

Reticular contraction frequency and ruminal gas dome development in goats do not differ between grass and browse diets

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Abstract

In investigations of differences between ruminant species feeding on browse or grass, it is often unclear whether observed differences are animal- or forage-specific. Ruminant species have been classified as ‘moose-type’, with little rumen content stratification, or ‘cattle-type’ with a distinct rumen contents stratification, including a gas layer. To which extent putative differences in forestomach motility are involved in these patterns is unknown. Using sonography, we investigated the frequency of reticular contractions and the stratification of rumen contents in goats fed exclusively on grass hay ($n = 6$) or dried browse ($n = 5$) directly after feeding, and after another 6 and 12 h with no access to feed. The frequency of reticular contractions decreased from immediately after feeding ($1.8 \pm 0.3 \text{ min}^{-1}$) to 6 h afterwards ($1.2 \pm 0.2 \text{ min}^{-1}$) and then remained constant, with no difference between diets. A gas dome became more visible over time, but neither its incidence nor its extent differed between diets. The results are in accord with classifying goats as ‘cattle-type’ in terms of their digestive physiology, and they add to a growing body of evidence that differences in digestive physiology between ruminant species are more due to species characteristics than different kinds of ingested forages.

KEYWORDS

browser, *capra hircus*, digestive physiology, grazer, motility, stratification

1 | INTRODUCTION

Ruminants have for a long time been classified based on their natural diet as browsers, intermediate feeders or grazers (Hofmann & Stewart, 1972; van Zyl, 1965). A large variety of anatomical and physiological characteristics have been linked to this diet classification (Codron et al., 2019; Hofmann, 1989). Some characteristics can be considered species-specific and independent of the actual diet ingested by the individual that is measured, for example the shape

of the muzzle or the hypsodonty of the teeth (Janis, 1988; Janis & Ehrhardt, 1988). For other characteristics, the diet that the specific specimens under investigation consumed prior to measurement may be more relevant, for example for measures of tooth wear (Clauss et al., 2007) or the papillation of the rumen (Hofmann & Nygren, 1992). Hence, evaluating which measures are independent of the actual diet consumed and hence completely species-specific, and which measures are a consequence of the actual diet is a question important for comparative ruminant digestive anatomy and physiology.

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One key measure in which ruminants differ is the degree to which their stomach contents are stratified. The rumen contents of domestic ruminants are typically stratified, with a large fibre mat on top of a more liquid layer with a sludge-type sediment at the bottom, and with a gas dome above the fibre mat (reviewed in Hummel et al., 2009). Hofmann (1973, 1989) noted that this stratification is absent in non-domestic species that feed mainly on browse. In subsequent investigations, the fact that ruminants differ with respect to rumen contents stratification was confirmed using a variety of proxies. These included the moisture and particle size gradient in rumen contents as well as the viscosity of rumen fluid (Clauss, Fritz, Bayer, Hummel, et al., 2009; Clauss, Fritz, Bayer, Nygren, et al., 2009; Codron & Clauss, 2010; Hertaeg et al., 2021; Lechner et al., 2010; Sauer et al., 2017), the gradient of the intraruminal papillation pattern (Clauss et al., 2009), and differences in the pH in different rumen locations (Ritz et al., 2013). Additionally, sonography proved to be a useful tool to demonstrate the presence or absence of a gas dome in the rumen (Braun et al., 2011, 2012, 2013; Imran et al., 2011), which was absent in a single browsing ruminant (a moose, *Alces alces*) (Tschuor & Clauss, 2008).

When providing hypothetical explanations for this difference, the focus was initially on physical and biochemical differences of the forages (Clauss et al., 2003; Hummel et al., 2006). Differences in forestomach physiology between grazing and browsing ruminants were interpreted as adaptations to reinforce the tendency of the natural diet to induce a stratification. But evidence accumulated for species-specific differences that persist even when different forages are fed (Lechner et al., 2010; Przybyło et al., 2019; Renecker & Hudson, 1990). Therefore, the difference in rumen contents stratification was summarized in a concept of classifying ruminants in terms of their forestomach physiology as 'cattle-type' (with a high fluid throughput and stratified contents including, amongst other strata, a gas dome, and natural diets consisting predominantly of grass or a grass/browse mix), and as 'moose-type' (with a low fluid throughput and homogenous, unstratified contents without a gas dome, and a natural diet constrained to very high proportions of browse) (Clauss et al., 2010). To date, no larger data collection on rumen motility of non-domestic species exists to link motility to this concept. The only comparative study we are aware of is one series of investigations (Dziuk, 1965; Dziuk et al., 1963; Dziuk & McCauley, 1965) that covered several cattle-type ruminants (domestics and the American bison, *Bison bison*) and a moose-type ruminant (the white-tailed deer, *Odocoileus virginianus*) and did not suggest a difference between the species. Theoretically, one might nevertheless assume that contents that are more homogenous and without a gas dome, as found on browse-only diets in moose-type ruminants, are produced by more frequent reticuloruminal contractions that maintain a thoroughly mixed, unstratified state.

The question to which degree a natural diet influences forestomach physiology is still not conclusively answered. Observations that grass-based diets induce a more pronounced 'filter-bed effect' in the rumen than browse-based diets (Clauss et al., 2011; Lauper et al., 2013) lead to the conclusion that within a ruminant species, grass tends to induce a higher degree of rumen contents stratification

than browse, without over-writing general species-specific differences. In order to further investigate whether grass or browse itself determines rumen contents stratification and forestomach motility, we used the opportunity of a feeding experiment in domestic goats fed either grass or browse (Braun et al., 2011; Clauss et al., 2017; Codron et al., 2012). Given a distinct difference between fluid and particle retention in the reticulorumen (Lechner-Doll et al., 1990), an inhomogenous intraruminal papillation pattern (Clauss, Hofmann, et al., 2009) as well as the general presence of a dorsal gas dome in live animals (Braun, Jacquat, et al., 2011), goats are classified as 'cattle-type' ruminants of an intermediate feeding type. We performed this study to test whether the reticular contractions and the presence and extent of the gas dome differed between goats fed on grass hay and on dried browse leaves. Our rationale was that if there would be a difference between the groups, this would indicate a fundamental difference between the forage types in terms of inducing motility and a gas dome, whereas no difference would support the view that differences in stratification observed across species in the literature are rather due to species-specific characteristics.

2 | MATERIAL AND METHODS

2.1 | Animals, diets and experimental design

This experiment was part of a study on the abdominal anatomy (Braun, Irmer, Augsburg, Jud, et al., 2011; Braun, Irmer, Augsburg, Müller, et al., 2011; Braun et al., 2011) and digestive physiology of goats (Clauss et al., 2017; Codron et al., 2012; Zeitz et al., 2016) and performed under animal experiment licence Zurich 69/2008 of the cantonal veterinary office. Eleven female adult non-lactating Saanen goats were kept in groups in indoor enclosures (app. 5 x 5 metres) on woodchips and fed exclusively on either whole (non-chopped) grass hay (n = 6) or whole dried browse leaves (n = 5) (aspen—*Populus tremula*, raspberry—*Rubus idaeus* and sweet chestnut—*Castanea sativa* leaves 1:1:1 as fed, Alfred Galke GmbH, Gittelde, Germany) for at least 20 days (maximum 30 days). While there is no direct evidence that the animals did not consume woodchips, they were never observed to do so, and when they were slaughtered at the end of the study and their gastrointestinal contents inspected (Clauss et al., 2017), no woodchips were detected visually. The animals did not receive any additional feeds or supplements during the trial period. Feed intake was not quantified. Feed was offered for *ad libitum* consumption, so that there were always relevant amounts left over at the next feeding, by spreading the forage along the sides of the enclosure to ensure all animals had equal access to it. New feed was offered twice daily. The chemical composition of the diets is shown in Table 1. Water was available at all times. In the third week of the experiment, 6 of the animals fed grass hay and 5 animals fed browse leaves were investigated by ultrasound directly after the morning feeding, and then, the leftovers were removed and the animals were kept without access to feed and again investigated at 6 and 12 h after the initial feeding.

TABLE 1 Nutrient composition of the diets fed to the experimental goats (from Zeitz et al., 2016)

	Dry matter ¹	Organic matter ¹	Crude protein ²	NDF ³	ADF ³	ADL ³	Gross energy ⁴
	% as fed	% Dry matter					MJ/kg DM
Grass hay	91.7	94.7	7.5	57.3	36.9	3.3	18.7
Aspen	92.1	94.0	12.5	35.4	25.4	7.2	20.5
Raspberry	90.9	90.7	18.1	34.3	20.8	5.1	18.8
Chestnut	91.6	95.5	11.3	41.3	23.0	4.1	19.6
Browse average	91.5	92.8	13.8	37.0	23.1	5.5	19.7

Note: Analyses following AOAC (1995); specifically: ¹AOAC no. 942.05, ²AOAC no. 977.02, ³NDF neutral detergent fibre (AOAC no. 2002.04), ADF acid detergent fibre and ADL acid detergent lignin (AOAC no. 973.18); detergent fibre values without residual ash; ⁴bomb calorimetry (C7000 IKA-Werke GmbH, Staufen, Germany)

2.2 | Ultrasound examination

Ultrasonographic examinations were performed as described by Braun and Jacquat (2011) and Braun, Jacquat, et al. (2011) on standing, non-sedated animals using a 5–13 MHz linear transducer with a penetration depth of approximately 3–10 cm. Skin regions for ultrasonography were clipped, and contact gel was used. Reticular motility was recorded at the left sternal region; after identifying the reticulum, contractions were counted during a 3-min period without differentiating between monophasic and biphasic contractions (we note, however, that it appeared that most contractions were biphasic). Rumen contents stratification was assessed in the left flank caudal to the last rib. The gas dome was identified by the typical reverberation lines (artefacts) and was classified as either absent (0), moderate if only a small area could be detected (1) or distinct (2). Its distance to the dorsal midline of the animal was measured using a soft measuring tape during the measurement 12 h after feeding. Because the border between the fibre mat and the fluid layer was difficult to detect, this measure was ultimately discarded.

2.3 | Statistical analysis

We tested the hypotheses that time since feeding (0, 6 and 12 h) and diet regime (grass or browse) influence the rate of ruminal contractions and development of a dorsal gas dome. Effects on ruminal contraction rate were tested using a Repeated Measures ANOVA (RM ANOVA) to ensure appropriate error terms were compared with each effect, with time since feeding as the within-subjects factor, and diet as the between-subjects factor. Depth of the gas dome produced by each individual was only measured 12 h after feeding, thus we only tested for the effect of diet (one-way ANOVA). Multiple comparisons were carried out using Tukey's post hoc test. In all cases, studentized residuals were normally distributed (Kolmogorov–Smirnov test, p ranged from 0.100 to 0.722) and had equal variances (Levene's test $p = 0.999$). However, because sample

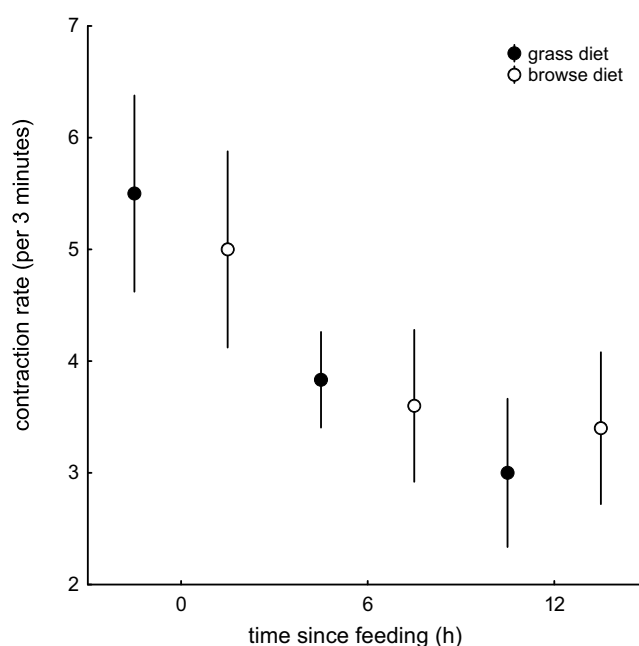


FIGURE 1 Reticular contraction rates decreased with time since feeding (RM ANOVA $p < 0.001$), levelling off between 6 and 12 h since feeding ($p = 0.215$), for animals on both the grass (black circles) and browse (white circles) diets. Symbols are means and error bars are 95% confidence intervals. RM ANOVA revealed a significant effect of time since feeding ($p < 0.001$) but not of diet ($p = 0.389$)

sizes were small ($n = 11$ individuals), we explored non-parametric alternatives to hypothesis testing, for the former using Friedman's ANOVA with Kendall's concordance for comparison of multiple dependent groups, and for the latter the Mann–Whitney U test for comparison of independent groups. Results of the non-parametric tests did not differ qualitatively from those of the parametric tests, which increases confidence that arising trends were not biased due to the small sample size; thus, we only reported results of the parametric analyses for effects on ruminal contraction rate and depth of the gas dome.

Count data describing the propensity of animals to develop a gas dome was analysed using Pearson's chi-square. Categories included in the count data were 0 (no gas dome detected), 1 (a moderate gas dome) and 2 (a distinct gas dome). Two contingency tables were used, the first dividing groups according to time since feeding, the other according to diet. To ensure that interpretations were not biased by small sample size, we based the significance tests on 2-tailed *p* values derived from 10,000 Monte Carlo simulations and reported the associated 95% confidence intervals (CI). Statistical tests were performed using the GLM module of STATISTICA 8.0 (Statsoft_Inc, 2007).

3 | RESULTS

Results showed a decrease in reticular contraction rate (number of contractions per 3 min time interval) over time since feeding (Figure 1). RM ANOVA confirmed a significant effect of time on contraction rate ($F_{2,18} = 23.198$; $p < 0.0001$); however, the change only occurred between 0 and 6 h after feeding (means = 5.3 ± 0.8 SD., $n = 11$, and 3.7 ± 0.5 , $n = 11$, respectively; $p < 0.001$), whereas there was no significant change between 6 and 12 h (3.2 ± 0.6 , $n = 11$) after feeding ($p = 0.215$). Contraction rates were similar for both diets (4.1 ± 0.6 , $n = 6$, and 4.1 ± 1.2 , $n = 5$, for grass and browse diets, respectively; $F_{1,9} = 0.818$; $p = 0.389$), and diet regime had no influence on the time-dependent decrease in contraction rate (time since feeding x diet interaction $F_{2,18} = 1.090$; $p = 0.357$).

Gas domes were detected as described in the literature by the abrupt cessation of reverberation lines indicating a gas-filled structure (Figure 2). The propensity for individuals to develop a gas dome increased with time since feeding. Immediately after feeding, gas was only present in two individuals on the grass diet and was absent from all individuals on browse (Figure 3). By 6 h after feeding, five individuals on grass and three on browse had moderate amounts

of gas, and one individual on the grass diet had formed a distinct gas dome. Twelve hours after feeding, five of the six individuals on the grass diet had a distinct gas dome, as well as four individuals on browse. The increased frequency of gas dome detection with time since feeding is significant ($X^2 = 28.800$; $df = 2$; $p < 0.0001$ (95% CI: <0.0001 – 0.001)), whereas this propensity is not different across grass and browse diets ($X^2 = 2.440$; $df = 2$; $p = 0.311$ (95% CI: 0.299 – 0.323)). The depth of the gas dome that had developed by 12 h after feeding also did not differ across the diets (15.8 ± 8.3 cm, $n = 6$, and 13.7 ± 6.9 cm, $n = 5$, for grass and browse diets, respectively; one-way ANOVA $F_{1,9} = 0.191$; $p = 0.6721$), even excluding the two individuals that had not produced gas by this time ($F_{1,7} = 1.135$; $p = 0.322$).

4 | DISCUSSION

The results indicate no effect of the diet, dried grass or dried browse, on forestomach motility or rumen content stratification in live goats. They thus support the post-mortem findings in the same animals at the end of the experiment that also did not indicate a difference in stratification as measured by the dry matter concentration in content of different forestomach regions (Clauss et al., 2017), and the general observation of a gradient of the intraruminal papillation in goats with a dorsal area of no or very reduced papillae (Schnorr & Vollmerhaus, 1967).

Several limitations apply to the present study. In contrast to previous ultrasonographic investigations of goats and other ruminants (Braun, Jacquat, et al., 2011; Tschuor & Clauss, 2008), the fibre mat and the underlying fluid layer could not be differentiated with certainty, making it impossible to assess this aspect of rumen contents stratification. Similar difficulties have been described in other sonographic studies (some animals in Braun et al., 2012, 2013; Braun,

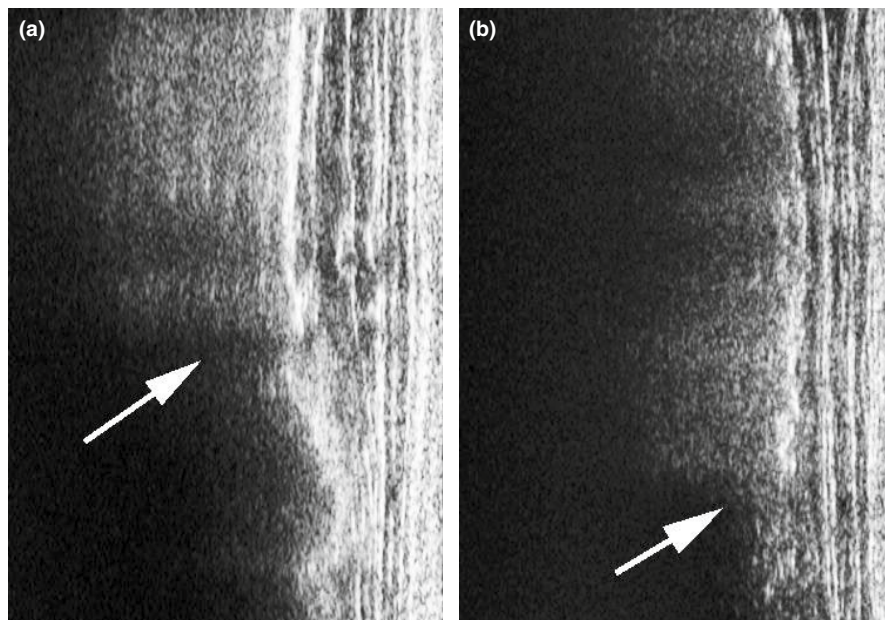


FIGURE 2 Examples of reverberation line artefacts on ultrasonographic pictures indicating a gas-filled structure; the cessation of the reverberation lines indicates the transition from gas to solid contents in the rumen. (a) a goat fed grass hay 6 h after feeding; (b) a goat fed on dried browse 12 h after feeding

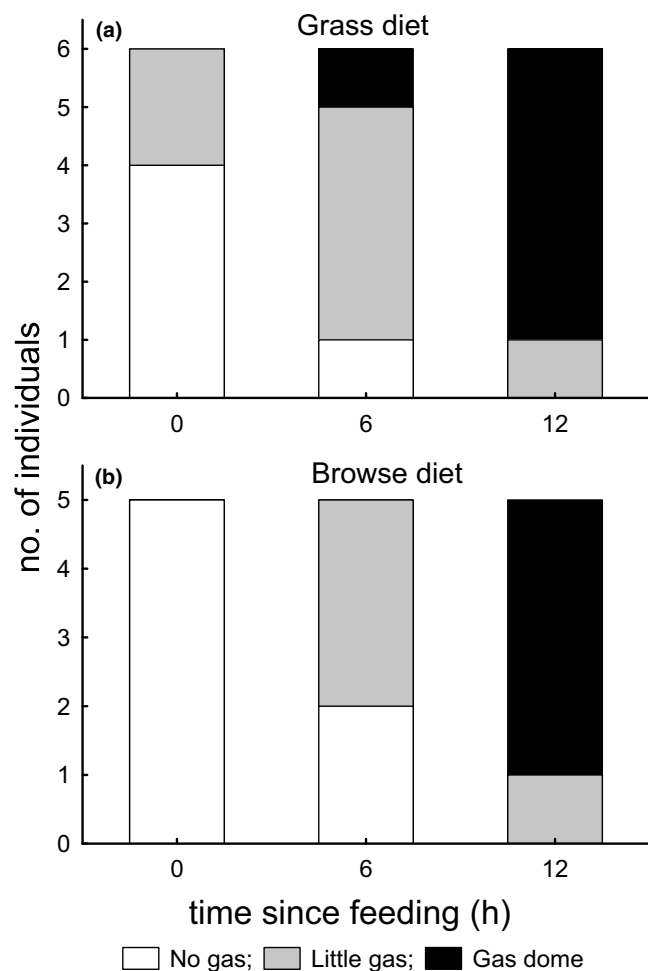


FIGURE 3 Propensity for gas dome detection in the dorsal rumen increased with time since feeding (chi-squared test $p < 0.001$) in goats fed grass (a) and browse (b), but was not different between these diet regimes ($p = 0.311$)

Jacquat, et al., 2011). Due to the husbandry system, it was not possible to feed the goats individually and relate differences in the occurrence and dimension of the gas dome to the individual animal's food intake. Several reports suggest that in ruminants that generally accept browse, such as moose, giraffe (*Giraffa camelopardalis*) or goats, food intake may be higher on a diet actually containing browse (Clauss et al., 2013; Hatt et al., 2005; Okoruwa & Ikhimioya, 2020; Teague, 1989). As this likely would lead to a higher rumen fill with less space for a gas dome, the (non-significant) difference between the grass and browse diet of our study considering the presence of a gas dome at 6 h after feeding (Figure 3) might have resulted of a higher rumen fill on the browse diet.

In ruminants, forestomach contractions are more frequent during than after feeding (Braun et al., 2012; Ulyatt et al., 1984; Waghorn & Reid, 1983), a pattern also found in the goats of the present study. A parsimonious explanation is that the distension of the reticulorumen by intake increases the contraction frequency; this is corroborated when comparing the total number of reticular contractions in the same animals at different dry matter intake (Malbert & Baumont,

1989). Differences in forestomach contraction frequency between diets were found for cattle fed whole or finely ground forage (Colvin & Daniels, 1965). However, this result was not repeated in a similar experiment with sheep (Pharr et al., 1967). In a comparison of grass hay and lucerne hay fed to sheep, Malbert and Baumont (1989) recorded a higher frequency of reticular contractions on the lucerne hay, which was also ingested in a larger amount; there was no difference between when the animals' intake of lucerne was restricted to the intake level of the grass hay. Given that the grass and browse diet were both comprised of whole forages, it appears plausible that even if physical differences between grass and browse have been suggested (Cornelissen & Thompson, 1997; Sanson, 2006), their overall consistency was not sufficiently different to cause different reticular contraction rates.

Differences in the physical fractionation pattern between grass and browse have been described repeatedly (Hummel et al., 2020), and these differences have been linked hypothetically to a higher propensity of grass ingesta to stratify (Clauss et al., 2003). However, in vitro stratification assays did not show a difference between rumen content of browsing or grazing ruminants (Clauss, Fritz, Bayer, Nygren, et al., 2009), which shifts the main responsibility for the consistency of the rumen contents to the ruminant species and not the kind of forage ingested. The results of the present study support this concept, as do results from retention time studies in various ruminant species that indicate that species-specific properties are more important for digesta kinetics than the nature of different forages ingested by the animals (Dittmann, Hummel, et al., 2015; Lechner et al., 2010; Przybyło et al., 2019; Renecker & Hudson, 1990). This conclusion is based on the comparison of different forages and does not contradict the finding that diets containing relevant amounts of non-forage components can significantly alter the stratification of the rumen contents (Tahas et al., 2017; Zebeli et al., 2007).

The fact that the stratification of rumen contents changed over time has been previously described in cattle, with the main difference between the time of feed intake and later measurements (Hummel et al., 2009). During feed intake, the stratification is least pronounced. Later, the decrease in rumen fill, with the concomitant reduction of the fibre mat (Kovács et al., 1997; Welch, 1982) due to the outflow of digested particles, allows for a larger space for the gas dome in 'cattle-type' ruminants, as in the goats of the present study. It should be noted that under conditions of free feed intake, as in free-ranging animals or animals kept at pasture, a fasting period of 12 h is unlikely to occur. Therefore, the distension of the gas dome in the goats at this time point probably overestimates the condition in a natural feeding situation.

In conclusion, the observations on reticular motility and rumen contents stratification of the present study support the concept that for ruminant species consuming different forages, differences in stratification are more likely to be the result of species-specific factors relating to rumen fluid viscosity than to forage-specific properties. The forestomach motility of different ruminant species remains to be compared comprehensively. Yet, the current evidence does not suggest fundamental differences between individual species (Dziuk,

1965; Dziuk et al., 1963; Dziuk & McCauley, 1965), and neither do comparisons of the particle sorting mechanism (Dittmann, Runge, et al., 2015) or the rumination frequency (Lauper et al., 2013) between species. Comparisons on different forages, including those of the present study, do not suggest that they should require different motility patterns.

ACKNOWLEDGEMENTS

We thank Prof. Dr. Dr. hc Ueli Braun, director emeritus of the Clinic for Ruminants of the Vetsuisse Faculty Zurich, for his support of this study. Open access funding provided by Universitat Zurich.

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.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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How to cite this article: Clauss, M., Tschuor, A., Codron, D., & Hummel, J. (2022). Reticular contraction frequency and ruminal gas dome development in goats do not differ between grass and browse diets. *Journal of Animal Physiology and Animal Nutrition*, 106, 1208–1215. <https://doi.org/10.1111/jpn.13663>