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ORIGINAL ARTICLE

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Comparative study of feeding and rumination behaviour of goats and sheep fed mixed grass hay of different chop length

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Abstract

Rumination is reported to be more pronounced in sheep compared to goats. This study compared the feeding and rumination behaviour of small ruminants and consisted of two experiments (E1 and E2). In E1, four sheep and four goats were offered low-quality hay (NDFom: 692 g/kg dry matter [DM]), processed to two chop lengths (long hay [LH]: 35 mm; short hay [SH]: 7 mm) in a 2 × 2 factorial (2 species × 2 chop lengths), cross-over design. In E2, the same animals were offered moderate-quality hay (NDFom: 636 g/kg DM) processed as LH and SH. Hay was offered for ad libitum consumption. Feeding and rumination behaviour was evaluated using video recordings. Aspects of rumination like chewing frequency were evaluated for 30 min per day. Faecal samples were analysed for faecal-N and particle size. There was no species effect on feed intake and organic matter digestibility (faecal N as proxy); however, goats consumed more LH than SH in E1 and E2. There was an effect of species on rumination:eating duration (R:E) ratio (higher in sheep) in E1 but not in E2, where there was a tendency for a species effect on rumination duration. In E1 and E2, sheep had a higher R:E ratio for SH than for LH. For rumination behaviour, there was a species effect for number of daily boli, chewing frequency and chews per day (more in sheep) in E1 and E2. No effect of species was found for faecal particle size. Despite much concordance, feed comminution behaviour differed in some aspects between sheep and goats. In an evolutionary context, a shift of significance of rumination could be triggered by a higher amount of abrasives in natural diets of sheep, rendering a shift of chewing towards ruminally prewashed material a rewarding strategy.

KEYWORDS

chewing behaviour, goats, grass hay, rumination, sheep

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1 | INTRODUCTION

In all ruminant species including domesticated cattle, sheep and goats, digestive physiology is following the same basic principle. However, the more detailed the perspective becomes, the more differences become obvious (Hackmann & Spain, 2010), starting with distinct preferences for particular plants. Herbivore-relevant characteristics of plant types vary; features such as low overall cell wall (neutral-detergent fibre), high indigestible fibre (lignin) and low abrasive contents (silica) are typical for browse-dominated diets (Hummel et al., 2020). Hofmann (1989) compared African and European ruminants (e.g., gnu, impala, giraffe) regarding their feed choice (grass or browse) and suggested adaptive differences in digestive tract morphology and physiology. This concept was also applied to ruminants of the Northern hemisphere, including domestic species (Hofmann, 1995). Some of these suggested differences were actually corroborated later by statistical analyses (reviewed, e.g., in Clauss et al., 2008; Codron et al., 2019). Besides morphological and physiological aspects, Hofmann (1989) also suggested that feeding patterns are correlated to the natural diet, with more frequent and shorter feeding bouts on dicot/browse diets—as later statistically corroborated by Hummel et al. (2006).

When comparing domestic ruminants regarding feed choice, goats—while being opportunistic feeders—represent the species with the most distinct preference for dicot plants (Dulphy et al., 1995; McCammon-Feldman et al., 1981; Rahmann, 2004). Under free-ranging conditions, goats are reported to have a browse:grass ratio of 2.1, while it is only 0.5 in sheep (Van Wieren, 1996). Several particularities have been assigned to the functional traits of feeding and digestion of goats, such as a distinct selectivity on forage (Morand-Fehr et al., 1980), stable-fed diets (Brown et al., 1988; GfE, 2003) and even concentrates (Morand-Fehr, 2003), or a low tendency to decrease voluntary intake when dietary fibre content increases, at least when compared to other ruminants (Riaz et al., 2014). Goats are classified to have an advantage over sheep in terms of energy intake when feeding on low-quality feeds by AFRC (1998); as possible reasons, higher rumen ammonia contents, slower passage rates and larger rumen volume in goats are suggested. An advantage in goats compared to sheep in dry matter intake (DMI) and fibre digestibility on low-quality diets has also been described by Domingue et al. (1991b) and Rapetti et al. (2008).

Since feed intake is closely related to rumen fill and mechanical disintegration of fibrous feed particles, feed comminution (eating and rumination) is decisive for overall digestive performance in all ruminants. A detailed look at chewing-related behaviour is therefore essential for an understanding of subtle, but potentially relevant differences in feed processing strategies between ruminants. In this regard, most comparative studies have been conducted in sheep and cattle, which are rather similar regarding their diet type, but obviously different in body size. Some basic data comparing sheep and goats (similar body size, but different diet types) also exist, which suggest that feeding and rumination behaviour of goats may differ to some extent from that of sheep. A review based on 20 comparisons between goats and sheep (from six publications) indicates that goats have more feeding bouts (8.1 vs. 6.4 bouts/d), feed longer in total (248 vs. 221 min/d) as well as per unit of DMI (4.6 vs. 3.9 min/(kg DM*kg $BW^{0.75}$)) and spend considerably less time ruminating (407 vs. 500 min/d; 7.5 vs. 8.9 min/(kg DM*kg $BW^{0.75}$)) (Baumont et al., 2006; Dulphy et al., 1995). Overall, the total time spent chewing was slightly lower in goats compared to sheep. A further study also found a longer feeding (+3.1 h/d) and shorter rumination time (−2.2 h/d) for goats compared to sheep on a diet of chaffed lucerne (Domingue et al., 1991).

The present study was designed to test assumptions on characteristics of feeding behaviour based on the influential review of Dulphy et al. (1995). Relevant German breeds were used. In particular, we aimed to test (1) whether goats spend less time ruminating than sheep, resulting in a lower ratio of rumination to eating time (R:E ratio), (2) whether there are differences in detailed chewing behaviour (for example rumination boli and chewing frequency), (3) if such differences exist, whether there is a systematic difference in faecal particle size as the final result of feed comminution processes and (4) whether goats have a tendency to feed in smaller, more frequent bouts.

2 | MATERIALS AND METHODS

This study was conducted in accordance with the German legal and ethical requirements of appropriate animal procedures. The experimental protocol was reviewed and approved by the institutional animal welfare committee of the University of Goettingen (reference no. E4–20).

2.1 | Diets, animals and experimental design

This study consisted of two experiments (E1 and E2) conducted under identical conditions with the same animals in consecutive periods.

Four mature nonpregnant female goats (Weiße Deutsche Edelziege; E1: 78 ± 2.5 kg body weight [BW], E2: 75 ± 1.7 kg BW) and four mature nonpregnant female sheep (German black-headed mutton sheep; E1: 83 ± 3.7 kg BW, E2: 84 ± 2.4 kg BW) were housed in two separate free stall pens (each 3.6 × 2.5 m), bedded with wood shavings. Both pens were equipped with four Calan Broadbent Feeding units (American Calan). The system allows individual feed intake measurements by restricting access to a particular trough to one single animal. All animals had free access to water and a trace mineral-fortified salt block. Goats and sheep were fed twice daily (equal portions at 07:00 and 16:00 h) for ad libitum consumption. The quantity of offered hay for each animal was determined during the adaption period and adjusted as necessary during the experiment. The refusals were collected every morning before feeding and weighed. Refusals of hay were 10.7% for sheep and 11.0% for goats in E1 and 8.6% for sheep and 10.7% for goats in E2. Significant feed

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TABLE 1 Nutrient and energy content of hay ($n = 4$).

Item	Hay Experiment 1	Hay Experiment 2
DM (g/kg)	910	900
Organic matter (g/kg DM)	924	937
Crude protein (g/kg DM)	101	100
aNDFom[1] (g/kg DM)	692	636
ADFom[2] (g/kg DM)	381	337
Ether extracts (g/kg DM)	13.8	17.8
24 h gas production[3] (mL/200 mg DM)	32.8	39.9
Metabolizable energy (MJ/kg DM)	7.7	8.7

[1]Neutral detergent fibre exclusive residual ash, assayed with heat-stable amylase.

[2]Acid detergent fibre exclusive residual ash.

[3]Determined by Hohenheim gas test.

selection in terms of nutrients was not detected. Compared to the average acid detergent fibre (ADFom) content of the offered hay (E1: 381 ± 4.4 and E2: 337 ± 11.3 g/kg DM), actually ingested ADFom was similar (sheep: 381 ± 3.8 [E1] and 335 ± 12.1 [E2], goats: 385 ± 3.4 [E1] and 338 ± 11.9 [E2] g/kg DM).

In both experiments, goats and sheep were offered mixed grass hay processed to two theoretical chop lengths 'short hay [SH]'—7 mm (longest particle 6 cm) and 'long hay [LH]'—35 mm (longest particle 15 cm) in a 2 × 2 factorial design. The different chop lengths were prepared by using a stationary electric forage chopper (Silo- und Blashäcksler Baureihe 28; Gebrüder Botsch). While both hays can be characterized as relatively high in fibre, ADFom content of hay 1 was 11.5% higher and metabolizable energy (ME) 11.5% lower than that of hay 2 (Table 1). The CP content of both hays was identical.

During the first 10 days of each period, the animals were adapted to the respective treatment. Subsequently, DMI was recorded over five consecutive days. Leftovers were collected every day before the morning feeding at 7:00 h. Samples of the leftovers were mixed, dried and stored for later analysis. During these five days of measurements, the chewing behaviour was recorded over two consecutive 24 h periods. After the feed intake measurement, faeces from every sheep and goat were spot sampled directly off the ground after defecation. The faeces were stored at −20°C until further analysis.

2.2 | Behavioural measurements

Behavioural observations were made with video cameras over 48 h during the five days of recording the DMI. Three video cameras (Berghoch) were mounted above the two pens and positioned to cover the entire surface area of both pens. Chewing behaviour (eating and ruminating) was evaluated continuously over 48 h for each individual animal.

'Eating' was defined as event during which an animal lowered its head continuously into the feed trough for more than 30 s. 'Rumination' was defined as the time span between regurgitation of the first bolus and swallowing of the last bolus of one rumination bout.

The number of rumination boli was counted twice during the daytime and twice during the nighttime per animal, each time for 15 min. The chews per bolus were counted for the same 15 min blocks and later extrapolated to 24 h. Reported chewing frequencies reflect true chewing time, exclusive of time for swallowing/regurgitation.

2.3 | Wet sieving of the faeces

Wet sieving of the faeces was carried out using a vibrating sieve analyser (model AS 200; Retsch GmbH) equipped with a series of sieves (pore sizes: 8.0, 4.0, 2.0, 1.0, 0.50, 0.250, 0.125 and 0.063 mm). Before sieving, the faecal samples (10 g; wet weight) were thawed overnight in 1 L H_2O in a beaker with magnetic stirrers to achieve near complete suspension of particles. The samples were sieved for 10 min with a vibration amplitude of approximately 2 mm and a water flow rate of 2 L/min. After 10 min, the particles retained on each sieve were rinsed on filter paper (ashless/Black ribbon 589/1; Whatman) and dried overnight at 60°C and subsequently for 1 h at 103°C.

The weighted average particle size (WAPS) was calculated as

WAPS (mm) = ∑ (faecal particles (g/sieve)/total faeces (g)) × average pore size upper and lower sieve (mm).

This value does not include the amount of material passing through the 0.063 sieve, which can be very small feed particles, faecal microbes and also soluble faecal components (e.g., minerals). The value for the fraction not retained on the 0.063 mm sieve is reported in Figures 1 and 2.

2.4 | Chemical analysis

All oven-dried feed and refusal samples were ground (cutting mill SM 200; Retsch GmbH) through a 1 mm screen prior to chemical analysis. The faecal samples were freeze-dried before milling.

All chemical analyses were conducted according to standardized methods recommended by the Association of German Agricultural Analytic and Research Institutes (VDLUFA, 2012). To determine the analytical DM, samples of the hay and refusals were dried for 24 h at 103°C (method 3.1). Organic matter (OM; 1000-ash g/kg) was determined after combusting the samples at 550°C (method 8.1). Crude protein (CP) was analysed by Kjeldahl titration (method 4.1.1). Fat was determined according to method 5.1.1. Neutral detergent fibre (aNDFom) and acid detergent fibre (ADFom; both expressed exclusive of residual ash) were analysed using an Ankom Fibre Analyzer (ANKOM Technology) (methods 6.5.1 and 6.5.2). The total gas production after 24 h (GP_{24h}) of in vitro incubation, which was necessary to calculate the ME content of the hay, was determined using the Hohenheim gas test

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(method 25.1). The metabolizable energy (ME) content of the hay for ruminants was estimated according to GfE (2008).

In the faecal samples, only ash and CP were analysed.

2.5 | Statistical analyses

Data of both experiments were analyzed using the mixed procedure of SAS (Version 9.4). The model for both experiments included the fixed effects of species, chop length and their interaction. Animal was considered as a random effect. Treatment means were compared by Tukey–Kramer test. For all parameters, significance was declared at $p < 0.05$. Trends were discussed at $0.05 \le p \le 0.10$. If a percentage is given to further quantify the size of an effect, the higher value is always taken as 100%, and the lower value is expressed in relation.

Due to the limited number of animals available, it was decided to investigate variable hay quality in separate experiments rather than in a design with hay quality as the third fixed variable (besides species and chop length). In this approach, E2 can act as an internal control for the results of E1. Effects proving to be significant in E1 and E2 can be considered particularly relevant. While sample sizes of around four animals are not uncommon in comparable studies (e.g., Focant et al., 1986; Masson et al., 1989), obviously a larger sample size would be considered in future studies. This contributes not only to detecting all relevant, but also to avoiding false significances (Button et al., 2013). A further point to be considered in future studies will also be the representativeness of the respective breed (e.g., dairy or fattening) for the entirety of the species.

3 | RESULTS

3.1 | Feed intake

In both, E1 and E2, an interaction between chop length and species was detected for DMI ($p < 0.001$; Table 2). Goats consumed more LH (E1: 1818 g DM/d; E2: 1954 g/d) compared to SH (E1: 1445 g DM/d; E2: 1436 g/d), while the DMI of sheep was not different between chop lengths. The results followed the same pattern when the DMI was adjusted for differences in BW (g/kg BW, g/kg $BW^{0.75}$). In both experiments, no effect of species on intake was found. Compared to E1 (with hay of a 11.5% higher ADFom content), average DMI (g/d) was approximately 10% higher in E2.

3.2 | Chewing activity

Goats spent more time eating the short hay compared to sheep in E1 (275 vs. 175 min; $p < 0.05$; Table 3). When offered LH, sheep spent more time eating (222 min/d) compared to SH in E1 and E2 ($p < 0.05$). Independent of species and chop length, animals spent on average between 550 and 590 min/d ruminating in E1 and between 509 and 572 min/d in E2. In contrast to one of our major hypothesis, there were no differences in the duration of total daily rumination time between sheep and goats in E1; however, in E2 sheep and goats tended to differ in rumination time (shorter rumination in goats). Total mastication time was 762–830 min/d and increased (E2: $p = 0.008$) or tended to increase (E1: $p = 0.066$) with chop length. The R:E ratio was lower in goats compared to sheep in E1 ($p = 0.002$) but not in E2 (only sheep on SH had a higher ratio than goats on SH; $p < 0.05$). In E1 and E2, sheep had a higher R:E ratio in response to SH than LH (E1: 3.41 vs. 2.66; E2: 3.16 vs. 2.43; $p < 0.05$), while there was no difference in R:E ratio in goats due to chop length.

For all chewing effort variables, an interaction of species and chop length was detected in E1 and E2. In E1 and E2, chewing effort (min/g DM) for eating was higher for LH than for SH in sheep ($p < 0.001$). For rumination and total mastication (min/g DM), differences were only present for goats; in E1 and E2, they needed more time per g DM for SH than for LH ($p < 0.001$).

TABLE 2 Dry matter intake (DMI) of sheep and goats in Experiment 1 (E1) and Experiment 2 (E2).

	E1								E2							
	Sheep		Goats			*p* Value			Sheep		Goats			*p* Value		
Item	SH[1]	LH[2]	SH	LH	SEM	Species	Chop length	S × CL[3]	SH	LH	SH	LH	SEM	Species	Chop length	S × CL[3]
DMI (g/d)	1562[ab]	1527[ab]	1445[a]	1818[b]	127.9	0.640	<0.001	<0.001	1959[b]	1710[ab]	1436[a]	1954[b]	96.7	0.265	0.083	<0.001
DMI (g/kg BW)	18.8[ab]	18.5[ab]	18.4[a]	23.9[b]	1.96	0.393	<0.001	<0.001	23.4[ab]	20.3[ab]	19.5[a]	25.5[b]	1.45	0.724	0.155	<0.001
DMI (g/kg $BW^{0.75}$)	56.7[ab]	55.7[ab]	54.8[a]	70.6[b]	5.59	0.435	<0.001	<0.001	70.8[ab]	61.5[ab]	57.2[a]	75.5[b]	4.14	0.974	0.133	<0.001

[1]Short hay (7 mm chop length).

[2]Long hay (35 mm chop length).

[3]Interaction species × chop length.

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TABLE 3 Eating and rumination behaviour in Experiment 1 (E1) and Experiment 2 (E2).

	E1								E2							
	Sheep		Goats			*p* Value			Sheep		Goats			*p* Value		
Item	SH[1]	LH[2]	SH	LH	SEM	Species	Chop length	S x CL[3]	SH	LH	SH	LH	SEM	Species	Chop length	S x CL[3]
Duration of behaviour (min/d)																
Eating	175^{a}	222^{b}	275^{b}	271^{b}	14.8	0.010	0.001	<0.001	185^{a}	236^{bc}	202^{ab}	245^{c}	13.5	0.491	<0.001	0.682
Ruminating	588	574	555	564	17.5	0.392	0.807	0.230	572	570	509	547	18.4	0.067	0.327	0.274
Mastication	762	795	830	843	29.7	0.202	0.066	0.422	757^{ab}	806^{b}	711^{a}	792^{ab}	23.9	0.282	0.008	0.473
R:E ratio	3.41^{c}	2.66^{b}	2.03^{a}	2.09^{a}	0.136	0.002	<0.001	<0.001	3.16^{b}	2.43^{a}	2.64^{ab}	2.25^{a}	0.211	0.227	0.001	0.259
Chewing effort (min/g DM)																
Eating	0.11^{a}	0.15^{b}	0.19^{c}	0.15^{b}	0.007	0.005	0.651	<0.001	0.10^{a}	0.14^{b}	0.14^{b}	0.13^{ab}	0.010	0.223	0.122	<0.001
Ruminating	0.38^{ab}	0.38^{ab}	0.38^{b}	0.32^{a}	0.037	0.381	0.002	0.002	0.31^{ab}	0.33^{ab}	0.37^{b}	0.28^{a}	0.030	0.832	0.043	0.002
Masticating	0.50^{ab}	0.53^{ab}	0.57^{a}	0.47^{b}	0.032	0.860	0.022	<0.001	0.41^{ab}	0.46^{ab}	0.52^{b}	0.41^{a}	0.037	0.616	0.173	<0.001

[1]Short hay (7 mm chop length).
[2]Long hay (35 mm chop length).
[3]Interaction species × chop length.

3.3 | Rumination behaviour

The species differed in the number of rumination boli in E1 ($p = 0.009$) and E2 ($p = 0.028$), with more boli in sheep (Table 4). The rumination frequency (chews/s) was not affected by chop length but by species in E1 ($p = 0.050$) and E2 ($p = 0.014$), indicating a higher frequency in sheep. Species also had an effect on rumination chews per day, with sheep ruminating longer compared to goats (E1: $p = 0.048$; E2: $p = 0.012$). In a simple calculation based on the means, the numerical effect is of a magnitude of 20% less rumination chews/day in goats.

3.4 | Through visits

Goats visited the trough more often compared to sheep in E1 and E2 ($p = 0.003$ and $p = 0.016$). The number of visits was not affected by chop length. Species tended to have an influence on duration of through visits in both experiments (indicating longer stays in sheep).

3.5 | Faecal variables

There were no differences in WAPS in response to species or chop lengths in E1 and E2 (Table 5); however in E2 there was an interaction between species and chop length ($p = 0.044$). The overall distribution of faecal particles was similar in sheep and goats (Figures 1 and 2).

For faecal N, an effect of chop length ($p = 0.002$) was present in E1, but not in E2. No effect of species and no significant interactions were found.

4 | DISCUSSION

Ruminants are known to be the herbivores that chew diets most thoroughly with consistently small faecal particles (Fritz et al., 2009). Still, relevant differences between species can be present. Detailed comparative insights on chewing behaviour are not only interesting from an evolutionary point of view, but also help to evaluate adequateness of fibre supply (Lu et al., 2005) and can represent prerequisites for the development of systems for the evaluation of structure effectiveness of diets (Hoffmann, 1990). This aspect can be regarded as particularly relevant in high-yielding dairy goats due to their high-performance potential, but relatively little is known in this respect (GfE, 2003; NRC, 2007). Besides that, detailed data on the feed comminution process will also contribute to classify a ruminant species regarding its fibre processing potential and in consequence its capacity to make efficient use of high-fibre feeds (AFRC, 1998). The chewing process can also be linked to important aspects of the digestive process of ruminants like mean retention time of digesta in the digestive tract (Zhang et al., 2022).

When characterizing the conditions of our study in general, it should be stated that the fibre levels applied represent the higher end of forages, which is reflected in the long rumination times of 8 h 30 min to 9 h 45 min observed; 9 h is often mentioned as the maximum for dairy cows (Van Soest, 1994), which matches the maximum observed so far across all ruminant species (Lauper et al., 2013). The conditions in the trials can in fact be considered as challenging in terms of forage comminution capacity, although animals only had maintenance requirements and were therefore on a corresponding, rather low intake level (Minson, 1990).

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TABLE 4 Rumination behaviour and trough visits in Experiment 1 (E1) and Experiment 2 (E2).

Item	E1 Sheep SH[1]	E1 Sheep LH[2]	E1 Goats SH	E1 Goats LH	E1 SEM	E1 *p* Value Species	E1 *p* Value Chop length	E1 *p* Value S x CL[3]	E2 Sheep SH	E2 Sheep LH	E2 Goats SH	E2 Goats LH	E2 SEM	E2 *p* Values Species	E2 *p* Values Chop length	E2 *p* Values S x CL[3]
Rumination																
Boli (N/d)	621^{b}	612^{b}	559^{a}	573^{ab}	12.8	0.009	0.876	0.365	600^{b}	604^{b}	483^{a}	544^{ab}	25.8	0.028	0.119	0.165
Duration (s/bolus)	49	48	51	49	1.9	0.464	0.160	0.298	49.1	47.9	53.9	51.9	2.19	0.188	0.068	0.596
Frequency (chews/s)	1.42	1.45	1.24	1.23	0.058	0.050	0.455	0.211	1.40^{b}	1.49^{c}	1.19^{a}	1.26^{b}	0.046	0.014	<0.001	0.421
Chews/bolus	69	70	64	61	9.7	0.535	0.479	0.150	69	71	64	65	3.9	0.354	0.251	0.595
Chews/day	42,677	43,020	34,223	33,520	2760.9	0.048	0.932	0.806	40,860^{b}	42,785^{b}	31,084^{a}	35,497^{ab}	1967.8	0.012	0.035	0.388
Trough visits																
Number/d	15^{a}	16^{a}	35^{b}	32^{b}	3.0	0.003	0.691	0.446	22^{ab}	21^{a}	44^{c}	40^{bc}	4.7	0.016	0.264	0.554
Duration (min/visit)	15.5	14.4	9.1	8.5	1.61	0.061	0.568	0.259	9.0^{a}	11.6^{b}	5.1^{a}	6.4^{ab}	1.53	0.070	0.005	0.279

[1]Short hay (7 mm chop length).
[2]Long hay (35 mm chop length).
[3]Interaction species × chop length.

4.1 | Duration of eating and rumination in sheep and goats

A difference between sheep and goats in daily rumination time and correspondingly in the R:E ratio, formed a central hypothesis of this study. A systematic difference in these traits would indicate some basal deviation in the processes of feed comminution and particle retention in the rumen, relevant for the aspects of feeding outlined above.

The results of E1 indicate the presence of the hypothesized difference in R:E ratio between sheep and goats; however, in this experiment, eating was the (significant) driver of this difference and not rumination, which is in contrast to Dulphy et al. (1995). While in a preliminary study (with four observations for each species) a corresponding difference was found (lower R:E ratio in goats) (Krone et al., 2021), the results of E2 indicate a trend for less rumination in goats ($p = 0.066$) but no difference in the R:E ratio.

While results of the present study give some support to a difference in chewing duration between sheep and goats, the size of this effect was lower than the level suggested, for example, by the data in Dulphy et al. (1995). In our study, rumination time in sheep was only 5% longer than in goats, compared to 23% higher rumination time for sheep in Dulphy et al. (1995) or 17% in Jalali et al. (2012). The R:E ratio was 23% higher in sheep in the present study, compared to 38% in Dulphy et al. (1995). However, another study only found a 7.5% higher value for sheep (Jalali et al. 2012).

4.2 | Detailed observation of rumination chewing

Besides the duration of feed comminution behaviour, further detailed aspects of rumination have been found to differ systematically between sheep and goats in this study. Species had a significant effect on the number of rumination boli/day in both experiments (more in sheep). There was also a clear difference in frequency of rumination chews of about 15% (1.44 chews/s in sheep vs. 1.23 chews/s in goats). While body size can have a substantial influence on such measures and a scaling of the duration of a chewing cycle has been proposed to be $BM^{0.17}$ for artiodactyls (Gerstner & Gerstein, 2008), our measured differences cannot be explained by size. This confirms previously published results indicating a 20% higher rumination chewing frequency in sheep (Domingue et al., 1991b), which is in contrast to older literature suggesting the opposite (Bürger, 1966). An unexpected but rather interesting result is based on combining rumination boli/d and chews/rumination bolus with daily ruminating behaviour (=daily rumination chews). There was an effect of species in E1 and E2 on the daily number of rumination chews; summing up the means of E1 and E2 results in 42,335 ± 994 rumination chews per day in sheep and 33,581 ± 1855 rumination chews/day in goats, indicating a 20% reduced number in goats compared to sheep. This strongly supports the view that rumination is of considerably more relevance in the overall comminution process in sheep than in goats.

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TABLE 5 Faecal particle size and faecal N content in experiment 1 (E1) and experiment 2 (E2).

	E1								E2							
	Sheep		Goats			*p* Value			Sheep		Goats			*p* Value		
	SH[1]	LH[2]	SH	LH	SEM	Species	Chop length	S × CL[3]	SH	LH	SH	LH	SEM	Species	Chop length	S × CL[3]
WAPS[4] (mm)	0.46	0.43	0.48	0.50	0.024	0.126	1.000	0.314	0.45	0.39	0.47	0.48	0.034	0.290	0.162	0.044
Faecal N (g/kg OM)	18.0[a]	19.0[b]	18.1[ab]	18.6[ab]	0.484	0.819	0.002	0.406	19.53	20.01	19.26	19.15	0.545	0.476	0.381	0.174

[1]Short hay (7 mm chop length).

[2]Long hay (35 mm chop length).

[3]Interaction species × chop length.

[4]Weighted average particle size.

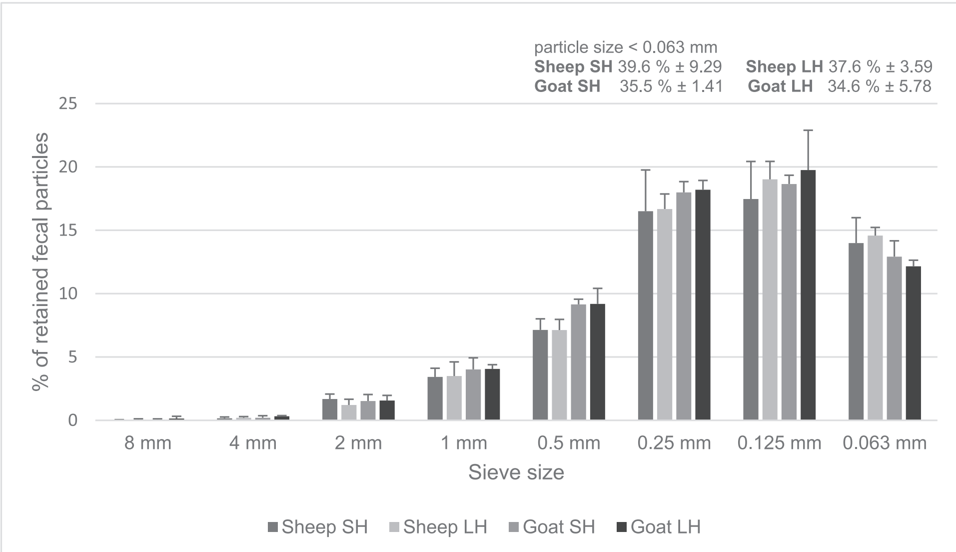

FIGURE 1 Distribution of faecal particles in Experiment 1.

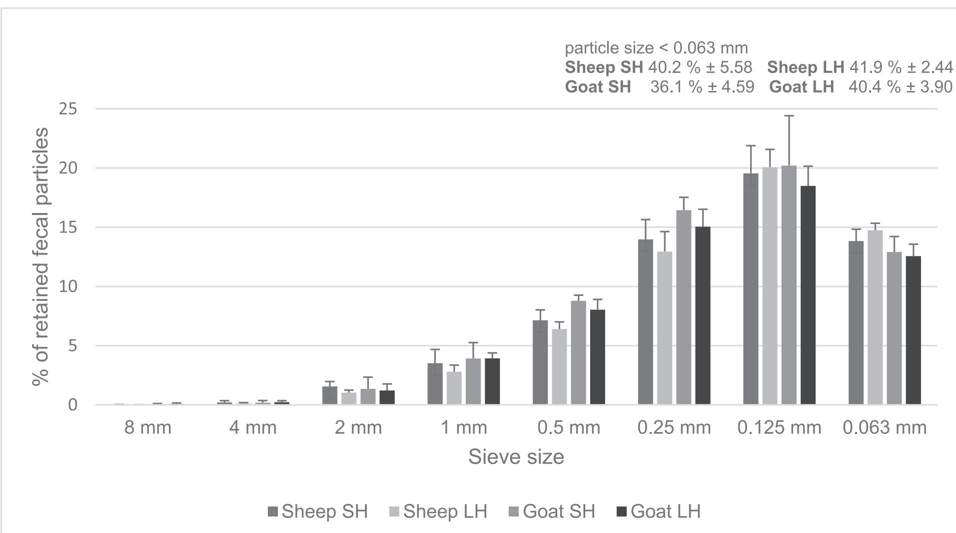

FIGURE 2 Distribution of faecal particles in Experiment 2.

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The question arises to what extent this variation in chewing behaviour influences feed particle disintegration as the major purpose of the overall feed comminution process. Because only limited feed particle disintegration is expected to happen beyond the oral cavity (after the processes of chewing during eating and ruminating) (McLeod & Minson, 1988), faecal particle size can be interpreted to represent mainly the result of chewing activity. Obviously, some interaction with the ruminal particle retention mechanism occurs, which has the potential to expose particles to a variable number of rumination cycles. In the present study, no difference in faecal particle size between the species was obvious, which is in line with comparable total mastication times of sheep and goats. This supports results of other studies (Uden & Van Soest, 1982) reporting an average faecal particle size of 0.46 mm for both sheep and goats, a value almost identical to those measured in the present study. So despite some variation in behaviour, the output of the system was identical in sheep and goats in terms of particle disintegration.

4.3 | Indications of goats as particularly good fibre processors

Overall, the observed intake levels were as expected for animals with maintenance requirements only (Minson, 1990). The absence of differences in faecal N levels contradicts significant differences in OM digestibility for sheep and goats. The faecal N concentrations measured would relate to a OM-digestibility of 56%–57% for hay 1 and of 58% for hay 2, based on a regression established for sheep [OM dig = 0.899 – 0.644 × exp(−0.5774 × faecal CP (g/kg OM)/100] by Wang et al. (2009). Calculating the maintenance energy requirements after established equations (GfE, 2003; Kirchgeßner, 1996), the animals met their requirements in E1 and ingested approximately 1.3× maintenance in E2.

While mostly considered to be particularly selective in feed intake, goats have also been reported to be especially capable of processing high-fibre forages (Riaz et al., 2014). Dulphy et al. (1995) report observations on the consumption of different forages in relation to consumption of grass hay; when shifting to straw, consumption was higher in goats compared to sheep (while the opposite was true for grass silages). While this was not the focus of the present study, two observations deserve to be mentioned. Goats in this study seemed to reduce their intake less than sheep on the hay with the higher fibre content; in sheep, intake of the hay with the higher fibre content was 84 ± 9.7% of that with the lower ADFom content, while it was still 96 ± 15% in goats. This difference between the species tended towards significance ($p = 0.076$; two-sided t test).

Furthermore, an unexpected observation was the distinct preference (higher intake) for the hay with the long chop length in goats. No such preference was evident in the sheep, while it was observed in both experiments for all goats. It has been described that the respiratory tract of goats is particularly sensible concerning finer particles (Ouédraogo et al., 1996), which may explain a negative correlation of intake to chopping length. Another report indicated species differences in preferences for forage particle sizes (Hadjigeorgiou et al., 2003); however, in that study the effect was rather due to the preference of sheep for the shorter chop length hay. The present study fits into a picture of goats as slightly superior fibre processors compared to sheep (AFRC, 1998; Domingue et al., 1991b; Rapetti et al., 2008), as indicated by a lower reduction in feed intake at higher fibre levels and a greater intake on longer forages.

4.4 | Feeding patterns and chewing differences

In both experiments, the frequency of the feeding trough visits was much higher in goats (37.8 vs. 18.4 visits/d by sheep) and it is tempting to relate this to the differences in feeding pattern as proposed for ruminant feeding types (Hofmann, 1989; Hummel et al., 2006). While these differences may be influenced by particularities of the stable, or even interactions between species and stable type, such a feeding pattern could result in a more even rumen fermentation process across the day, due to more and smaller feed units arriving in the fermentation chamber. This can be considered a relevant trait if animals are kept on a high-energy diet, like dairy goats. In fact, goats have been described to be less prone to ruminal acidosis than the average ruminant (Avondo et al., 2008; Mgasa & Mbassa, 1988; Mgasa & Arnbjerg, 1993; Rapetti et al., 2008). The relevance of frequent feeding bouts is emphasized by the observation that goats turn to more frequent, smaller meals when being fed on a diet prone to induce acidosis (Abijaoudé et al., 2000). In comparison to dairy sheep, a less direct positive correlation of dietary fibre content and milk fat (as a potential indicator of rumen stability) has been described for dairy goats (Bellof & Leberl, 2019).

4.5 | Advantage of more rumination chewing on a grass diet

The present study gives several indications for a more significant role of rumination in sheep than in goats. This is based on data of the activity budget (eating, ruminating), but is even more prominent when looking at the extrapolations on daily number of rumination chewing strokes (approximately 20% less in goats compared to sheep, as estimated above). Such distinct differences on the same diet may well indicate species-specific evolutionary adaptations, possibly to the respective natural diets (grass in sheep, browse in goats). In fact, a hypothesis linked to abrasiveness contamination of natural diet matches well with the observed pattern. Besides other, well-described advantages, the ruminant forestomach physiology also represents a mechanism that washes off dust, sand or grit from the ingested feed prior to rumination (Hatt, et al., 2019; Valerio et al., 2022). Free-ranging ruminants have been reported to ingest significant levels of soil inadvertently with their diet (Beyer et al., 1994; Fannin et al., 2022; Hummel et al., 2011; Madden, 2014;

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Sanson et al., 2017). Shifting the majority of mastication to that phase where these external abrasives have been removed from the feed will distinctively protect dental tissue from wear, and may therefore represent an important adaptation. Under the assumption that plants consumed farther away from the ground will be less contaminated with such external abrasives, a less pronounced focus on rumination chewing in browsing ruminants as compared to grazing ruminants, as determined in goats and sheep in the present study, appears understandable. In line with this concept, the only existing comparative evaluation across ruminant species found a significant, positive relationship between the percentage of grass in the natural diet and the observed minimum proportion of time spent ruminating (Lauper et al., 2013). Further comparative evaluations of feeding and rumination times in different species would be welcome. Due to the overruling effect of dietary fibre levels on rumination behaviour (Lauper et al., 2013), such comparisons might be particularly insightful when performed under controlled conditions on an easily accessible common forage (e.g., lucerne hay) across the species.

5 | SUMMARY AND CONCLUSION

In the present study, some relevant differences in feed comminution behaviour between sheep and goats were present. Results point to a difference in terms of duration of rumination and in terms of the ratio of the duration of rumination and eating (sheep > goats); although these differences were of a lesser magnitude than hypothesized based on literature, a further difference was present in terms of daily rumination chews (sheep > goats). This can be interpreted as rumination playing a somewhat more important role in sheep than in goats. A feeding habit resulting in a diet containing less internal and external abrasives might be linked to less relevance of rumination in the overall chewing and comminution process. For systems evaluating structure effectiveness of fibre, sheep and goats will have to be considered separately.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data of the manuscript will be available for interested persons on request.

ANIMAL WELFARE STATEMENT

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to and the appropriate ethical review committee approval has been received. The authors confirm that they have followed EU standards for the protection of animals used for scientific purposes.

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