

## Body weight and sex effects on digesta mean retention time in growing Saanen goats

Marcelo Gindri,<sup>†,\*</sup> Rafael Fernandes Leite,<sup>†</sup> Carla Joice Härter,<sup>†</sup> Simone Pedro da Silva<sup>†</sup>, Normand St-Pierre,<sup>‡</sup> Márcia Helena Machado da Rocha Fernandes,<sup>†</sup> Telma Teresinha Berchielli,<sup>†</sup> and Izabelle Auxiliadora Molina de Almeida Teixeira<sup>†,1</sup>

<sup>†</sup>Department of Animal Sciences, Universidade Estadual Paulista, Jaboticabal, SP 14884-900, Brazil; <sup>‡</sup>Perdue AgriBusiness LLC, Salisbury, MD 21804

**ABSTRACT:** Despite the important role of digesta mean retention time (MRT) on digestive efficiency of ruminants, it is poorly investigated in total gastrointestinal tract (GIT) of growing ruminants, especially in goats. The objective of this study was to evaluate the effect of body weight (BW) and sex on GIT MRT of particles and solutes in growing Saanen goats. A dataset from two studies, comprising 103 individual records of castrated males ( $n = 36$ ), females ( $n = 34$ ), and intact males ( $n = 33$ ) Saanen goats slaughtered at 15, 22, 30, 37, and 45 kg BW, was used. Goats were fed basically with total mixed ration composed by dehydrated corn plant (*Zea mays*) milled to pass a 10-mm screen, cracked corn grain, and soybean (Glycine max) meal. Variables evaluated were BW, feed intake, feed intake level, composition of ingested diet, wet weight of GIT tissues, wet digesta pool size, digesta composition (dry matter and neutral detergent fiber [NDF]), indigestible NDF:NDF ratio of ingested diet and GIT digesta, MRT of particles ( $MRT_{iNDF}$ ) and solutes ( $MRT_{Cr}$ ), and reticulorumen selectivity factors (large particles/solutes). Reticulorumen, omasum, abomasum, small intestine, cecum, and colon–rectum segments were

evaluated. The dataset was analyzed as mixed models considering sex, BW, and sex  $\times$  BW interaction as fixed effects, and study and residual error as random effects. Sex did not affect  $MRT_{iNDF}$  in any GIT segments. Females and intact males presented similar reticulorumen  $MRT_{Cr}$  (5.6 h;  $P = 0.92$ ) and they presented lower reticulorumen  $MRT_{Cr}$  than castrated males (7.0;  $P \leq 0.04$ ). Total GIT  $MRT_{Cr}$  was similar between castrated males and females (15.7 h;  $P = 0.11$ ) and between females and intact males (14.2 h;  $P = 0.76$ ). Body weight (BW) did not affect  $MRT_{iNDF}$  in reticulorumen and colon–rectum and total GIT  $MRT_{Cr}$  ( $P \geq 0.11$ ). Reticulorumen and omasum  $MRT_{Cr}$  increased as BW increased ( $P < 0.01$ ), and abomasum  $MRT_{Cr}$  decreased as BW increased ( $P = 0.02$ ). Feed intake, and wet tissues and wet pool size of all GIT segments increased as BW increased, except abomasum wet pool size ( $P \leq 0.01$ ). The mechanism related to sex effect on MRT has to be elucidated. Reticulorumen  $MRT_{iNDF}$  and total GIT  $MRT_{Cr}$  were modulated by intake and capacity of reticulorumen and GIT, respectively. On the other hand, reticulorumen  $MRT_{Cr}$  seemed to be regulated by reticulo-omasal orifice opening and saliva secretion.

**Key words:** dairy goat, digesta kinetic, digesta washing, gastrointestinal tract fill, sorting mechanism

© The Author(s) 2020. Published by Oxford University Press on behalf of the American Society of Animal Science.

This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<http://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact [journals.permissions@oup.com](mailto:journals.permissions@oup.com)

Transl. Anim. Sci. 2020.4:883–900  
doi: 10.1093/tas/txaa028

<sup>1</sup>Corresponding author: [izabelle.teixeira@unesp.br](mailto:izabelle.teixeira@unesp.br)

Received October 29, 2019.

Accepted March 11, 2020.

## INTRODUCTION

Digesta mean retention time (MRT) is an important factor on digestive efficiency (Okine et al., 1998) because it is related to digestibility of plant cell wall (Allen and Mertens, 1988), rate and extent of protein digestion (Ørskov and McDonald, 1979), amount of protein which escapes from degradation in the reticulorumen (Fox et al., 2004), efficiency of microbial growth (Harrison and McAllan, 1980; Evans, 1981), and extent of methane losses (Okine et al., 1998). In this sense, MRT has an important role in compartmental models of feeding systems to predict the ruminal digestibility of carbohydrate and protein fractions (Cannas et al., 2004; Fox et al., 2004).

Studies carried out in the past reported relationship between BW and MRT in herbivores (Demment, 1983; Robbins, 1983; Gordon and Illius, 1994). These studies justified this relationship because the gastrointestinal tract (GIT) capacity in herbivores increases in the same proportion of BW ( $BW^{1.0}$ ) (Demment and Van Soest, 1985; Illius and Gordon, 1992), whereas the energy requirements/feed intake increases in the range of  $BW^{0.75}$  (Kleiber, 1932; Bourlière, 1975; Blaxter et al., 1982). However, currently, the relationship between BW and MRT is considered a controversial subject. Previous studies with several species of herbivores did not find a significant relationship between MRT and BW for browsing and grazing ruminants (Clauss et al., 2007b; Steuer et al., 2011). On the other hand, recent studies also studying several species of herbivores, reported that the relationship between MRT and BW was confirmed for ruminants (Müller et al., 2013; Dittmann et al., 2015). Importantly, few studies in the literature have evaluated this relationship accounting for possible sex effects on MRT in ruminants.

Sex and BW are accounted into the species-specific physiological responses of MRT because they are related to ingested feed, feed intake, GIT capacity, and feed digestibility (Gross et al., 1995b). Feed intake and ingested feed are considered the driving force of MRT, and both are dependent on energy requirements (Clauss et al., 2007b; Meyer et al., 2010; Souza et al., 2017; Müller et al., 2013). In addition, recent meta-analytical studies with growing Saanen goats have shown sex and BW effects on net energy requirements for maintenance and growth (Souza et al., 2017; Souza et al., 2020). Therefore, considering a possible BW and sex effect on MRT, and the lack of studies with Saanen goats, the aim of this study was to evaluate the effects of

BW and sex on MRT of particles and solutes in Saanen goats throughout the growing phase.

## MATERIALS AND METHODS

### Dataset

A dataset including 103 individual records of castrated males ( $n = 36$ ), females ( $n = 34$ ), and intact males ( $n = 33$ ) Saanen goats from 15 to 45 kg BW was analyzed. This dataset was combined from two studies in which goats were slaughtered at 15, 22, and 30 kg BW (Leite et al., 2015a, 2015b) and at 30, 37, and 45 kg BW (Silva, 2013). Males were castrated when they were around 1 and 5 months old for Leite et al. (2015a, 2015b), and Silva (2013) studies, respectively. Goats were weaned when they were around 2 months old and 12 kg BW, for all studies (Silva, 2013; Leite et al., 2015a, 2015b). And the experiments started when goats were  $3.2 \pm 0.67$  and  $10.2 \pm 1.76$  months old for Leite et al. (2015a, 2015b), and Silva (2013) studies, respectively. All procedures used across studies were reviewed by the University's Animal Care Committee (Comissão de Ética e Bem-Estar Animal, CEBEA; Universidade Estadual Paulista, Jaboticabal, Brazil).

### Experimental Procedures and Calculations

All goats were housed in individual 0.5 m<sup>2</sup> pens with free access to water. Goats were fed with similar diets ad libitum for all experiments (Table 1) and the diets were formulated to meet the daily requirements of goat kids. The whole diet was milled to pass a 10-mm screen (Figure 1). The daily feed intake was calculated by subtracting orts from the offered diet during the whole experiments (139 d), but only the feed intake in the last 5 d before slaughter was used to calculate the MRT and, therefore, only these data are presented. During the same experimental period (i.e., last 5 days) Cr-EDTA was administered to determine the MRT of solutes. In the offered diet and orts, the dry matter (DM), organic matter (OM), neutral detergent fiber (NDF), and indigestible NDF (iNDF) concentration were determined, and posteriorly intake of DM (DMI), OM (OMI), NDF (NDFI), iNDF (iNDFI), potentially degradable NDF (pdNDFI) were calculated. In addition, we calculated the feeding level as multiples of metabolizable energy (ME) requirements for maintenance intake (L), using ME requirements for maintenance of growing Saanen goats (Souza et al., 2020). The ME in the diet was estimated when goats were around 22 and 37 kg BW for

**Table 1.** Ingredients and chemical composition of the experimental diets

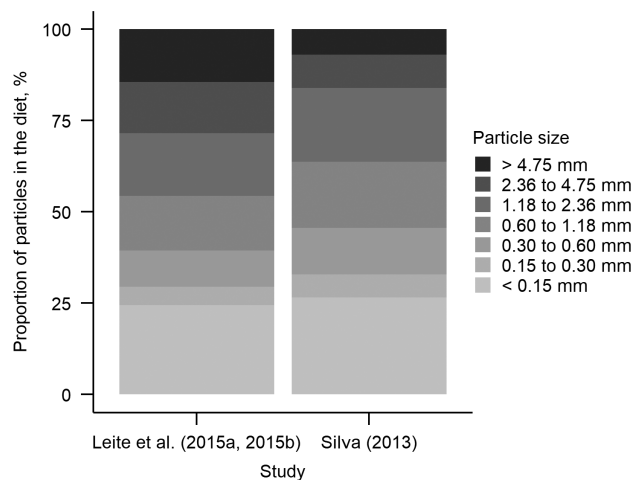
Item	Leite et al. (2015a, 2015b)	Silva (2013)
Dietary ingredient, % DM		
Dehydrated corn plant <sup>a</sup>	45.40	44.70
Cracked corn grain	26.60	30.50
Soybean meal	22.30	15.10
Soybean oil	1.60	2.50
Limestone	1.00	1.30
Mineral supplement <sup>b</sup>	2.20	6.00
Ammonium chloride	0.90	0.00
Diet chemical composition <sup>c</sup> , g/kg of DM ± SD		
DM	854 ± 10.9	865 ± 3.13
OM	935 ± 2.00	902 ± 3.27
CP	204 ± 5.40	154 ± 6.57
Crude fat	80 ± 4.90	51 ± 0.79
NDF	355 ± 25.00	313 ± 7.54
iNDF <sup>d</sup>	108 ± 10.50	113 ± 8.97
Lignin	57 ± 3.40	n.a.

<sup>a</sup>Dehydrated corn plant was made from whole corn plants harvested and chopped when the kernel milk line was approximately two-thirds of the distance down the kernel, air-dried for approximately 72 h or to a DM content of approximately 90%, and milled to pass a 10-mm screen (Mexon charger 15.0 hay mill; G3 Mexon Maquinas Agricolas, Cajuru, Sao Paulo, Brazil).

<sup>b</sup>Composition, per kg, as-fed basis: 190 g of Ca; 92 g of Cl; 73 g of P; 62 g of Na; 44 g of Mg; 1.35 g of Zn; 1.06 g of Fe; 0.94 mg of Mn; 0.73 g of F; 0.34 g of Cu; 18 mg of Se; 16 mg of I; 3 mg of Co.

<sup>c</sup>Mean and standard deviation of 10 composite samples. The chemical composition of the diet was calculated from the individual ingredients.

<sup>d</sup>iNDF = Indigestible NDF.



**Figure 1.** Particle size of diet offered to the goats during the studies (Leite et al., 2015a, 2015b; Silva, 2013).

study (Leite et al., 2015a, 2015b) and (Silva, 2013), respectively. The ME concentration in the diet (kcal/kg of DM) was estimated from gross energy intake, total energy losses from feces, urine, and gaseous products of digestion. Fecal and urinary excretions were obtained from their total collection (Souza et al., 2020). Energy loss from gaseous products of digestion was predicted according to Blaxter and Clapperton (1965) equation, as described by Souza et al. (2020). The feed intake was expressed as g and % of BW.

Goats were slaughtered as they reached approximately 15, 22, 30, 37, and 45 kg BW. Castrated males goats were 82 ± 12, 195 ± 52, 220 ± 80, 253 ± 31, and 291 ± 77 days old at slaughter weight 15, 22, 30, 37, and 45 kg BW, respectively, females goats were 116 ± 12, 178 ± 24, 263 ± 75, 361 ± 21, and 503 ± 54 days old at slaughter weight 15, 22, 30, 37, and 45 kg BW, respectively, and intact males were 92 ± 20, 214 ± 44, 237 ± 75, 249 ± 25, and 280 ± 72 days old at slaughter weight 15, 22, 30, 37, and 45 kg BW, respectively.

After goats were slaughtered (2.2 ± 0.8 h after morning feeding), GIT was removed and separated into reticulorumen, omasum, abomasum, small intestine, cecum, and colon-rectum (colon and rectum free of fat and mesenteries). The segments were weighed before and after emptying to determine the mass of wet digesta and the wet weight of each segment tissues.

For all studies, the reticulorumen digesta was separated into solid and liquid fractions by straining the contents through four layers of cheesecloth. These fractions were weighed and sampled according to the proportions determined to obtain a representative sample. The digesta from omasum, abomasum, small intestine, and cecum were individually placed into trays and mixed/homogenized before sampling. Colon and rectum digesta were collected separately and placed into trays. The

rectum digesta was minimally and manually broken up and then mixed with colon digesta until we got a very homogeneous colon–rectum paste, then samples were taken.

In the digesta of each segment, the DM, OM, NDF, iNDF, and Cr concentrations were determined. We considered the wet weight of the total GIT tissues as the sum of the wet weight of individual tissues of GIT segments, and total GIT pool size (wet digesta and DM) as the sum of individual pool size of GIT segments. We expressed the wet pool size and the wet weight of tissues grams.

The MRT was determined as the inverse of the digesta passage rate ( $k_p$ ) (i.e.,  $MRT = 1/k_p$ ). The  $k_p$  was assessed by using the method of emptying GIT compartments in slaughtered animals and using iNDF and Cr-EDTA as markers for particles grams ( $MRT_{iNDF}$ ) and solutes  $MRT_{Cr}$ , respectively. The details about preparation, administration, and analysis of both markers were previously published (Leite et al., 2015a, 2015b). The  $k_p$  of particles and solutes in different segments of the GIT were determined by the flux/compartamental pool method using the Eq. (1) (Ellis et al., 1994):

$$k_p \text{ of indigestible entity (IE) = intake rate of IE / compartmental mass of IE,} \quad (1)$$

where  $k_p$  is the fractional rate of IE escape per hour, intake rate of IE is expressed in grams per hour, and compartmental mass in the segment is expressed in grams.

The total MRT in the GIT was calculated by the sum of MRT in the reticulorumen, omasum, abomasum, small intestine, cecum, and colon–rectum. Moreover, the reticulorumen selectivity factors of particles and solutes (particles:solutes), that indicate digesta washing was calculated as the quotient between MRT estimated by iNDF and Cr-EDTA (Lechner et al., 2010; Müller et al., 2011).

### Statistical Analyses

The data was analyzed using PROC MIXED of SAS (v 9.4, SAS Inst. Inc., Cary, NC) by the model (Eq. [2])

$$Y_{ijkl} = |\mu| + |S_i| + |W_j| + |S_i \times W_j| + |T_k| + |e_{ijkl}|, \quad (2)$$

where  $Y_{ijkl}$  is the dependent variable,  $\mu$  is the overall mean,  $S_i$  is the fixed effect of sex  $i$ ,  $W_j$  is the fixed effect of BW  $j$ ,  $S_i \times W_j$  is the interaction between sex  $i$  and BW  $j$ ,  $T_k \sim iidN(0, \sigma_T^2)$  is the random effect of study  $k$ , and  $e_{ijkl} \sim iidN(0, \sigma_e^2)$  is the random

residual error. Moreover, residual variances were modeled using distinct grouping (i.e., no grouping, study, sex, BW, or interaction between sex and BW) using the REPEATED/GROUP function of PROC MIXED. The best grouping for each variable was chosen using the lowest Akaike information criterion (Akaike, 1974), corrected for small samples (AICc) (Sugiura, 1978). Residuals were plotted against the predicted means to check the model assumptions regarding homoscedasticity, independence, and normality of the errors. Outliers were removed when their Studentized residuals were  $>|3|$ . For cecum wet tissues, abomasum wet digesta, iNDF:NDF ratio of cecum content, MRT of particles in cecum, and MRT of solutes in abomasum, 1 data point each was removed. For small intestine wet tissues, iNDF:NDF ratio of colon–rectum content, and MRT of solutes in reticulorumen, omasum, and cecum, 2 data points each were removed. For iNDF:NDF of ingested diet and abomasum wet tissues, 3 data points each were removed.

Orthogonal polynomial contrasts were used to determine linear and quadratic effects of BW when it was significant ( $P \leq 0.05$ ) using the CONTRAST statement of PROC MIXED of SAS (v 9.4, SAS Inst. Inc., Cary, NC). The effects of sex and sex within BW were compared by Tukey's test. When the interaction between sex and BW was significant ( $P \leq 0.05$ ), polynomial regressions were used to determine linear or quadratic effects of BW within sex using the PROC MIXED of SAS (v 9.4, SAS Inst. Inc., Cary, NC), by the model (Eq. [3]) as follow:

$$Y_{ijkl} = |\mu| + |S_i| + |W^1(S_c)| + |\dots| + |W^j(S_c)| + |W^1(S_f)| + |\dots| + |W^j(S_f)| + |W^1(S_m)| + |\dots| + |W^j(S_m)| + |T_k| + |e_{ijkl}|, \quad (3)$$

where  $Y_{ijkl}$  is the dependent variable,  $\mu$  is the overall mean,  $S_i$  is the fixed effect of sex  $i$ ,  $W^1(S_c) + \dots + W^j(S_c)$  are the fixed effects of BW raised by the exponent  $j$  (1–4) within castrated males,  $W^1(S_f) + \dots + W^j(S_f)$  are the fixed effects of BW raised by the exponent  $j$  (1–4) within females,  $W^1(S_m) + \dots + W^j(S_m)$  is the fixed effect of BW raised by the exponent  $j$  (1–4) within intact males,  $T_k \sim iidN(0, \sigma_T^2)$  is the random effect of study  $k$ , and  $e_{ijkl} \sim iidN(0, \sigma_e^2)$  is the random residual error with a variance  $\sigma_e^2$ . Statistical significance was set at  $P \leq 0.05$ .



## RESULTS

Castrated males had greater DM intake, relative DM intake, and L than females (915 vs. 809 g, 3.19 vs. 2.91% BW, and 3.24 vs. 2.93, respectively;  $P \leq 0.05$ ), and both were similar to intact males (912 g, 3.11% BW, and 3.18, respectively;  $P \geq 0.07$ ; Table 2). Moreover, DM intake (Figure 2) increased at a decreasing rate as BW increased ( $P < 0.01$ ; Table 2). The relative DM intake decreased linearly as BW increased ( $P < 0.01$ ) and L decreased at an increasing rate as BW increased, with the lowest means observed at 45 kg BW ( $P \leq 0.03$ ; Table 2). There was a significant interaction between sex and BW ( $P < 0.01$ ) in NDF content and iNDF:NDF ratio of the ingested diet (Table 2; Figure 2).

Sex did not affect wet tissues, wet pool size, DM and NDF contents of reticulorumen and omasum, and the ratio between DM intake and reticulorumen wet pool size (DM intake:RR wet pool size ratio;  $P \geq 0.07$ ; Table 3; Figure 3). The ratio between DM intake and reticulorumen wet tissues (DM intake:RR wet tissues ratio) was greater for males than females ( $P \leq 0.04$ ), and it was similar between males ( $P = 0.95$ ; Figure 3). Reticulorumen and omasum wet tissues and wet pool size increased at a decreasing rate as BW increased ( $P < 0.01$ ; Table 3). Reticulorumen DM content increased at an increasing rate as BW increased ( $P = 0.01$ ; Table 3). The DM intake:RR wet tissues ratio linearly decreased as BW increased ( $P \leq 0.05$ ; Figure 3). BW did not affect reticulorumen and omasum NDF contents, omasum DM content, and the DM intake:RR wet pool size ratio ( $P \geq 0.11$ ; Table 3; Figure 3).

Sex did not affect reticulorumen iNDF:NDF ratio and  $MRT_{iNDF}$  (Figure 3) and omasum  $MRT_{Cr}$  ( $P \geq 0.30$ ; Table 3). However, females and intact males presented similar reticulorumen  $MRT_{Cr}$  (5.6 h;  $P = 0.92$ ) and they presented lower reticulorumen  $MRT_{Cr}$  than castrated males (7.0;  $P \leq 0.04$ ; Table 3; Figure 3). The reticulorumen iNDF:NDF ratio increased from 15 to 30 kg BW and then decreased from 30 to 45 kg BW ( $P < 0.01$ ; Table 3). BW did not affect reticulorumen  $MRT_{iNDF}$  ( $P \geq 0.11$ ; Table 3; Figure 3). However, reticulorumen and omasum  $MRT_{Cr}$  increased linearly as BW increased ( $P < 0.01$ ; Table 3; Figure 3). Reticulorumen selectivity factor of particles:solutes in females decreased at a decreasing rate as BW increased ( $P < 0.01$ ) and remained similar in males as BW increased ( $P \geq 0.41$ ; Table 3).

Even though castrated males demonstrated greater abomasum wet tissues than females and intact males only at 37 kg BW ( $P < 0.01$  for interaction

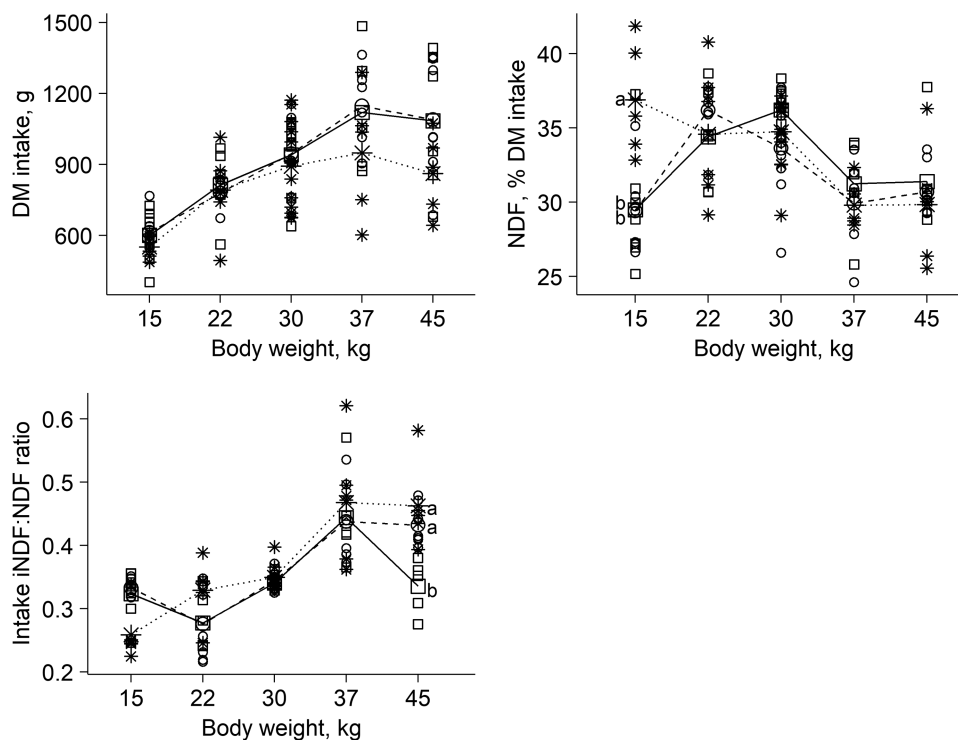
sex and BW; Table 3), castrated males had greater abomasum wet pool size (563 g) and  $MRT_{Cr}$  (0.66 h) than females and intact males at all evaluated BW ( $P < 0.01$ ; Table 3). Females and intact males had similar abomasum wet pool size and  $MRT_{Cr}$  (429 g and 0.46 h, respectively;  $P \geq 0.99$ ; Table 3). Regardless the interaction between sex and BW, abomasum wet tissues increased as BW increased, for all sexes ( $P < 0.01$ ); different from abomasum wet pool size that did not present clear pattern with the increase of BW. Abomasum  $MRT_{Cr}$  decreased linearly as BW increased ( $P = 0.02$ ; Table 3).

Small intestine wet tissues were greater for castrated males than females (681 vs. 599 g;  $P \leq 0.04$ ; Table 4). Small intestine wet tissues were similar between castrated males and intact males (668 g) and between females and intact males (627 g;  $P \geq 0.09$ ). On the other hand, small intestine wet pool size, DM content, and  $MRT_{Cr}$  were not affected by sex ( $P \geq 0.69$ ). Small intestine wet tissues and wet pool size increased at a decreasing rate as BW increased ( $P < 0.01$ ) and small intestine DM content and  $MRT_{Cr}$  remained similar as BW increased ( $P \geq 0.12$ ; Table 4). Moreover, small intestine NDF content decreased linearly as BW increased for males ( $P \leq 0.04$ ) and remained similar as BW increased for females ( $P \geq 0.06$ ; Table 4). Females had lower small intestine NDF content than intact males at 15 kg BW ( $P < 0.01$ ; Table 4). Castrated males and intact males had similar small intestine NDF content for all evaluated BW ( $P \geq 0.77$ ; Table 4).

Sex did not affect the variables evaluated in cecum ( $P \geq 0.17$ ; Table 4). Cecum wet tissues, wet pool size, NDF content, and iNDF:NDF ratio increased linearly as BW increased ( $P \leq 0.01$ ; Table 4). Cecum  $MRT_{iNDF}$  increased at an increasing rate as BW increased ( $P = 0.02$ ). Cecum  $MRT_{Cr}$  increased linearly as BW increased for females ( $P = 0.02$ ) and increased at an increasing rate as BW increased for intact males ( $P = 0.01$ ). Cecum  $MRT_{Cr}$  remained similar as BW increased for castrated males ( $P \geq 0.42$ ; Table 4).

In the colon-rectum, sex only affected  $MRT_{Cr}$  ( $P < 0.01$ ; Table 4). The lowest colon-rectum  $MRT_{Cr}$  was observed for intact males (4.76 h;  $P \leq 0.02$ ). Females and castrated males had similar colon-rectum  $MRT_{Cr}$  ( $P = 0.91$ ; Table 4). Colon-rectum wet tissues, wet pool size, and iNDF:NDF ratio increased at a decreasing rate as BW increased ( $P \leq 0.01$ ; Table 4). Colon-rectum DM content increased linearly as BW increased in castrated males and females ( $P \leq 0.01$ ) and increased at an increasing rate as BW increased in intact





**Figure 2.** Castrated males had greater DM intake than females (915 vs. 809 g;  $P = 0.05$ ), and both were similar to intact males (912 g;  $P \geq 0.07$ ). BW quadratically affect DM intake ( $P < 0.01$ ). Means in the same body weight with different letters (a and b) are different according to Tukeys' test ( $P \leq 0.05$ ). Body weight linearly affected NDF content and the ratio between indigestible NDF (iNDF) and NDF (iNDF:NDF ratio) of the ingested diet of females ( $P \leq 0.01$ ). Body weight quadratically affect NDF content of ingested diet of males and iNDF:NDF ratio of the ingested diet of males ( $P \leq 0.02$ ). The symbol  $\circ$  and dashed line represents castrated males, \* and dotted line represents females,  $\square$  and solid line represents intact males.

males ( $P < 0.01$ ). Colon–rectum  $MRT_{iNDF}$  and  $MRT_{Cr}$  were not affected by BW growth ( $P \geq 0.11$ ; Table 4).

Total GIT wet tissues were greater for castrated males than females (1,950 vs. 1,784 g;  $P = 0.01$ ; Table 4; Figure 4). Total GIT wet tissues were similar between females and intact males (1,833 g;  $P = 0.24$ ) and between castrated males and intact males (1,916 g;  $P = 0.47$ ; Table 4; Figure 4). Total GIT  $MRT_{Cr}$  was similar between castrated males and females (15.7 h;  $P = 0.11$ ) and between females and intact males (14.2 h;  $P = 0.76$ ). Sex and BW did not affect the ratio between DM intake and total GIT wet tissues (DM intake:Total GIT wet tissues ratio) and the ratio between DM intake and total GIT wet pool size (DM intake:Total GIT wet pool size ratio) ( $P \geq 0.30$ ; Figure 4). Total GIT wet tissues and wet pool size increased at a decreasing rate as BW increased ( $P < 0.01$ ). Total GIT DM content increased at an increasing rate as BW increased ( $P < 0.01$ ). Total GIT  $MRT_{Cr}$  was greater to castrated males than intact males (16.8 vs. 13.8 h;  $P < 0.01$ ; Table 4). Total GIT  $MRT_{Cr}$  was not affected by BW ( $P \geq 0.45$ ; Table 4).

## DISCUSSION

### Sex Effect on MRT

The effect of sex on  $MRT_{iNDF}$  and  $MRT_{Cr}$  in total GIT and GIT segments was tested in goats. Sex did not affect  $MRT_{iNDF}$  in any GIT segments. However, sex affected  $MRT_{Cr}$  in reticulorumen, abomasum, and total GIT.

Previous study indicated that MRT can be modulated by feed intake and GIT capacity, in which whether intake increases and GIT capacity remains constant MRT decreases, or whether GIT capacity increases and intake remains constant MRT increases (Clauss et al., 2007a). Our similar results on reticulorumen  $MRT_{iNDF}$  between sexes do not fully support this, since castrated males showed greater DM intake than females and similar reticulorumen capacity, thus one would expect a lower reticulorumen  $MRT_{iNDF}$  in castrated males. On the other hand, the DM intake:RR wet pool size ratio was similar among sexes, that agrees with the absence of effect of sex on reticulorumen  $MRT_{iNDF}$ . Our findings indicate that  $MRT_{iNDF}$  is modulated by intake and capacity (Clauss et al., 2007a). Composition of ingested diet was not consistently different among sex in our study, differences





**Table 3.** Continued

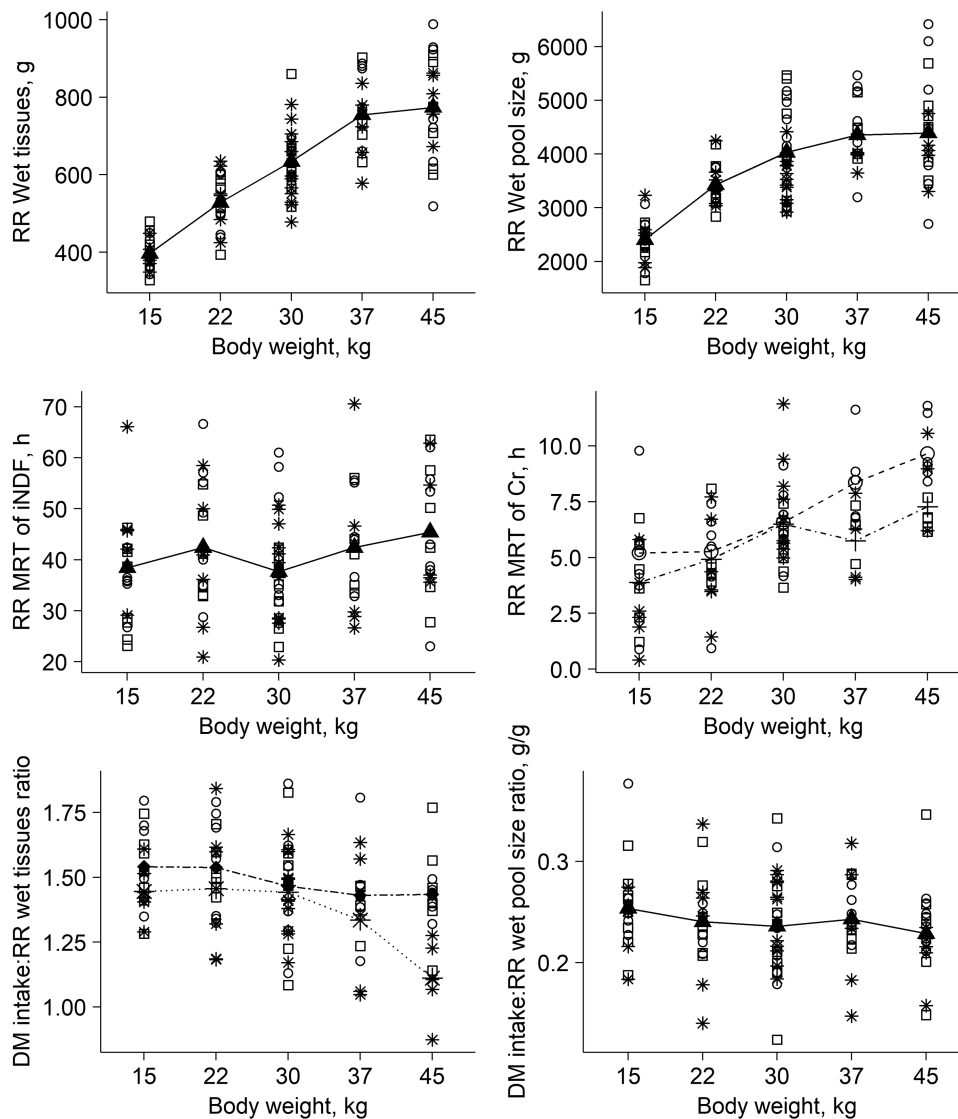
Item	BW (kg) and sex																P-value <sup>e</sup>																	
	15						22						30						37						45						Sex <sup>b</sup>	BWL	BWQ	Sex* BW <sup>c</sup>
	C	F	I	C	F	I	C	F	I	C	F	I	C	F	I	C	F	I	C	F	I	C	F	I	SEM									
Wet pool size, g	474.1	459.1	433.7	537.9	477.0	486.3	568.0	375.5	416.2	830.6	525.0	442.0	405.8	298.8	377.9	120.24	0.01	0.08	0.61	<0.01	0.39	0.08	<0.01	0.07										
DM, % wet pool size	14.5	13.7	14.4	12.2	11.1	9.9	11.5	12.9	10.6	16.7	12.9	11.6	16.9	12.6	14.8	1.25	-	-	-	-	-	-	-	0.04										
NDF, % DM	30.7	35.2	34.4	42.7	44.9	43.4	37.2	37.3	45.4	33.5	38.7	37.8	34.1	40.5	39.2	5.15	0.03	0.86	0.01	0.01	0.63	0.01	0.63	0.63										
MRT <sub>C<sub>r</sub></sub> , h	0.67	0.59	0.67	0.73	0.72	0.49	0.62	0.48	0.43	0.74	0.23	0.34	0.55	0.28	0.36	0.130	<0.01	0.02	0.94	0.94	0.52	<0.01	0.15	0.15										

a, b: Means in the same row with different superscripts are different according to Tukey's test within of BW ( $P \leq 0.05$ ).

<sup>a</sup>Main effects and interaction sex  $\times$  BW (Sex  $\times$  BW). BW<sub>L</sub> = linear effect of BW; BW<sub>Q</sub> = quadratic effect of BW.

<sup>b</sup>Females and intact males presented similar reticulorumen MRT<sub>C<sub>r</sub></sub> (5.6 h;  $P = 0.92$ ) and they presented higher reticulorumen MRT<sub>C<sub>r</sub></sub> than castrated males (7.0;  $P \leq 0.04$ ). Castrated males had greater abomasum wet pool size and MRT<sub>C<sub>r</sub></sub> than females and intact males at all evaluated BW (563 g vs. 427 and 431 g, and 0.66 vs. 0.46 and 0.46 h, respectively;  $P < 0.01$ ). Females and intact males had similar abomasum wet pool size and MRT<sub>C<sub>r</sub></sub> (429 g, and 0.46 h, respectively;  $P \geq 0.99$ ). Intact males had greater abomasum NDF content than castrated males (40.0% vs. 35.6% DM;  $P = 0.04$ ). Females had similar abomasum NDF content than males (39.3% vs. 37.8% DM;  $P \geq 0.10$ ).

<sup>c</sup>When the interaction between sex and BW was significant the effect of BW was evaluated within each sex.

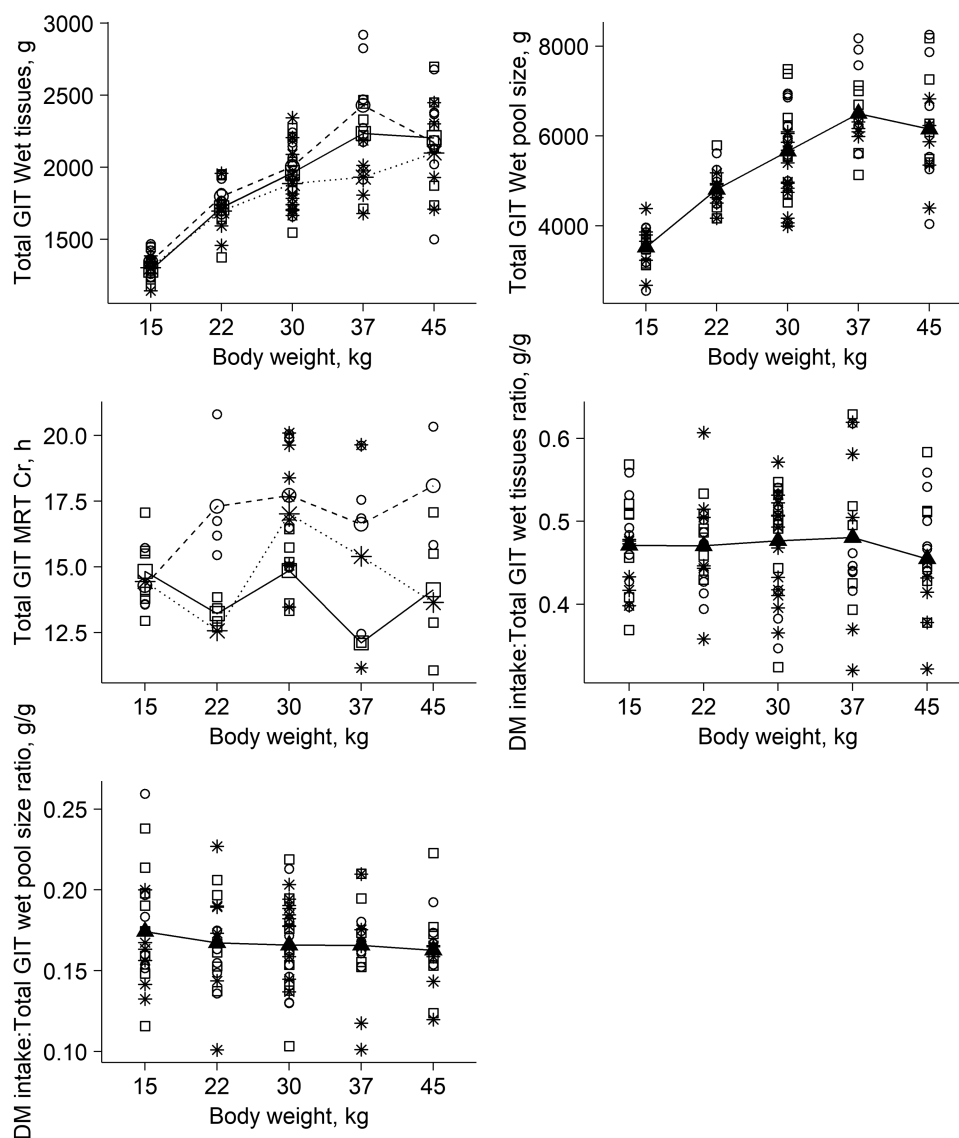


**Figure 3.** Sex did not affect wet tissues, wet pool size, DM, and NDF contents of reticulorumen (RR), and the ratio between DM intake and reticulorumen wet pool size (DM intake:RR wet pool size ratio) ( $P \geq 0.07$ ). Females and intact males presented similar reticulorumen digesta mean retention time (MRT) of solutes ( $MRT_{Cr}$ ) (5.6 h;  $P = 0.92$ ) and they presented greater reticulorumen  $MRT_{Cr}$  than castrated males (7.0;  $P \leq 0.04$ ). The ratio between DM intake and reticulorumen wet tissues (DM intake:RR wet tissues ratio) was greater for males than females ( $P \leq 0.04$ ), and it was similar between males ( $P = 0.95$ ). Body weight quadratically affected reticulorumen wet tissues and wet pool size ( $P < 0.01$ ). Body weight linearly affected reticulorumen  $MRT_{Cr}$  and the DM intake:RR wet tissues ratio ( $P \leq 0.05$ ). Body weight did not affect reticulorumen  $MRT_{INDF}$  and the DM intake:RR wet pool size ratio ( $P \geq 0.11$ ). The symbol  $\circ$  and dashed line represent castrated males, \* and dotted line represent females,  $\square$  and solid line represent intact males, + and dash-dotted line represent females and intact males mean,  $\diamond$  and dash-short-dashed line represent males mean, and  $\blacktriangle$  and solid line represent all sexes mean.

between sexes were observed only at 15 and 45 kg BW. Thus, this suggests composition of ingested diet may have contributed to the absence effect of sex on reticulorumen  $MRT_{INDF}$ .

Females and intact males had similar reticulorumen  $MRT_{Cr}$  and lower than castrated males. Therefore, the assumption made by Clauss et al. (2007a) also does not fully support that reticulorumen  $MRT_{Cr}$  is modulated by intake and capacity. This demonstrates that other factors are affecting reticulorumen  $MRT_{Cr}$ . Saliva secretion has been shown negatively related to reticulorumen  $MRT_{Cr}$  (Seo et al., 2007). Gross et al. (1995a, 1995b)

found that females Nubian ibexes (*Capra ibex nubiana*) had lower reticulorumen  $MRT_{Cr}$  than males, because females were around 50% lesser efficient chewers than males, and chewing stimulates saliva secretion. On the other hand, we do not think that chewing efficiency in females was the unique reason for the differences on reticulorumen  $MRT_{Cr}$  among sexes in our study. Our goats had the opportunity of diet searching and they were fed with diet that did not challenge the goats for having high chewing investment. Thus, sex effect on reticulorumen  $MRT_{Cr}$  is not clearly understood and must be further investigated with



**Figure 4.** Total Gastrointestinal tract (GIT) wet tissues were greater for castrated males than females (1,950 vs. 1,784 g;  $P = 0.01$ ). Total GIT wet tissues were similar between females and intact males (1,833 g;  $P = 0.24$ ) and between castrated males and intact males (1,916 g;  $P = 0.47$ ). Total GIT digesta mean retention time (MRT) of solutes (MRT<sub>Cr</sub>) was similar between castrated males and females (15.7 h;  $P = 0.11$ ) and between females and intact males (14.2 h;  $P = 0.76$ ). Total GIT MRT<sub>Cr</sub> was greater to castrated males than intact males (16.8 vs. 13.8 h;  $P < 0.01$ ). Sex and body weight did not affect the ratio between DM intake and total GIT wet tissues (DM intake:Total GIT wet tissues ratio) and the ratio between DM intake and total GIT wet pool size (DM intake:Total GIT wet pool size ratio) ( $P \geq 0.30$ ). body weight quadratically affected total GIT wet tissues and wet pool size ( $P < 0.01$ ). body weight did not affect total GIT MRT<sub>Cr</sub> ( $P \geq 0.45$ ). The symbol  $\circ$  and dashed line represent castrated males, \* and dotted line represent females,  $\square$  and solid line represent intact males. The symbol  $\blacktriangle$  and solid line represents all sexes mean.

diets with high fiber content, that would require great chewing investment, and with feeding levels that would not allow diet searching.

Omasum is one of the GTI segments responsible by reducing digesta moisture (Holtenius and Björnhag, 1989). The greatest MRT<sub>Cr</sub> observed in reticulorumen of castrated males was not observed in omasum MRT<sub>Cr</sub>, that would indicate that omasum fulfilled its function on reducing digesta moisture. Abomasum also demonstrated greater MRT<sub>Cr</sub> for castrated males than females and intact males; however, in this case, it must be related to greater abomasum capacity in castrated males. Moreover,

small intestine was not affected by great MRT<sub>Cr</sub> in the abomasum of castrated males, as demonstrated by the absence effect of sex on small intestine wet pool size and MRT<sub>Cr</sub>. On the other hand, even though sex did not affect cecum capacity and MRT<sub>Cr</sub>, castrated males and females had great MRT<sub>Cr</sub> in colon-rectum than intact males. Thus, our data did not show a clear pattern on the effect of sex on wet tissues, wet pool size, and MRT<sub>Cr</sub> of GTI segments, and further studies may have to elucidate how sex would affect MRT in GTI segments.

As observed in the GTI sections, total GIT MRT<sub>Cr</sub> was also different among sexes. This does

**Table 4.** Wet tissues, pool size (wet digesta and composition), and digesta mean retention time (MRT) of indigestible NDF (iNDF) (MRT<sub>iNDF</sub>) and MRT of Cr (MRT<sub>Cr</sub>) of intestine segments and total GIT of castrated males (C), females (F), and intact males (I) Saanen goats slaughtered at five different BW

Item	BW (kg) and sex															P-value <sup>a</sup>				
	15			22			30			37			45			Sex <sup>b</sup>	BW <sub>L</sub>	BW <sub>Q</sub>	Sex <sup>b</sup> *BW <sup>c</sup>	
	C	F	I	C	F	I	C	F	I	C	F	I	C	F	I	C	F	I	SEM	
Small intestine																				
Wet tissues, g	533.4	467.4	463.2	707.9	629.7	618.8	731.5	665.8	696.5	772.8	605.6	773.7	661.0	626.1	721.5	67.66	0.01	<0.01	<0.01	0.40
Wet pool size, g	280.2	291.4	336.3	333.0	320.1	332.2	449.2	372.9	470.0	503.0	704.0	499.4	462.3	391.0	499.7	61.33	0.78	0.01	0.01	0.09
DM, % wet pool size	9.9	9.5	10.1	8.8	9.7	9.5	9.3	9.8	9.0	10.2	9.3	9.8	10.8	10.2	9.2	0.61	0.74	0.67	0.12	0.49
NDF, % DM	27.5ab	20.5b	29.8a	21.5	23.8	23.6	22.0	22.8	24.9	20.9	20.9	20.4	21.8	18.1	16.5	1.81	-	-	-	0.02
MRT <sub>Cr</sub> , h	1.3	1.2	1.1	1.0	1.0	1.1	1.3	1.0	1.4	1.0	1.0	0.9	1.1	1.2	1.1	0.19	0.69	0.80	0.49	0.76
Cecum																				
Wet tissues, g	24.2	27.0	25.8	33.2	35.1	34.1	34.4	36.5	37.5	47.6	36.5	40.4	39.9	45.9	48.2	2.63	0.71	<0.01	0.18	0.10
Wet pool size, g	98.6	144.0	121.1	179.6	137.2	108.1	174.3	168.5	167.0	217.0	199.8	197.2	223.9	245.8	268.6	25.75	0.87	0.01	0.34	0.29
DM, % wet pool size	15.1	13.1	14.9	12.9	13.2	13.3	13.5	13.2	12.6	12.9	14.6	15.2	13.9	13.3	14.5	0.79	0.25	0.93	0.03	0.10
NDF, % DM	45.7	42.6	44.8	44.1	44.7	45.3	45.3	42.8	45.2	35.7	41.1	39.7	40.1	43.0	39.1	2.44	0.71	0.01	0.61	0.09
iNDF:F:iNDF ratio	0.57	0.54	0.55	0.65	0.59	0.58	0.67	0.66	0.62	0.74	0.58	0.66	0.60	0.64	0.68	0.047	0.32	0.01	0.09	0.63
MRT <sub>iNDF</sub> , h	1.3	2.2	1.8	2.4	1.4	1.3	1.7	1.4	1.2	1.7	1.9	1.6	1.6	2.6	2.4	0.33	0.54	0.67	0.02	0.06
MRT <sub>Cr</sub> , h	1.3	1.5	1.6	1.7	1.4	0.9	1.2	1.6	1.2	1.2	2.2	1.5	1.2	2.3	1.9	0.40	-	-	-	0.02
Colon-rectum																				
Wet tissues, g	204.9	234.0	215.6	313.3	284.4	304.8	330.2	345.2	331.4	478.9	313.4	415.9	414.5	351.8	406.6	29.72	0.08	0.56	0.01	0.12
Wet pool size, g	231.0	276.1	253.8	416.7	315.7	437.3	467.4	444.6	470.3	539.6	564.0	552.5	534.6	529.9	545.0	61.92	0.76	0.02	0.01	0.94



**Table 4.** Continued

Item	BW (kg) and sex																		P-value <sup>a</sup>		
	15			22			30			37			45			Sex <sup>b</sup>	BW <sub>L</sub>	BW <sub>Q</sub>	Sex *BW <sup>c</sup>		
	C	F	I	C	F	I	C	F	I	C	F	I	C	F	I					SEM	
DM, % wet pool size	19.6	19.0	21.7	16.8	17.4	18.7	21.8	21.4	18.0	22.2	27.1	21.9	22.2	25.0	25.3	1.37	-	-	0.04		
NDF, % DM	45.3	43.7	45.5	46.3	44.2	44.9	45.7	43.3	47.7	42.3	43.8	43.3	44.2	42.2	40.0	4.89	0.48	0.22	0.16	0.61	
iNDF:F:NDF ratio	0.57	0.60	0.53	0.65	0.59	0.68	0.63	0.66	0.62	0.61	0.70	0.81	0.65	0.64	0.59	0.041	0.69	0.04	<0.01	0.08	
MRT <sub>INDF</sub> <sup>h</sup>	5.3	8.4	6.3	8.8	4.5	9.7	7.2	7.3	6.3	4.4	10.2	6.5	7.0	8.7	7.0	1.21	-	-	-	0.01	
MRT <sub>Ct</sub> <sup>h</sup>	5.4	5.4	5.1	6.0	4.5	5.3	6.4	6.9	4.9	6.1	7.6	3.9	7.0	7.4	4.5	1.49	<0.01	0.33	0.95	0.22	
Total GIT	1,344.7	1,304.4	1,286.4	1,798.7	1,697.3	1,718.9	2,006.0	1,887.7	1,962.9	2,430.1	1,932.2	2,235.2	2,171.8	2,099.0	2,205.1	92.40	0.02	<0.01	<0.01	0.47	
Wet tissues, g	3,510.7	3,602.3	3,462.0	4,897.1	4,724.2	4,813.1	5,933.3	5,070.2	5,977.5	6,978.0	6,203.6	6,316.3	6,271.5	5,738.5	6,451.3	326.70	0.09	<0.01	<0.01	0.61	
DM, % wet pool size	15.6	13.6	14.9	14.2	13.3	13.7	14.5	14.9	13.8	17.0	15.7	16.5	18.8	17.0	16.3	1.45	0.06	<0.01	<0.01	0.62	
NDF, % DM	45.6	47.4	46.3	46.1	50.5	45.8	47.5	46.7	48.7	44.5	43.1	47.1	44.9	44.8	47.1	3.83	0.35	0.41	0.29	0.21	
MRT <sub>Ct</sub> <sup>d</sup> , h	14.3	14.4	14.8	17.3	12.6	13.2	17.7	17.0	14.9	16.6	15.4	12.1	18.1	13.6	14.1	3.09	<0.01	0.69	0.45	0.47	

a, b: Means in the same row with different superscripts are different according to Tukey's test within of BW ( $P \leq 0.05$ ).

<sup>a</sup>Main effects and interaction sex  $\times$  BW (Sex  $\times$  BW). BW<sub>L</sub> = linear effect of BW; BW<sub>Q</sub> = quadratic effect of BW.

<sup>b</sup>Small intestine wet tissues were greater for castrated males than females (681 vs. 599 g;  $P \leq 0.04$ ). Small intestine wet tissues were similar between castrated males and intact males (668 g) and between females and intact males (627 g;  $P \geq 0.09$ ). Colon-rectum MRT<sub>Ct</sub> was lower for intact males than females and castrated males (4.76 vs. 6.37 and 6.17 h;  $P \leq 0.02$ ). Females and castrated males had similar colon-rectum MRT<sub>Ct</sub> ( $P = 0.91$ ). Total GIT wet tissues were greater for castrated males than females (1,950 vs. 1,784 g;  $P = 0.01$ ). Total GIT wet tissues were similar between females and intact males (1,833 g;  $P = 0.24$ ) and between castrated males and intact males (1,916 g;  $P = 0.47$ ). Total GIT MRT<sub>Ct</sub> was similar between castrated males and females (15.7 h;  $P = 0.11$ ) and between females and intact males (14.2 h;  $P = 0.76$ ).

<sup>c</sup>When the interaction between sex and BW was significant the effect of BW was evaluated within each sex.

<sup>d</sup>Total GIT MRT<sub>Ct</sub> = Sum of MRT<sub>Ct</sub> of reticulorumen, omasum, abomasum, small intestine, cecum, and colon-rectum tissues.

not fully agree with the assumption that  $\text{GIT MRT}_{\text{Cr}}$  is modulated by feed intake and GIT capacity, because sex did not affect DM intake:Total GIT wet tissues ratio and DM intake:Total GIT wet pool size ratio. On the other hand, total GIT represents the sum of all GIT sections, and the differences among GIT segments have to be considered. The greater castrated males  $\text{MRT}_{\text{Cr}}$  in reticulorumen, abomasum, and colon-rectum than intact males were also observed in total GIT. However, females, that presented lower  $\text{MRT}_{\text{Cr}}$  in reticulorumen and abomasum than castrated males, presented total GIT  $\text{MRT}_{\text{Cr}}$  similar to castrated males. This similarity between females and castrated males total GIT  $\text{MRT}_{\text{Cr}}$  was also observed in colon-rectum, that is associated with water absorption (Clauss et al., 2016). This suggests females had greater water absorption in colon-rectum section even though the absence effect of sex on colon-rectum wet tissues. Therefore, our results suggest females may have naturally greater water absorption capacity in colon-rectum than males as a mechanism to compensate great chewing investment and saliva secretion and low  $\text{MRT}_{\text{Cr}}$  and consequently avoid great fecal water losses (Gross et al., 1995a, 1995b). Moreover, our results also suggest that differences of sex on water absorption among GIT segments affect total GIT  $\text{MRT}_{\text{Cr}}$ .

### ***BW Effect on MRT***

The effect of BW on  $\text{MRT}_{\text{iNDF}}$  and  $\text{MRT}_{\text{Cr}}$  in total GIT and GIT segments was tested in goats. BW affected only cecum  $\text{MRT}_{\text{iNDF}}$ . However, BW affected  $\text{MRT}_{\text{Cr}}$  in reticulorumen, omasum, abomasum, and cecum of females and intact males.

Reticulorumen wet tissues and wet pool size increased similar to DM intake as BW increased (i.e., increased at a decreasing rate). On the other hand, the DM intake:RR wet pool size ratio was not affected by BW, while the DM intake:RR wet tissues ratio was great in goats slaughtered at 15 kg BW and linearly decreased as BW increased. This demonstrates the distention capacity of reticulorumen (Clauss et al., 2016) and supports the assumptions that  $\text{MRT}_{\text{iNDF}}$  is modulated by intake and capacity (Clauss et al., 2007a). Moreover, the reticulorumen MRT of particles has been related to the composition of ingested diet (Seo et al., 2009). Composition of ingested diet affects changes on functional specific gravity of particles (FSH) (Seo et al., 2009) because of its relationship to rate of fermentation and hydration of the particles (Hooper and Welch, 1985). However, our results do

not support this, because BW affected the composition of ingested diet.

Additionally, reticulorumen  $\text{MRT}_{\text{Cr}}$  was lower at young goats (i.e., 15 kg BW), and linearly increased as BW increased. This indicates that other factors than intake and capacity (Clauss et al., 2007a) must also be considered on reticulorumen MRT of solutes. Reticulorumen MRT of solutes has been positively related to frequency and duration of reticulo-omasal orifice opening and the amount of solutes in the reticulorumen, that comes mainly from water intake and saliva secretion (Seo et al., 2007). Water intake was not recorded in the studies of Leite et al. (2015a, 2015b) and Silva (2013). However, our results demonstrated that young goats, slaughtered at 15 kg BW, had low DM content in reticulorumen and it increased at an increasing rate as BW increased. Thus, this suggests great input of water in the reticulorumen of young goats that would come from saliva secretion (Seo et al., 2007). The major factor for secretory responses of salivary glands is chewing movements (Bartley, 1976), that is positively related to feed intake level (Galvani et al., 2010; Grimaud et al., 2010) and negatively related to BW (i.e., young ruminants are lesser efficient chewers than old ruminants, spending more time chewing per kilogram of ingested diet; Bae and Welch, 1983; Grandl et al., 2016, 2018). Moreover, frequency and duration of reticulo-omasal orifice opening depend on duration, amplitude, and frequency of primary reticular contractions, that extremally depends on intake level (Okine and Mathison, 1991; Seo et al., 2007). Our results demonstrated intake level (DM and L) was great at young goats, slaughtered at 15 kg BW, and decreased as BW increased. Thus, our results suggest, reticulorumen MRT of solutes is linearly and positively related to BW growth because frequency and duration of reticulo-omasal orifice opening and saliva secretion probably were great in young goats and decreased with aging.

Reticulorumen and omasum are related segments and it was very evident in our results. Wet tissues and wet pool size of reticulorumen and omasum increased similarly as BW increase. However, different than that observed for reticulorumen, BW did not affect omasum DM content. Water absorption is the main function of omasum (Holtenius and Björnhag, 1989). Thus, this demonstrated omasum absorbed solutes from the digesta that escape from reticulorumen. The omasum absorption in our study was around 12%, smaller than the absorption found by Holtenius and Björnhag (1989), that was around 18%. On the other hand,

omasum  $MRT_{Cr}$  linearly increased as BW increased. Thus, even though omasum reduced the moisture content of digesta that escape from reticulorumen, the low  $MRT_{Cr}$  observed in reticulorumen of young goats and increase as BW increased was also observed in omasum and abomasum. Additionally, in the past omasum was not accounted in total NDF digestibility (Holtenius and Björnhag, 1989); however, more recent studies have suggested that the omasum plays a role on fiber digestion, that may contribute to around 7% of total NDF digestibility in dairy cows (Ahvenjärvi et al., 2000, 2001). Our results demonstrated that NDF content decreased around 19% from reticulorumen to omasum. Thus, this may indicate NDF digestion in the omasum of growing goats.

Abomasum is one of the first GIT segment to reach the maximum growth rate, that is around 15 days of life in goats (Andrade et al., 2020). This happens because abomasum is responsible by enzymatic digestion during the suckling phase. Its importance in feed digestion begins to decrease at the weaning phase, that started for our goats when they were around 2 months old. According to Andrade et al. (2020), after goats start the transition period and eat solid feed diet more effectively they become functional ruminants in 15 days, that is the period to reticulorumen reaches the maximum growth rate. Our goats started at the experiment when they were around 3 months old, 30 days after the beginning of solid feed diet, and 15 days after they become functional ruminants. The abomasum wet tissues are able to distend in young ruminants and the abomasum capacity may increase without changes on wet tissues size (Ortigue and Doreau, 1995). However, the abomasum distention ability decreases with aging by the increase on tissues thickness (Ortigue and Doreau, 1995). Our results demonstrated young goats may had great digesta content in abomasum even though they did not have great wet tissues. The abomasum distention ability and great abomasum wet pool size in young goats and decrease as BW increase led to great abomasum  $MRT_{Cr}$  at 15 kg BW and linear decrease as BW increased even though omasum  $MRT_{Cr}$  was low at 15 kg BW and linearly decreased as BW increased. Thus, we suggest abomasum of young is able to distend to avoid the influence of omasum  $MRT_{Cr}$  on abomasum  $MRT_{Cr}$ .

Small intestine, similar to abomasum, has early development in goats, and it reaches the maximum growth rate when goats are around 15 days

old (Andrade et al., 2020). The early development of small intestine is mainly explained by its function of enzymatic digestions, that is basically the main site for nutrient digestion during the suckling phase. Thus, because our goats were early weaned, they started the experiment when their small intestine growth rate was decreasing, as demonstrated by the non-linear relationship between small intestines wet tissues and BW.

Small intestine is considered tubular segment and its flow has been considered laminar (Ellis et al., 1994; Faichney, 2005). However, based on  $iNDF:NDF$  ratio in small intestine, studies have questioned the general assumption of laminar flow in small intestine (Hristov et al., 2019). Our results demonstrated BW did not affect small intestine  $MRT_{Cr}$  even though abomasum  $MRT_{Cr}$  was greater in young goats (i.e., at 15 kg BW) and decreased as BW increased. The differences on  $MRT_{Cr}$  between abomasum and small intestine were possible because small intestine wet pool size increased as BW increased, indicating increase on digestion retention as BW increased and supporting the hypothesis that small intestine may not have laminar flow.

Additionally, small intestine  $MRT$  of solutes and particles have been demonstrated similar (Leite et al., 2015a, 2015b). Thus, due to the absence of BW on small intestine  $MRT_{Cr}$ , we suggest BW did not affect small intestine  $MRT_{iNDF}$ . Based on that and the similarity on the increase of cecum and small intestine wet pool size as BW increased, the absence of effect of BW on cecum  $MRT_{iNDF}$  would be expected. However, cecum  $MRT_{iNDF}$  increased as BW increased.  $MRT$  of particles is positively related to NDF digestibility (Allen and Mertens, 1988), and cecum is known by digesting fiber. The  $iNDF:NDF$  ratio in cecum increased as BW increased while reticulorumen  $iNDF:NDF$  ratio did not. This suggests fiber digestion in the segments between reticulorumen and cecum increased a BW increased, and it would be related to the increase on  $MRT_{iNDF}$  as BW increased, as demonstrated in cecum. Thus, even though BW did not affect small intestine  $MRT_{Cr}$ , the results of  $MRT_{iNDF}$  and  $iNDF:NDF$  ratio in cecum suggest mixing of digesta and NDF digestion may occurred in small intestine, and small intestine  $MRT_{Cr}$  and  $MRT_{iNDF}$  were not similar.

Despite cecum  $MRT$  increased as BW increased and colon–rectum wet tissues and wet pool size increased as BW increased, BW did not affect colon–rectum  $MRT_{iNDF}$  and  $MRT_{Cr}$ . Colon and rectum, specially distal colon and rectum, are associated with water absorption (Clauss et al.,

2016). Thus, we would expect great colon–rectum DM content in young goats and decrease as BW increased as a way to reduce digesta volume in young goats and keep constant colon–rectum MRT. However, our data demonstrated colon–rectum DM content increased as BW increased, indicating decrease on fecal water losses as BW increased. Thus, our results indicate colon–rectum efficiency on water absorption is low in young goats and increase as BW increased, that demonstrates the importance of ad libitum drinking water, especially for young goats.

Despite BW affected  $MRT_{Cr}$  in reticulorumen, omasum, abomasum, and cecum of females and intact males, BW did not affect total GIT  $MRT_{Cr}$ , DM intake, total GIT wet tissues, and wet pool size demonstrated similar growth as BW increased. This was also demonstrated by the absence effect of BW on the DM intake:Total GIT wet tissues ratio and the DM intake:Total GIT wet pool size ratio. This demonstrates that despite the differences on GIT segments capacity, compensations on  $MRT_{Cr}$  occur among the GIT segments. Therefore, in general terms our results support that for total GIT of growing goats the  $MRT_{Cr}$  is modulated by feed intake and GIT capacity.

## CONCLUSIONS

Sex did not affect  $MRT_{iNDF}$  in any evaluated GIT segments and affected  $MRT_{Cr}$  in reticulorumen, abomasum, and total GIT. However, the mechanism related to sex effect on MRT has to be elucidated. BW was positively related to reticulorumen  $MRT_{Cr}$ , but it was not related to reticulorumen  $MRT_{iNDF}$  and total GIT  $MRT_{Cr}$  in growing Saanen goats. Reticulorumen  $MRT_{iNDF}$  and total GIT  $MRT_{Cr}$  were modulated by intake and capacity of reticulorumen and GIT, respectively. On the other hand, reticulorumen  $MRT_{Cr}$  seemed to be regulated by reticulo-omasal orifice opening and saliva secretion.

## ACKNOWLEDGMENTS

We thank the São Paulo Research Foundation (FAPESP; Grant 2008/57302-0) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes - Brazil; Finance code PVE 061/2011) for providing financial support for this project. M.G. received funding from National Council for Scientific and Technological Development (CNPq - Brazil; Scholarship 141615/2017-6).

*Conflict of interest statement.* None declared.

## LITERATURE CITED

- Ahvenjärvi, S., B. Skiba, and P. Huhtanen. 2001. Effect of heterogeneous digesta chemical composition on the accuracy of measurements of fiber flow in dairy cows. *J. Anim. Sci.* 79:1611–1620. doi:10.2527/2001.7961611x.
- Ahvenjärvi, S., A. Vanhatalo, P. Huhtanen, and T. Varvikko. 2000. Determination of reticulo-rumen and whole-stomach digestion in lactating cows by omasal canal or duodenal sampling. *Br. J. Nutr.* 83:67–77. doi:10.1017/S0007114500000106
- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Trans. Automat. Contr.* 19:716–723. doi:10.1109/TAC.1974.1100705.
- Allen, M. S., and D. R. Mertens. 1988. Evaluating constraints on fiber digestion by rumen microbes. *J. Nutr.* 118:261–270. doi:10.1093/jn/118.2.261.
- Andrade, M.E.B., C.J. Härter, M. Gindri, K.T. Resende, and I.A.M.A. Teixeira. 2020. Visceral organ growth patterns in Saanen goats. *J. Agric. Sci.* 1–22. doi:https://doi.org/10.1017/S0021859620000039.
- Bae, D.H., J.G. Welch, and B.E. Gilman. 1983. Mastication and rumination in relation to body size of cattle. *J. Dairy Sci.* 66:2137–2141. doi:10.3168/jds.S0022-0302(83)82060-8.
- Bartley, E.E. 1976. Bovine saliva: Production and function. In Weinberg, M.S. and L.S. Sheffner, editors. *Buffers in ruminant physiology and metabolism*. New York (NY): Church and Dwight; p. 61–81.
- Blaxter, K.L., V.R. Fowler, and J.C. Gill. 1982. A study of the growth of sheep to maturity. *J. Agric. Sci.* 98:405–420. doi:10.1017/S0021859600041952.
- Blaxter, K.L., and J.L. Clapperton. 1965. Prediction of the amount of methane produced by ruminants. *Br. J. Nutr.* 19:511–522. doi:10.1079/bjn19650046.
- Bourlière, F. 1975. Mammals, small and large: the ecological implications of size. In Frank, G.B., K. Petrusewicz, and L. Ryszkowski, editors. *Small mammals: their productivity and population dynamics*. 1st ed. New York (NY): Cambridge University Press; p. 1–8.
- Cannas, A., L.O. Tedeschi, D.G. Fox, A.N. Pell, and P.J. Van Soest. 2004. A mechanistic model for predicting the nutrient requirements and feed biological values for sheep. *J. Anim. Sci.* 82:149–169. doi:10.2527/2004.821149x.
- Clauss, M., W. Jürgen Streich, A. Schwarm, S. Ortmann, and J. Hummel. 2007a. The relationship of food intake and ingesta passage predicts feeding ecology in two different megaherbivore groups. *Oikos* 116:209–216. doi:10.1111/j.2006.0030-1299.15461.x.
- Clauss, M., A. Schwarm, S. Ortmann, W.J. Streich, and J. Hummel. 2007b. A case of non-scaling in mammalian physiology? Body size, digestive capacity, food intake, and ingesta passage in mammalian herbivores. *Comp. Biochem. Physiol. A. Mol. Integr. Physiol.* 148:249–265. doi:10.1016/j.cbpa.2007.05.024.
- Clauss, M., M. Stewart, E. Price, A. Pailon, T. Savage, I. Van Ekris, and A. Munn. 2016. The effect of feed intake on digesta passage, digestive organ fill and mass, and digesta dry matter content in sheep (*Ovis aries*): flexibility in digestion but not in water reabsorption. *Small Rumin. Res.* 138:12–19. doi:10.1016/j.smallrumres.2016.03.029.
- Demment, M.W. 1983. Feeding ecology and the evolution of body size of baboons. *African J. Ecol.* 21:219–233. doi:10.1111/j.1365-2028.1983.tb00323.x.



- Demment, M.W., and P.J. Van Soest. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125:641–672. doi:10.1086/284369.
- Dittmann, M.T., J. Hummel, S. Hammer, A. Arif, C. Hebel, D.W.H. Müller, J. Fritz, P. Steuer, A. Schwarm, M. Kreuzer, and M. Clauss. 2015. Digesta kinetics in gazelles in comparison to other ruminants: Evidence for taxon-specific rumen fluid throughput to adjust digesta washing to the natural diet. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 185:58–68. doi:10.1016/J.CBPA.2015.01.013.
- Ellis, W.C., J.H. Matis, T.M. Hill, and M.R. Murphy. 1994. Methodology for estimating digestion and passage kinetics of forages. In Fahey, G.C. Jr., M. Collins, D.R. Mertens, and L.E. Moser, editors. *Forage quality, evaluation and utilization*. 1st ed. Madison (WI): American Society of Agronomy; p. 682–756.
- Evans, E. 1981. An evaluation of the relationships between dietary parameters and rumen solid turnover rate. *Can. J. Anim. Sci.* 61:97–103. doi:10.4141/cjas81-014.
- Faichney, G.J. 2005. Digesta flow. In Dijkstra, J., J.M. Forbes, and J. France, editors. *Quantitative aspects of ruminant digestion and metabolism*. 2nd ed. Wallingford: CABI Publishing; p. 49–86.
- Fox, D.G., L.O. Tedeschi, T.P. Tytlutki, J.B. Russell, M.E. Van Amburgh, L.E. Chase, A.N. Pell, and T.R. Overton. 2004. The Cornell net carbohydrate and protein system model for evaluating herd nutrition and nutrient excretion. *Anim. Feed Sci. Technol.* 112:29–78. doi:10.1016/j.anifeedsci.2003.10.006.
- Galvani, D.B., C.C. Pires, T.P. Wommer, F. Oliveira, and M.F. Santos. 2010. Chewing patterns and digestion in sheep submitted to feed restriction. *J. Anim. Physiol. Anim. Nutr. (Berl)*. 94:e366–e373. doi:10.1111/j.1439-0396.2010.01022.x.
- Gordon, I.J., and A.W. Illius. 1994. The functional significance of the browser-grazer dichotomy in African ruminants. *Oecologia* 98:167–175. doi:10.1007/BF00341469.
- Grandl, F., S.L. Amelchanka, M. Furger, M. Clauss, J.O. Zeitz, M. Kreuzer, and A. Schwarm. 2016. Biological implications of longevity in dairy cows: 2. Changes in methane emissions and efficiency with age. *J. Dairy Sci.* 99:3472–3485. doi:10.3168/jds.2015-10262.
- Grandl, F., A. Schwarm, S. Ortman, M. Furger, M. Kreuzer, and M. Clauss. 2018. Kinetics of solutes and particles of different size in the digestive tract of cattle of 0.5–10 years of age, and relationships with methane production. *J. Anim. Physiol. Anim. Nutr. (Berl)*. 102:639–651. doi:10.1111/jpn.12862.
- Grimaud, P., D. Richard, M.P. Vergeron, J.R. Guilleret, and M. Doreau. 2010. Effect of drastic undernutrition on digestion in zebu cattle receiving a diet based on rice straw. *J. Dairy Sci.* 82:974–981. doi:10.3168/jds.s0022-0302(99)75317-8.
- Gross, J.E., P.U. Alkon, and M.W. Demment. 1995a. Grouping patterns and spatial segregation by Nubian ibex. *J. Arid Environ.* 30:423–439. doi:10.1006/jare.1995.0037.
- Gross, J.E., M.W. Demment, P.U. Alkon, and M. Kotzman. 1995b. Feeding and chewing behaviours of Nubian ibex: compensation for sex-related differences in body size. *Funct. Ecol.* 9:385. doi:10.2307/2390001.
- Harrison, D.G., and A.B. McAllan. 1980. Factors affecting microbial growth yields in the reticulo-rumen. In *Proceedings of the 5th International Symposium on Ruminant Physiology*, Clermont—Ferrand. Dordrecht, NL: Springer Netherlands; p. 205–226.
- Holtenius, K., and G. Björnag. 1989. The significance of water absorption and fibre digestion in the omasum of sheep, goats and cattle. *Comp. Biochem. Physiol. A. Comp. Physiol.* 94:105–109. doi:10.1016/0300-9629(89)90792-5.
- Hooper, A.P., and J.G. Welch. 1985. Effects of particle size and forage composition on functional specific gravity. *J. Dairy Sci.* 68:1181–1188. doi:10.3168/jds.S0022-0302(85)80945-0.
- Hristov, A.N., A. Bannink, L.A. Crompton, P. Huhtanen, M. Kreuzer, M. McGee, P. Nozière, C.K. Reynolds, A.R. Bayat, D.R. Yáñez-Ruiz, et al. 2019. Invited review: nitrogen in ruminant nutrition: a review of measurement techniques. *J. Dairy Sci.* 102:5811–5852. doi:10.3168/jds.2018-15829.
- Illius, A.W., and I.J. Gordon. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Oecologia* 89:428–434. doi:10.1007/BF00317422.
- Kleiber, M. 1932. Body size and metabolism. *Hilgardia A J. Agric. Sci.* 6:315–353. doi:10.3733/hilg.v06n11p315.
- Lechner, I., P. Barboza, W. Collins, J. Fritz, D. Günther, B. Hattendorf, J. Hummel, K.H. Südekum, and M. Clauss. 2010. Differential passage of fluids and different-sized particles in fistulated oxen (*Bos primigenius f. taurus*), muskoxen (*Ovibos moschatus*), reindeer (*Rangifer tarandus*) and moose (*Alces alces*): rumen particle size discrimination is independent from contents. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* 155:211–222. doi:10.1016/j.cbpa.2009.10.040.
- Leite, R.F., S.J. Krizsan, F.O. Figueiredo, V.B. Carvalho, I.A. Teixeira, and P. Huhtanen. 2015a. Contribution of different segments of the gastrointestinal tract to digestion in growing Saanen goats. *J. Anim. Sci.* 93:1802–1814. doi:10.2527/jas.2014-8423.
- Leite, R.F., S.J. Krizsan, F.O. Figueiredo, V.B. Carvalho, I.A. Teixeira, and P. Huhtanen. 2015b. Retention time of digesta in the gastrointestinal tract of growing Saanen goats. *J. Anim. Sci.* 93:3969–3978. doi:10.2527/jas.2014-8763.
- Meyer, K., J. Hummel, and M. Clauss. 2010. The relationship between forage cell wall content and voluntary food intake in mammalian herbivores. *Mamm. Rev.* 40:221–245. doi:10.1111/j.1365-2907.2010.00161.x.
- Müller, D.W., J. Caton, D. Codron, A. Schwarm, R. Lentle, W.J. Streich, J. Hummel, and M. Clauss. 2011. Phylogenetic constraints on digesta separation: variation in fluid throughput in the digestive tract in mammalian herbivores. *Comp. Biochem. Physiol. A. Mol. Integr. Physiol.* 160:207–220. doi:10.1016/j.cbpa.2011.06.004.
- Müller, D.W.H., D. Codron, C. Meloro, A. Munn, A. Schwarm, J. Hummel, and M. Clauss. 2013. Assessing the Jarman–Bell Principle: scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* 164:129–140. doi:10.1016/j.cbpa.2012.09.018.
- Okine, E.K., and G.W. Mathison. 1991. Reticular contraction attributes and passage of digesta from the ruminoreticulum in cattle fed roughage diets. *J. Anim. Sci.* 69:2177–2186. doi:10.2527/1991.6952177x.
- Okine, E.K., G.W. Mathison, M. Kaske, J.J. Kennelly, and R.J. Christopherson. 1998. Current understanding of the role of the reticulum and reticulo-omasal orifice in the control of digesta passage from the ruminoreticulum of sheep and cattle. *Can. J. Anim. Sci.* 78:15–21. doi:10.4141/A97-021.

- Ørskov, E.R., and I. McDonald. 1979. The estimation of protein degradability in the rumen from incubation measurements weighted according to rate of passage. *J. Agric. Sci.* 92:499. doi:[10.1017/S0021859600063048](https://doi.org/10.1017/S0021859600063048).
- Ortigue, I., and M. Doreau. 1995. Responses of the splanchnic tissues of ruminants to changes in intake: absorption of digestion end products, tissue mass, metabolic activity and implications to whole animal energy metabolism. *Ann. Zootech.* 44:321–346. doi:[10.1051/animres:19950401](https://doi.org/10.1051/animres:19950401).
- Robbins, C.T. 1983. *Wildlife feeding and nutrition*. 1st ed. San Diego (CA): Academic Press.
- Seo, S., C. Lanzas, L. O. Tedeschi, and D. G. Fox. 2007. Development of a mechanistic model to represent the dynamics of liquid flow out of the rumen and to predict the rate of passage of liquid in dairy cattle. *J. Dairy Sci.* 90:840–855. doi:[10.3168/jds.S0022-0302\(07\)71568-0](https://doi.org/10.3168/jds.S0022-0302(07)71568-0).
- Seo, S., C. Lanzas, L.O. Tedeschi, A.N. Pell, and D.G. Fox. 2009. Development of a mechanistic model to represent the dynamics of particle flow out of the rumen and to predict rate of passage of forage particles in dairy cattle. *J. Dairy Sci.* 92:3981–4000. doi:[10.3168/jds.2006-799](https://doi.org/10.3168/jds.2006-799).
- Silva, S.P. da. 2013. *Taxa de passagem em caprinos submetidos ou não à restrição alimentar*. PhD Thesis. Jaboticabal, Brazil: Universidade Estadual Paulista Júlio de Mesquita Filho, Faculdade de Ciências Agrárias e Veterinárias.
- Souza, A.P., N.R. St-Pierre, M.H.R.M. Fernandes, A.K. Almeida, J.A.C. Vargas, K.T. Resende, and I.A.M.A. Teixeira. 2017. Sex effects on net protein and energy requirements for growth of Saanen goats. *J. Dairy Sci.* 100:4574–4586. doi:[10.3168/jds.2016-11895](https://doi.org/10.3168/jds.2016-11895).
- Souza, A.P., N.R. St-Pierre, M.H.M.R. Fernandes, A.K. Almeida, J.A.C. Vargas, K.T. Resende, and I.A.M.A. Teixeira. 2020. Energy requirements and efficiency of energy utilization in growing dairy goats of different sexes. *J. Dairy Sci.* 103:272–281. doi:[10.3168/jds.2018-15930](https://doi.org/10.3168/jds.2018-15930).
- Steuer, P., K.H. Südekum, D.W. Müller, R. Franz, J. Kaandorp, M. Clauss, and J. Hummel. 2011. Is there an influence of body mass on digesta mean retention time in herbivores? A comparative study on ungulates. *Comp. Biochem. Physiol. A. Mol. Integr. Physiol.* 160:355–364. doi:[10.1016/j.cbpa.2011.07.005](https://doi.org/10.1016/j.cbpa.2011.07.005).
- Sugiura, N. 1978. Further analysts of the data by Akaike's information criterion and the finite corrections. *Commun. Stat. Theor. M.* 7:13–26. doi:[10.1080/03610927808827599](https://doi.org/10.1080/03610927808827599).