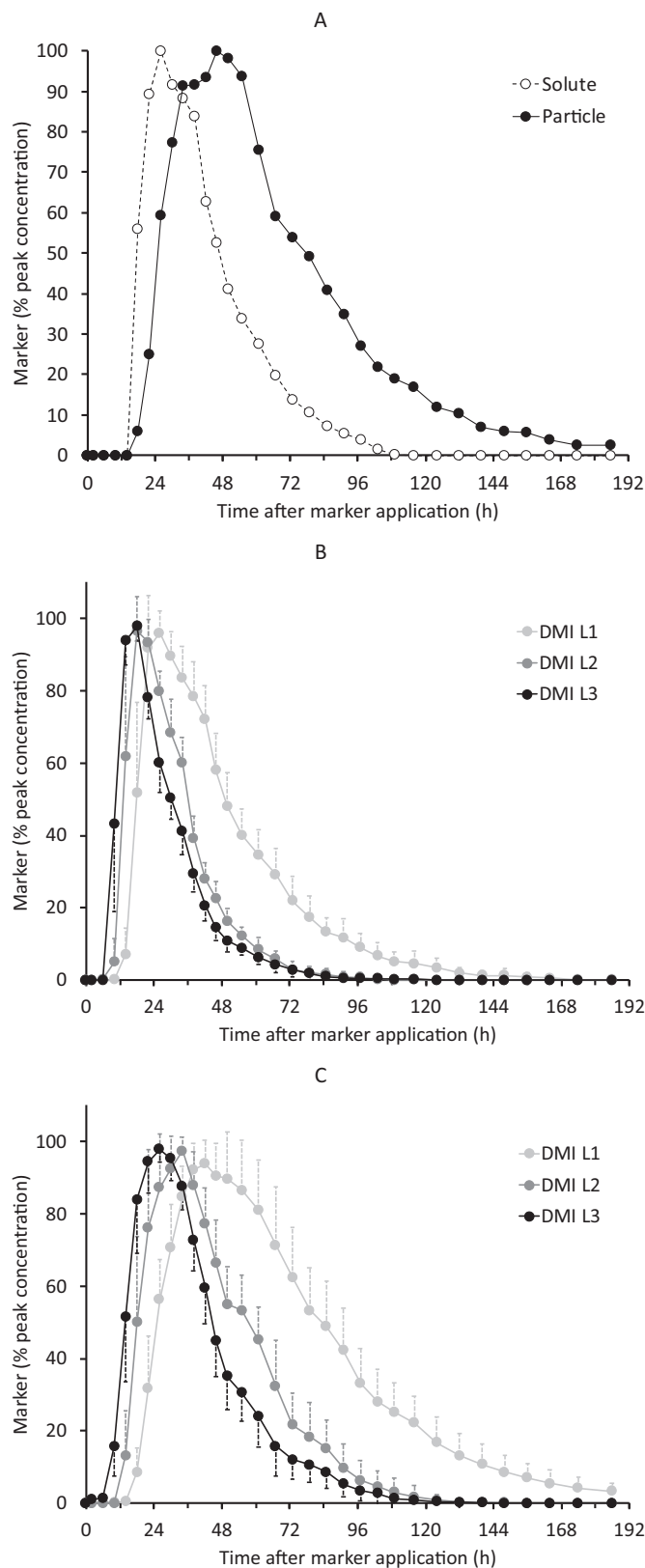


Fig. 2. Marker excretion graphs (solute marker: Co-EDTA; small particle (1-2 mm) marker: Cr-mordanted fibre) in goats (*Capra hircus*) on a consistent diet; (A) example in a single goat on maintenance dry matter intake (DMI L1) level; (B) mean (with standard deviation) solute marker excretion of 8 goats at three DMI levels; (C) mean (with standard deviation) particle marker excretion of 8 goats at three DMI levels. Note faster marker excretion on the higher DMI levels.

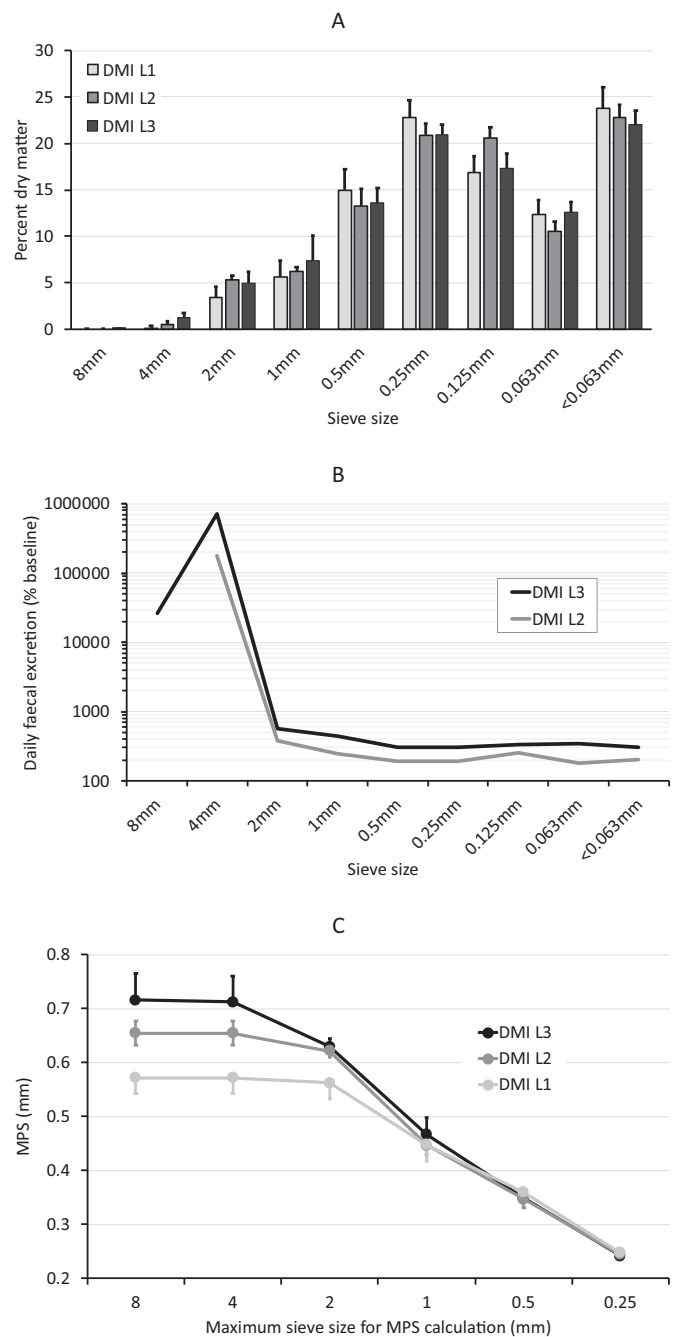


Fig. 3. Mean (with standard deviation) percentage of dry matter of faeces of goats (*Capra hircus*) submitted to wet sieve analysis; (A) particle size distribution of the faeces of 8 goats on a consistent diet at three levels (L1–L3) of dry matter intake (DMI). (B) The daily amount of particles of different size classes excreted in % of the excretion of the respective size class at DMI L1; note that particle sizes of 0.5 mm and less are excreted in proportion to the overall faecal output of 200 and 300% at DMI L2 and DMI L3, respectively. (C) Mean particle size (MPS) calculated using all sieves from the smallest one of 0.063 mm pore size up to different larger sieves.

interpretations regarding time constraints must remain speculative. Future studies should include visual or chewing-halter measurements of ingestive and rumination mastication as well as the number of regurgitated and swallowed boli.

Digestion is a multi-factorial process. Its efficiency is determined, among other factors, by dietary characteristics, by the time available for digestion, and by the size of the feed particles (Bjorndal et al., 1990;

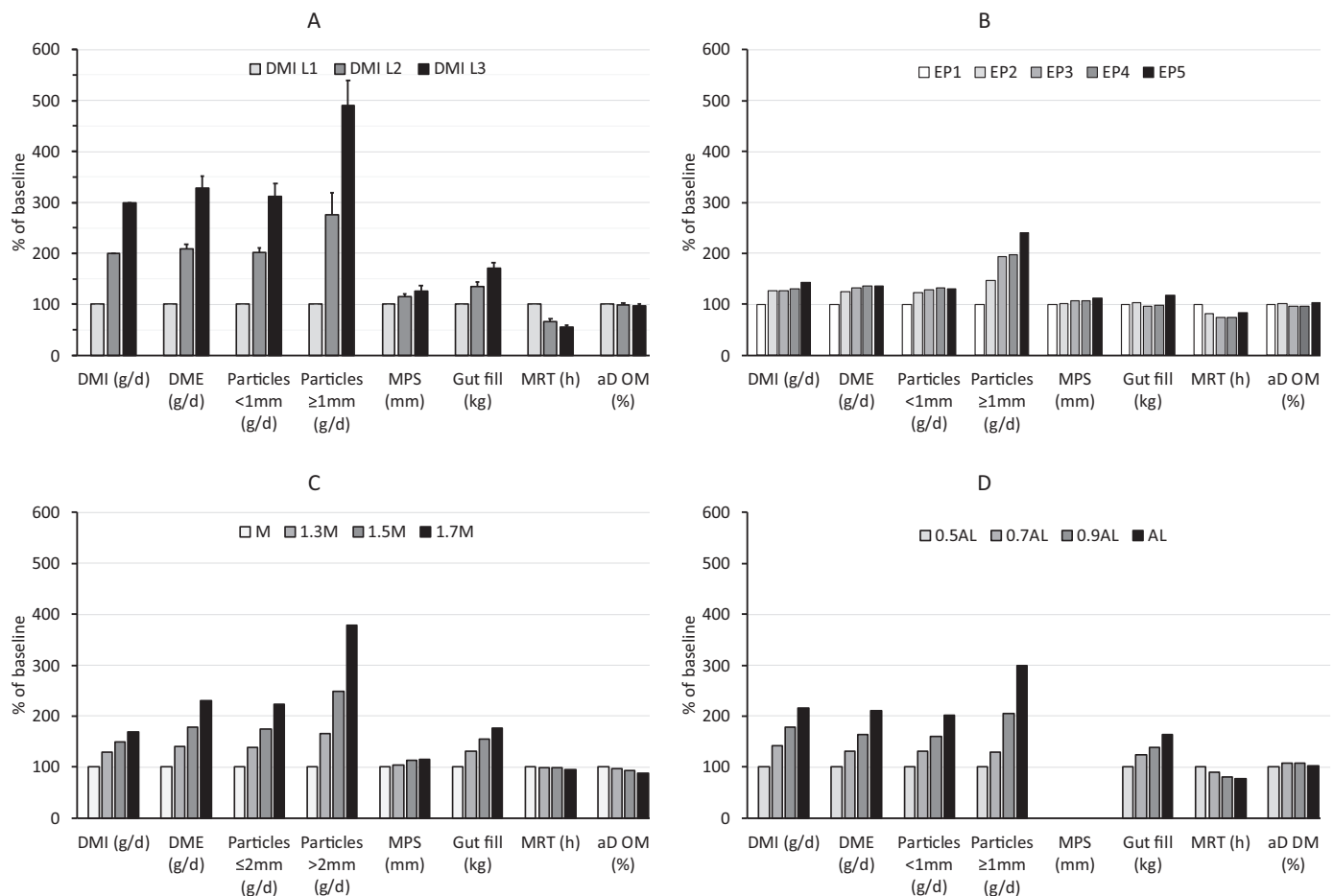


Fig. 4. Comparison of the proportional change of various measures of digestive physiology (dry matter intake DMI, dry matter faecal excretion DME, small particle mean retention time MRT, dry matter gut fill, mean particle size MPS, daily excretion of particles of different size groups, apparent digestibility of organic matter aD OM) in domestic ruminants in experiments with different intake levels of a consistent diet and measurement of faecal particle size. The treatment with the lowest intake is always set to 100%. Note that methods may vary between studies, so that the patterns but not the actual values should be compared. (A) Goats (*Capra hircus*) of the present study fed a consistent diet (hay:concentrate 1:1) at three levels L1-L3 of dry matter intake DMI at maintenance or in lactation. (B) Sheep (*Ovis aries*) in five experimental periods EP (I early, II middle, III late pregnancy, IV early and V later lactation; diet: grass hay) with ad libitum intake (Kaske and Groth, 1997). (C) Non-lactating cattle (*Bos primigenius taurus*) fed a consistent hay mixture at various multiples of maintenance requirements M (Okine and Mathison, 1991). (D) Steers (*Bos primigenius taurus*) fed grass hay at various fractions of ad libitum AL intake (Luginbuhl et al., 1990). Note general patterns of decreasing MRT and increasing gut fill with increasing intake and an increase in MPS, and that small particle excretion usually reflects the pattern of overall DME, whereas large particle excretion increases disproportionately at higher intakes.

Hume, 2005; Clauss et al., 2015). Generally, lower fibre and ash concentrations, longer retention times, and smaller particle sizes will increase digestibility. Acquiring additional energy at times of increased requirements, such as during lactation, can be conceptualized as a dilemma for free-ranging animals, because the necessary increased feed intake can.

- (i) constrain the ability to feed selectively; in other words, higher intended intakes may make it necessary to accept feed of lesser quality.
- (ii) reduce time available for digestion, as a higher input rate into a system may well translate into a higher throughput rate through that system.
- (iii) reduce time available for chewing, as the intended increased intake may make a faster intake rate with less masticatory processing necessary.

Constraint (i) may be real for free-ranging animals, and will depend largely on the spatial and temporal distribution of feed (patch distance, sward height) (Griffiths et al., 2003b; a) and of nutrients within the feed items (leaf:stem ratio, growth stage) (Van Soest, 1994). However, the

experimental conditions of the studies summarized in Fig. 4 rule out changes in diet quality as an influencing factor for the documented digestive processes. When comparing effects of intake levels on other measures of digestive physiology, the choice of the experimental diet will affect the magnitude of the effects. For example, the use of a 50:50 mixture of forage and concentrate might have facilitated a higher variation in intake (Fig. 4), as physical forestomach fill may have played a lesser role on this diet than on a whole forage-only diet (Baile and Forbes, 1974).

The magnitude of any of the mentioned effects will depend crucially on the spare (or 'buffering') capacity of the respective system. Buffering may occur on the level of body stores, on the level of gut capacity, and on the level of spare time.

On the level of the organism, the extent of the increase of feed intake at times of increased requirements will depend on available body stores that can be used to meet the requirements; this is often explained in the dichotomy of 'capital breeders' and 'income breeders' (Stearns, 1992). Although in contrast to marine mammals, pure 'capital breeding' is rare among terrestrial mammals with the notable exception of some bear species, the dichotomy has been used to describe differences even between ruminant species that may depend to varying degrees on the

mobilization of body stores during peak lactation or during rut (Kerby and Post, 2013; Apollonio et al., 2020). Domestic ruminants used for milk production, like the Saanen goats of the present study, invest body stores at peak lactation in parallel to increased intakes – a fact also evident in the body mass fluctuation between the different states of our animals.

On the level of digesta passage, an increased feed intake is linked to a decreased retention time, both in interspecific (Claus et al., 2013; Müller et al., 2013) and intraspecific comparisons (Munn et al., 2008; Munn et al., 2015). This effect can be buffered by an increased gut fill – i. e., an increase in the volume of the gut capacity that is actually used (Barboza et al., 2006). Quantifying this spare capacity by anatomical measurements is difficult; it is evident in the maximum water holding capacities of exenterated forestomachs as compared to their actual wet contents fill (Weckerly et al., 2003). Animal species may differ in the degree to which their digestive tract can expand and hence buffer the retention-shortening effect of intake (Barboza and Hume, 2006; Claus et al., 2007), and pregnancy may limit the expansion capacity of the gut in the abdominal cavity distinctively (Faichney and White, 1988). In the studies with domestic ruminants, an increase in gut fill with increasing intake is evident in parallel with a decrease in digesta retention (Fig. 4), suggesting that the animals employed a combined strategy in these experiments. The diets used in the experiments as well as the state of the animals will influence the response magnitude. For example, note that the increase in intake of a medium-quality hay in pregnant sheep was hardly accompanied by an increase in gut fill but mainly reduced digesta retention (Fig. 4B), whereas non-gravid animals had a more flexible gut fill response (Fig. 4A,C,D). As a side note, the negative scaling exponent of particle mean retention time with relative dry matter intake in the goats of the present study (-0.47) was identical to the one determined in ponies at different levels of feed restriction (Claus et al., 2014), contradicting an earlier hypothesis by Claus et al. (2007), based on the assumption of a linear relationship, that this scaling is less steep in equids than in ruminants.

On the level of digestibility, the extent to which an increased intake will reduce digestibility depends on how close the digesta retention time of the control intake level was already at the minimum required for optimal digestion of the diet used. In other words, the control low intake condition may or may not imply a state where retention is longer than necessary for optimal digestion. Whereas the digestibility of plant feed may vary distinctively with time during the first hours of microbial fermentation and digestion, changes after the initial 12–24 h are often less distinct (Hummel et al., 2006). This may explain the lack of effect of reduced retention times on digestibility in Fig. 4A, B and D, whereas the diet employed in the experiment depicted in Fig. 4C was possibly more susceptible to variation in retention times. In this respect, the compilation of studies in Fig. 4 warns against interpreting digesta retention times as the predominant factor constraining or facilitating digestion, and recommends to always consider relevant diet characteristics (Claus et al., 2013).

With respect to the main aim of the present investigation, increased intake levels were linked to increased faecal MPS. This had been expected based on previous studies in ruminants (Shaver et al., 1986; Kovács et al., 1997a and those depicted in Fig. 4), even though it is in contrast to other studies in ruminants (Bae et al., 1981), to the few observations in nonruminant mammals (Claus et al., 2014; Findeisen et al., 2021), and to the general concept that ‘oral processing’ (i.e., mastication) represents a rather inflexible constraint for instantaneous intake rates (Yearsley et al., 2001, and references cited in the introduction). While processes like digesta retention or digestion integrate the effects of a large number of separate events – many individual, swallowed feed boli entering and being mixed in the gut –, mastication preceding the swallowing of a feed bolus is considered a rather inflexible process. While particle size composition of a bolus may vary between different feeds (e.g. Trudell-Moore and White, 1983; Ulyatt et al., 1986; Grenet, 1989), mastication is performed until a certain consistency of

the bolus is achieved that facilitates swallowing, and that prevents bolus disintegration due to too intensive chewing (Prinz and Lucas, 1997). The production of saliva is a crucial component of this process: on the one hand, it is a prerequisite for coherent bolus formation and swallowing; on the other hand, too much saliva can disrupt bolus coherence (Prinz and Lucas, 1997). The fact that different feeds require different chewing investment is reflected, in domestic ruminant science, in positive relationships of fibre content or particle size with chewing time (Beauchemin, 2018). In particular, the concept of physically ‘effective fibre’ combines biochemical properties (the concentration of neutral detergent fibre) and physical properties (the proportion of particles above a certain size) of diet items into a quantitative values describing the required chewing intensity (Mertens, 1997, 2000).

Presumably, it is the consistency of the bolus that is detected by the animal, and the fact that different particle size compositions will lead to the threshold consistency in different feeds explains variation between feeds. The fact that the required bolus consistency is only achieved after a certain number of chews for a specific feed thus can explain the seemingly inflexible constraint of oral processing on instantaneous intake, because the sensory threshold would have to be deliberately overruled by the animal. The only situations in which this appears plausible is extreme greed after feed deprivation, in situations of extreme competition, or when feeding under a distinct predation risk. Cattle that were fasted prior to grazing had less chewing intensity (Greenwood and Demment, 1988). Higher intake rates with fewer chews per feed were documented at the beginning of a feeding bout in sheep compared to later stages of the feeding bout (Grenet, 1989). Drastic reduction in feed provision led to shorter intake times in cows, possibly linked to fewer chewing bouts per ingested feed (Santana et al., 2020). Social competition can lead to faster ingestion rates and reduced chewing intensity per intake (Olofsson, 1999; Melin et al., 2007). However, apart from such situations, ruminants might adjust time allocated to chewing or chewing frequency (Coulon et al., 1987; Blanchard, 2005; Hamel and Côté, 2008) to achieve the targeted ‘bolus consistency’ in this scenario. Notably, the constraints imposed by time that needs to be allocated to social interactions or vigilance, and the perceived competition due to group feeding, are absent in studies like those collated in Fig. 4. These investigations are performed in individually housed animals under protected conditions. A time constraint appears only plausible for diets that cause, due to their high content of ‘effective fibre’, a tradeoff between the time required for mastication (in particular, rumination), and the time available for ingestion (Dado and Allen, 1995; Weston, 1996; Beauchemin, 2018).

However, even though mastication by non-ruminants may be governed by a sensory setpoint of bolus consistency in the oral cavity, ruminants are peculiar in that different types of boli have been documented on consistent diets: boli swallowed after ingestive mastication have a higher proportion of large particles than boli swallowed after rumination (Reid et al., 1979; Trudell-Moore and White, 1983; Ulyatt et al., 1986; McLeod and Minson, 1988; Grenet, 1989). This is paralleled by different chewing patterns during ingestion and rumination (Dittmann et al., 2017). In other words, a ruminant should be used to admit boli of different consistency for swallowing, even under non-fasted and non-competitive conditions that do not impose a time constraint on chewing – because it does so on a daily basis, every time it switches from ingestion to rumination. In theory, this should give ruminants more behavioural leeway to flexibly adjust the chewing intensity to accommodate higher intake rates (Shaver et al., 1988).

While we cannot conclusively reject this hypothesis, we suggest an alternative one that appears to more plausibly match the observations in particle size distributions in our and similar experiments (Fig. 4). Rather than implying voluntary adjustments of the ‘bolus consistency swallowing setpoint’, one can also postulate two different, rather inflexible setpoints in ruminants for ingestive swallowing and swallowing after rumination. For example, the observation that intake did not affect the MPS of the ingested (Shaver et al., 1988) or ruminated boli (Kovács

et al., 1997b) on a consistent diet supports the concept of certain ingestion and rumination comminution setpoints for a given diet. In ruminants, it is not only the amount of feed ingested that determines the amount of feed that is actually chewed, but also the amount of feed that is regurgitated from the forestomach. The sorting mechanism in the ruminant forestomach generally ensures that large particles are regurgitated for rumination (Dittmann et al., 2015). However, a low proportion of large particles actually escapes from the forestomach unruminated (desBordes and Welch Des Bordes and Welch, 1984; Kaske et al., 1992), and this has been shown to occur comparatively soon after ingestion (Lauper et al., 2013; Hummel et al., 2018). It is plausible to assume that this may occur more under conditions of increased forestomach fill. Thus, even though the *calculated* chewing intensity, the ratio of observed chews and ingested feed, changes with feed intake (Shaver et al., 1988), this might not necessarily mean that a given amount of feed in the oral cavity is exposed to less chewing cycles (i.e., the animal accepting a different ‘bolus consistency setpoint’). Rather, this calculated ratio might simply reflect that a higher proportion of ingested feed is never again submitted to rumination. The observation that it is particularly the excretion of particles above the typical threshold for escape – roughly 1 mm in sheep and possibly 2 mm in cattle (Poppi et al., 1980; Poppi et al., 1985; Shaver et al., 1988) – that increases disproportionately at increasing intakes in our own study (Fig. 3) and the studies depicted in Fig. 4 supports this hypothesis. In order to fully test this, intense invasive studies using fistulated animals would be necessary to determine the amount of material actually submitted to rumination at different levels of intake.

To conclude, the chewing intensity may be a comparatively fixed process for a given feed, with a sensory setpoint given by a ‘bolus consistency’ that may be different for ingestion and rumination. To what extent animals voluntarily overrule or change this setpoint remains speculative. Existing data on effects of variation in intake level on digesta particle size provide evidence for an effect in ruminants (but so far not in other mammals), but this is probably an effect of increased escape of larger particles from the forestomach prior to rumination, rather than to a change in actual chewing intensity.

Declaration of Competing Interest

The authors declare no conflict of interest.

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