Retention time of digesta in the gastrointestinal tract of growing Saanen goats[1]

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ABSTRACT: This study examined the effect of increased BW on mean retention time (MRT) of both particulate and solute marker, gastrointestinal tract (GIT) development, and fiber digestion in the whole tract of growing Saanen goats using the slaughter technique. A total of 58 Saanen goats with initial BW of 15.7 ± 0.9 kg were allocated into 9 treatments with a 3 × 3 factorial arrangement consisting of 3 sexes (female, castrated males, and intact males) and 3 slaughter weights (initial, intermediate, and final; target BW of 16, 23, and 30 kg at slaughter, respectively). They were fed twice daily (0700 and 1600 h) with the identical diets for ad libitum intake. Mean retention time of particulate matter was estimated by in situ determination of indigestible NDF (iNDF), and the MRT of solute marker was determined by Cr-EDTA. Treatment effects were evaluated in a split-plot design, with sex as the main plot and slaughter weight as the subplot. Orthogonal polynomial contrasts were used to determine linear and quadratic effects of slaughter weight, whereas the effect of sex was compared using the Tukey test. The effects of sex and sex × slaughter weight were not significant for most of variables evaluated. The results showed that DMI (% BW) linearly decreased as slaughter weight increased ($P < 0.01$). Generally wet weight of the total GIT tissues (% BW) decreased and digesta pool sizes (g) linearly increased with increasing slaughter weight ($P \leq 0.05$). The ratio of iNDF:NDF for both ingested diet and reticulorumen digesta linearly increased as slaughter weight increased ($P \leq 0.05$). The MRT of particles did not change with increasing slaughter weight ($P = 0.94$). Mean retention time of particulate matter linearly increased in the omasum but linearly decreased in the abomasum with increasing slaughter weight ($P < 0.01$). Mean retention time of solute marker in the forestomachs linearly increased with increasing slaughter weight ($P < 0.01$). The results revealed a decreased selectivity with increasing BW, as supported by a greater ratio of iNDF:NDF for ingested diet. Increasing BW led to neither a longer particle MRT in the reticulorumen nor a digestive advantage. The results also indicated that, on average, 91% of fiber digestion occurred in the forestomachs of the goats.

Key words: fiber digestibility, mean retention time, pool size, slaughter weight

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INTRODUCTION

The gastrointestinal tract (**GIT**) of ruminants consists of sequential segments characterized by mixing or nonmixing digesta flows. Therefore, particulate matter has been suggested to have an age-independent or age-dependent distribution of residence times in different segments of the GIT (Ellis et al., 1994). Mean retention time (**MRT**) of digesta, especially in the reticulorumen, is one of the most important factors affecting the extent of digestion (Ellis, 1978). Additionally, when animals are fed ad libitum, physical constraints can limit intake because feed must disappear from the reticulorumen either by digestion or passage (Van Soest, 1994).

Growing animals increase their feed intake in response to increasing size (Lewis and Emmans, 2010).

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Additionally, the GIT development is characterized by increases in mass, volume, and surface area (Baldwin, 1999), and the volume of the GIT in herbivorous animals increases in proportion to BW (Parra, 1978; Demment and Van Soest 1985; Hackmann and Spain, 2010). However, other factors also may influence GIT development. Furthermore, rumen development clearly has a large impact on the digestive capabilities and supply of substrates to the growing ruminant (Baldwin et al., 2004).

Therefore, an increase of MRT is expected with increasing BW. However, Clauss et al. (2007) stated that the MRT is not much dependent on BW but rather on relative DMI. Therefore, it is essential to understand the differentiation in the various segments of GIT integrated to the feed intake, pool size, MRT, and fiber digestibility in growing animals.

The aim of this experiment was to evaluate the effect of increased BW on MRT of both particulate and solute marker, GIT development, and fiber digestion in the whole digestive tract of growing Saanen goats using the slaughter technique.

MATERIALS AND METHODS

The experiment was conducted at the goat facility at Universidade Estadual Paulista, Jaboticabal Campus, Sao Paulo, Brazil (21°14′ S, 48°17′ W, and 595 m above sea level). All animals were registered and cared for according to guidelines approved by the Human Animal Care and Handling Committee of the Faculty of Agricultural and Veterinarian Sciences, and the experiment was performed in accordance with the laws and regulations controlling experiments involving live animals in Brazil. During the experiment, the daily average minimum and maximum temperatures were 20.7 ± 1.86 and 35.7 ± 3.24°C, respectively, and the minimum and maximum relative humidities of the air were 36.1 ± 11.21 and 83.4 ± 6.72%, respectively.

Animals, Experimental Design, and Diets

A total of 58 Saanen goats (18 females, 20 castrated males, and 20 intact males) with initial BW 15.7 ± 0.9 kg were used in the experiment. The animals were housed in individual 0.5 by 1.0 m pens with free access to water. Treatments were administered in a 3 × 3 factorial arrangement consisting of 3 sexes (females, castrated males, and intact males) and 3 slaughter weights (initial, intermediate, and final with target BW of 16, 23, and 30 kg, respectively). The effects of treatments were evaluated in a split-plot design, with sex as the main plot and slaughter weight as the subplot. The goats within each sex were randomly allocated to 1 of 3 slaughter weights (20, 20, and 18 animals in the initial, intermediate, and final slaughter weights, respectively). All animals were fed the experimental diet before the start of the experiment, after they were weaned at 12 kg BW.

The animals were fed twice daily at 0700 and 1600 h. The experimental diet consisted of dehydrated corn plant (*Zea mays*), cracked corn grain, soybean (*Glycine max*) meal, soybean oil, limestone, mineral supplement, and ammonium chloride, and it was fed as a total mixed ration. Feeding rate was adjusted to yield orts of approximately 10% of intake. Orts were weighed and representative samples were taken on a daily basis. 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). The ingredients of the diet were individually sampled before the diet was mixed. All samples of feed ingredients and orts were stored at –10°C before further processing and chemical analyses. All animals were fed ad libitum during the whole experiment (139 d), but only the feed intake in the last 5 d before slaughter was used to calculate the MRT and, therefore, only those data are presented. Chemical composition of the diet was calculated from the individual ingredients (Table 1). The amount of ingested diet was calculated by subtracting orts from the offered diet.

Markers, Administration of Marker, and Slaughter

The retention time of particulate matter was estimated using in situ determined indigestible NDF (**iNDF**), and the solute marker was determined using Cr-EDTA prepared according to Downes and McDonald (1964). The Cr-EDTA was administered orally 4 times daily to all animals after reaching the target slaughter weight at 0100, 0700, 1300, and 1900 h during the 5-d period before slaughter. The average daily dose of Cr was 0.6 g.

To obtain measurements of MRT for different GIT compartments, different segments of the digestive tract were evacuated after the animals were slaughtered (2.2 ± 0.8 h after feeding). All animals were slaughtered in the morning, and a maximum of 3 animals were slaughtered per day. The slaughtering procedure took around 1 h per animal.

The GIT was removed and separated into reticulorumen, omasum, abomasum, small intestine, cecum, and colon (including rectum). The segments were weighed before and after emptying to determine the mass of digesta and the wet weight of each segment tissue. The

Table 1. Ingredients and chemical composition of the experimental diet

Item	Value
Dietary ingredient, % DM	
Dehydrated corn plant[1]	45.4
Cracked corn grain	26.6
Soybean meal	22.3
Soybean oil	1.6
Limestone	1.0
Mineral supplement[2]	2.2
Ammonium chloride	0.9
Diet chemical composition,[3] g/kg of DM ± SD	
DM	854 ± 10.9
OM	935 ± 2.0
CP	204 ± 5.4
Crude fat	80 ± 4.9
NDF	355 ± 25.0
iNDF[4]	108 ± 10.5
Lignin	57 ± 3.4

[1]Dehydrated corn plant consisted of whole corn plants harvested and chopped when the kernel milk line was approximately two-thirds of the distance down the kernel.

[2]Composition, per kilogram, 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, and 3 mg of Co.

[3]Mean and SD of 10 composite samples. Chemical composition of the diet was calculated from the individual ingredients.

[4]iNDF = indigestible NDF.

wet weight of the total GIT tissue and total GIT pool size were calculated from the sum of wet weight of individual tissue and individual pool size in the GIT, respectively. Pool size (wet digesta, DM, and NDF) was determined in each segment and expressed in grams. The reticulorumen digesta was separated into solid and liquid fractions by straining the contents through 4 layers of cheesecloth. These fractions were weighed and sampled according to the proportions determined to obtain a representative sample. The content from other segments (omasum, abomasum, small intestine, cecum, and colon) were individually placed into trays and mixed/homogenized before sampling. The pH of reticuloruminal and cecal digesta were measured using a digital potentiometer (TEC-5; Tecnal, Piracicaba, Sao Paulo, Brazil). The digesta from each GIT segment sampled were stored at –10°C for later processing and chemical analyses.

Mean Retention Time

Mean retention time of particulate and solute marker in different segments of the GIT was determined by the flux/compartmental pool method using Eq. [1] and [2], as described by Ellis et al. (1994):

$$K_e \text{ of IE} = \text{intake rate/compartmental mass}, \quad [1]$$

in which $\mathbf{K_e}$ is the fractional rate of escape per hour, **IE** is an indigestible entity with an intake rate expressed in grams per hour, a compartmental mass in the segment is expressed in grams, and

$$\text{MRT} = 1/K_e, \quad [2]$$

in which MRT is measured in hours.

The feed intake during the 5-d period before slaughter was used to determine the intake rate of the IE by iNDF. The amount of Cr administered during the same period was also used to determine the IE of solute marker. Total MRT in the GIT was calculated as the sum of MRT in the reticulorumen, omasum, abomasum, small intestine, cecum, and colon (including rectum).

Forestomach Contribution to Total Digested NDF

The forestomach contribution to total NDF digested was calculated using the ratio of iNDF:NDF in the ingested diet and cecum and colon digesta (Eq. [3]):

$$\text{NDF digestibility}_{\text{segment}} = \{1 - [(\text{iNDF:NDF}_{diet})/(\text{iNDF:NDF}_{segment})]\}, \quad [3]$$

in which $\text{iNDF:NDF}_{\text{diet}}$ is the ratio between iNDF and NDF in the ingested diet and $\text{iNDF:NDF}_{\text{segment}}$ is the ratio between iNDF and NDF in each segment. To calculate the forestomach contribution, it was assumed that no fiber digestion occurred between the omasum and the cecum. Hence, the proportion of NDF digested that occurred in the forestomach was determined by the ratio between NDF digestibility in the cecum and colon.

Chemical Analyses

The ingredients of diet and orts were oven-dried at 60°C for 72 h. The digesta from different GIT segments were freeze-dried for 96 h. Thereafter, all samples were milled to pass a 1-mm screen using a Wiley mill (Arthur H. Thomas Co., Philadelphia, PA). Concentrations of DM, ash, NDF, and Cr were determined in diet ingredients, orts, and digesta collected from the different segments of the GIT. The CP, crude fat, and lignin concentrations were also determined for all diet ingredients.

The concentration of DM was quantified by drying the material in an oven at 105°C for 24 h (AOAC, 1995; method 930.15) and ash content determined by complete combustion in a muffle furnace at 600°C for 3 h (AOAC, 1990; method 942.05). The concentration of NDF was analyzed according to the technique described by Mertens et al. (2002), using heat-stable α-amylase but without sodium sulfite, in an Ankom 220 Fiber Analyzer (Ankom Technology Corp.,

Fairport, NY). Furthermore, the concentration of NDF was expressed free of residual ash. The concentration of CP was estimated using the Dumas combustion method (LECO FP-528; LECO Corp., St. Joseph, Michigan; AOAC, 1990; method 990.03). The crude fat concentration was determined by extraction with petroleum ether in a Soxhlet apparatus for 6 h (AOAC, 1990; method 930.15). The lignin was analyzed by solubilization of cellulose in 12 *M* sulfuric acid after extraction with an acid detergent (AOAC, 1990; method 973.18). The concentration of Cr was determined after adding 5 mL of a 5:1 mixture of nitric and perchloric acids to 0.2 g DM of sample. Samples were then kept in the acidic solution overnight and thereafter gradually heated until completely digested. Marker concentration was analyzed with an atomic absorption spectrometer (Varian, model Spectra AA 220 FS; Alchem Technology, Denver, CO) with an acetylene and nitrous oxide flame (de Vega et al., 1998).

The iNDF content in the diet, orts, and digesta from all GIT segments was quantified by incubating 0.6-g DM samples in F57 bags (Ankom Technology Corp.) in the rumen of fistulated cattle for 288 h (Valente et al., 2011). After the in situ incubation, the bags were manually washed for 30 min and the content of iNDF was determined using an Ankom 220 Fiber Analyzer (Ankom Technology Corp.), as described by Mertens et al. (2002).

Statistical Analyses

The data, 58 observations (individual animals as the experimental unit), were analyzed using PROC MIXED (SAS Inst. Inc., Cary, NC) by the model

$$Y_{ij} = \mu + S_i + W_j + S_i \times W_j + e_{ij},$$

in which Y_{ij} is dependent variable, μ is the overall mean, S_i is the effect of sex i (main plot), W_j is the effect of slaughter weight j, $S_i \times W_j$ is the interaction between sex i and slaughter weight j (main plot error), and $e_{ij} \sim N(0, \sigma_e^2)$ is the random residual error with a variance σ_e^2. The effect of sex, slaughter weight, and their interactions were considered fixed effects. Orthogonal polynomial contrasts were used to determine linear and quadratic effects of slaughter weight. The effects of sex and sex within slaughter weight were compared by Tukey test. Statistical significance was set at $P \leq 0.05$.

Residuals were plotted against the predicted values to check the model assumptions regarding homoscedasticity, independence, and normality of the errors. A data point was deemed to be an outlier and removed from the database if the Studentized residual was outside the ±3.0 range.

RESULTS

Body Weight and Feed Intake

Intact males had a greater BW ($P < 0.01$) than castrated males or females (24.5 vs. 23.5 and 23.1 kg, respectively). There was a significant effect of sex × slaughter weight on BW ($P = 0.01$), with the intact males slaughtered at intermediate and final weight having a greater BW than castrated males and females ($P \leq 0.03$). Intake of DM, OM, and NDF as a percentage of BW linearly decreased with increasing slaughter weight ($P \leq 0.03$). Intake of iNDF (% BW) did not changed with increasing slaughter weight ($P = 0.77$; Table 2).

Measurements of pH and Wet Weights of Gastrointestinal Tissues

The pH of ruminal digesta quadratically changed as slaughter weight increased ($P = 0.01$), with the highest values observed with animals slaughtered at the intermediate weight. Castrated males had greater wet weight of small intestine tissue (3.1% BW) and total GIT tissue (7.5% BW) than intact males (2.7 and 6.8% BW, respectively; $P < 0.01$), but neither of them differed from females (2.8 and 7.2% BW, respectively; $P \geq 0.24$). Castrated males and females had greater wet weight of colon tissue compared with intact males (1.3 vs. 1.2% BW, respectively; $P \leq 0.03$). The wet weight (% BW) of reticulorumen, abomasum, small intestine, and cecum tissues linearly decreased with increasing slaughter weight ($P \leq 0.01$). The wet weight (% BW) of colon and total GIT tissues quadratically decreased as the slaughter weight increased and reached the smallest values in animals at final slaughter weight ($P \leq 0.03$).

Digesta Pool Size and Indigestible NDF:NDF Ratio

Castrated males had greater DM content of reticulorumen and total GIT than females (501 vs. 432 g and 710 vs. 613 g, respectively; $P \leq 0.02$), but neither of them differed significantly in these values from intact males (479 and 686 g, respectively; $P \geq 0.07$). Intact and castrated males had greater omasum pool size (104 and 101 g of wet digesta, 26 and 25 g of DM, and 10 and 9 g of NDF content, respectively) compared with females (75, 18, and 7 g for wet, DM, and NDF content, respectively; $P \leq 0.05$). Intact males had greater NDF content in the small intestine compared with castrated males and females (10 vs. 8 g, respectively; $P \leq 0.03$). Pool size (wet digesta, DM, and NDF) of the reticulorumen, omasum, cecum, colon, and total GIT linearly increased as slaughter weight increased ($P < 0.01$; Table 3). Wet digesta, DM, and NDF content in

Table 2. Body weight, feed intake before slaughter, pH of digesta in the reticulorumen and cecum, and wet weight of the gastrointestinal tissue (without digesta) in goats of different sexes and slaughtered at 3 different target weights (initial, intermediate, and final)

	Initial			Intermediate			Final				*P*-value[1]			
Item	Females	Castrated males	Intact males	Females	Castrated males	Intact males	Females	Castrated Males	Intact males	SEM	Sex	SW_L	SW_Q	Sex × SW
No.	6	7	7	6	7	7	6	6	6	–	–	–	–	–
BW, kg	17.0	16.4	16.6	22.2[b]	22.9[b]	24.2[a]	30.0[b]	31.2[b]	32.6[a]	0.43	<0.01	<0.01	<0.01	0.01
Intake,[2] % BW														
DM	3.5	4.0	3.9	3.8	3.6	3.5	3.0	3.3	3.1	0.19	0.39	<0.01	0.25	0.44
OM	3.3	3.7	3.6	3.5	3.3	3.3	2.7	3.1	2.9	0.18	0.39	<0.01	0.25	0.39
NDF	1.3	1.2	1.2	1.3	1.3	1.2	1.0	1.1	1.1	0.08	0.91	0.03	0.13	0.78
iNDF[3]	0.29	0.34	0.36	0.40	0.32	0.30	0.32	0.34	0.36	0.032	0.98	0.77	0.92	0.12
pH														
Reticulorumen	5.6	5.7	5.6	5.8	5.9	5.7	5.7	5.7	5.6	0.06	0.07	0.22	0.01	0.52
Cecum	6.4	6.3	6.2	6.2	6.6	6.6	6.4	6.5	6.4	0.10	0.41	0.07	0.26	0.19
Wet weight tissues, % BW														
Reticulorumen	2.3	2.4	2.4	2.4	2.2	2.2	2.0	2.1	1.9	0.09	0.27	<0.01	0.12	0.13
Omasum	0.24	0.24	0.25	0.22	0.29	0.26	0.26	0.27	0.29	0.016	0.11	0.06	0.93	0.15
Abomasum	0.57	0.58	0.56	0.48	0.51	0.50	0.37	0.45	0.41	0.022	0.08	<0.01	0.61	0.59
Small intestine	3.1	3.5	3.1	3.0	3.3	2.7	2.4	2.6	2.3	0.15	<0.01	<0.01	0.06	0.66
Cecum	0.16	0.15	0.16	0.16	0.13	0.14	0.12	0.11	0.12	0.009	0.10	<0.01	0.23	0.87
Colon[4]	1.4	1.3	1.3	1.3	1.4	1.3	1.2[a]	1.2[a]	1.0[a]	0.052	0.01	<0.01	0.03	0.02
Total GIT[5]	7.7	8.2	7.8	7.6	7.8	7.1	6.3	6.6	5.6	0.235	<0.01	<0.01	0.01	0.49

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

[1]Main effects and interaction of sex × slaughter weight. SW_L = linear effect of slaughter weight; SW_Q = quadratic effect of slaughter weight; Sex × SW = interaction of sex × slaughter weight.

[2]Intake = ingested diet (offered diet – orts).

[3]iNDF = indigestible NDF.

[4]Colon represents the colon and rectum.

[5]Total GIT is the sum of wet weight of reticulorumen, omasum, abomasum, small intestine, cecum, and colon tissues.

the small intestine quadratically changed as slaughter weight increased, with the greatest values observed for animals slaughtered at the final weight ($P \leq 0.05$).

The ratio of iNDF:NDF for both ingested diet and reticuloruminal digesta linearly increased as slaughter weight increased ($P \leq 0.05$; Table 4). The ratio of iNDF:NDF in abomasal digesta quadratically changed as slaughter weight increased, with the smallest ratios observed in the animals slaughtered at intermediate weight ($P = 0.02$). The ratio of iNDF:NDF in colon digesta quadratically changed as slaughter weight increased, with the greatest ratios observed in the animals slaughtered at final weight ($P = 0.04$). The NDF digestibility and the contribution of forestomach to the total digested NDF did not change with increasing slaughter weight ($P \geq 0.27$). On average, the forestomach was responsible for 91% of the total NDF digested (across all treatments).

Mean Retention Time

Reticulorumen retention time of particles did not change with increasing slaughter weight ($P = 0.94$). Mean retention time of digesta in the omasum linearly increased and MRT in the abomasum linearly decreased as slaughter weight increased ($P < 0.01$; Table 5). Furthermore, MRT of solute marker in the reticulorumen, omasum, and total GIT linearly increased with increasing slaughter weight ($P < 0.01$; Table 5).

DISCUSSION

The greater BW of intact males than castrated males and females at intermediate and final slaughter weight may explain most of the differences between sexes and the sex × slaughter weight interactions observed by Leite et al. (2015). Therefore, the effects of sex and sex × slaughter weight are not discussed further below.

Methodological Aspects

Accurate estimation of reticulorumen pool size requires steady state conditions. Alternatively, the average pool size can be determined by evacuating the reticulorumen to allow for a representative estimate (Ellis et al., 2002; Huhtanen et al., 2007). Huhtanen et al. (2007) stated that for a reliable estimation of reticulorumen pool

Table 3. Pool size of different gastrointestinal tract (GIT) segments in goats of different sexes and slaughtered at 3 different target weights (initial, intermediate, and final)

	Initial			Intermediate			Final				*P*-value[1]			
Item	Females	Castrated males	Intact males	Females	Castrated males	Intact males	Females	Castrated males	Intact males	SEM	Sex	SW_L	SW_Q	Sex × SW
Reticulorumen, g														
Wet	2,451	2,444	2,327	3,479	3,394	3,412	3,674	4,231	4,278	223.5	0.66	<0.01	0.23	0.45
DM	334	389	340	475	490	469	488	624	628	33.6	0.05	<0.01	0.64	0.20
NDF	170	179	166	244	226	221	236	311	303	18.8	0.37	<0.01	0.82	0.10
Omasum, g														
Wet	45	47	55	60	100	102	121	157	155	13.6	0.03	<0.01	0.34	0.62
DM	11	12	14	14	23	26	28	39	37	3.4	0.01	<0.01	0.34	0.62
NDF	5	4	6	6	9	10	10	14	15	1.4	0.04	<0.01	0.44	0.57
Abomasum, g														
Wet	360	375	334	378	438	387	325	439	329	46.1	0.14	0.83	0.22	0.86
DM	52	57	52	45	57	41	41	58	37	8.4	0.10	0.24	0.74	0.89
NDF	17	16	16	19	21	17	16	20	16	2.3	0.33	0.44	0.19	0.74
Small intestine, g														
Wet	317	306	346	346	359	358	492	468	545	38.0	0.42	<0.01	0.03	0.90
DM	30	30	36	34	32	35	41	46	53	4.1	0.18	<0.01	0.05	0.79
NDF	6	8	10	8	6	8	9	9	12	1.1	0.03	<0.01	0.04	0.43
Cecum, g														
Wet	136	90	113	131[ab]	171[a]	100[b]	179	141	169	17.4	0.36	<0.01	0.75	0.02
DM	17	13	16	17	21	13	23	19	21	2.4	0.49	0.01	0.44	0.06
NDF	7	6	7	7	9	5	9	8	9	1.0	0.82	0.01	0.47	0.12
Colon,[2] g														
Wet	294	249	272	334	434	455	533	454	553	35.7	0.22	<0.01	0.54	0.09
DM	57	50	58	59	73	85	118	97	101	9.0	0.55	<0.01	0.23	0.20
NDF	23	21	25	24	31	37	50	41	44	3.6	0.35	<0.01	0.22	0.15
Total GIT,[3] g														
Wet	3,602	3,511	3,459	4,724	4,897	4,813	5,234	5,890	6,005	288.8	0.51	<0.01	0.35	0.57
DM	501	551	522	627	697	669	711	882	867	47.4	0.05	<0.01	0.81	0.63
NDF	238	228	234	298	304	298	316	412	385	26.6	0.37	<0.01	0.91	0.33

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

[1]Main effects and interaction of sex × slaughter weight. SW_L = linear effect of slaughter weight; SW_Q = quadratic effect of slaughter weight; Sex × SW = interaction of sex × slaughter weight.

[2]Colon represents the colon and rectum.

[3]Total GIT is the sum of wet weight of reticulorumen, omasum, abomasum, small intestine, cecum, and colon tissues.

size and digesta kinetic parameters, at least 2 evacuations should be done (one close to its minimum and another close to its maximum value). In this study, the minimum and maximum reticulorumen pool size values occurred close to the feeding and at 4 h after feeding, respectively. To avoid maximum and minimum reticulorumen fill, the animals in the present study were slaughtered 2.2 ± 0.8 h after feeding in an attempt to obtain GIT close to steady state and near-average pool size.

Feed Intake, Wet Weights of Gastrointestinal Tissues, and pH

Increasing the slaughter BW caused increases in feed intake and wet weight of the measured tissues (data not shown), whereas intakes of DM, OM, and NDF and wet weight of most the measured tissues decreased when expressed as percentages of BW. This may be related to the fact that the maintenance energy requirement decreases with increasing BW, which can be related to the proportional decrease of the visceral organs (CSIRO, 2007). Previous studies showed that a large proportion of maintenance energy requirements in animals can be attributed to the visceral organs, especially the liver and GIT (Johnson et al., 1990; Fluharty and McClure, 1997; Nozière et al., 1999).

Low ruminal pH can affect fiber digestibility, because of the reduction in the fibrolytic microbial population, and it has been attributed to a reduction in the ability of fibrolytic bacteria to attach to feed particles when pH is lower than 6.0 (Cheng et al., 1980; Russell and Wilson, 1996). The low pH observed in this study is likely be related to the time at which it was measured (around 3 h after feeding). Usually, greatest ruminal pH

Table 4. Ratio of indigestible NDF (iNDF) to NDF (NDF) in different gastrointestinal tract segments of goats of different sexes and slaughtered at 3 different target weights (initial, intermediate, and final)

	Initial			Intermediate			Final				*P*-value[1]			
Item	Females	Castrated males	Intact males	Females	Castrated males	Intact males	Females	Castrated males	Intact males	SEM	Sex	SW_L	SW_Q	Sex × SW
iNDF:NDF														
Intake[2]	0.23	0.27	0.30	0.33	0.26	0.28	0.29	0.31	0.32	0.025	0.50	0.05	0.73	0.16
Reticulorumen	0.49	0.46	0.46	0.49	0.54	0.53	0.60	0.50	0.50	0.032	0.53	0.02	0.34	0.33
Omasum	0.52	0.51	0.49	0.44	0.57	0.52	0.62	0.56	0.50	0.048	0.49	0.17	0.48	0.39
Abomasum	0.79	0.79	0.86	0.67	0.66	0.64	0.77	0.79	0.60	0.063	0.63	0.09	0.02	0.21
Small intestine	0.44	0.38	0.38	0.49	0.48	0.49	0.47	0.50	0.43	0.041	0.66	0.06	0.09	0.73
Cecum	0.60	0.64	0.62	0.64	0.69	0.68	0.84	0.65	0.62	0.056	0.59	0.12	0.91	0.40
Colon[3]	0.70[a]	0.68[b]	0.58[b]	0.70[b]	0.76[ab]	0.82[a]	0.83[a]	0.76[ab]	0.71[b]	0.031	0.34	<0.01	0.04	0.01
NDF digestibility														
Forestomach	0.61	0.56	0.49	0.52	0.64	0.58	0.60	0.50	0.50	0.046	0.31	0.64	0.27	0.16
Contribution to total digested NDF, %														
Forestomach	91.7	95.6	88.8	90.6	93.8	88.2	99.2	82.9	87.5	5.47	0.53	0.66	0.98	0.54

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

[1]Main effects and interaction of sex × slaughter weight. SW_L = linear effect of slaughter weight; SW_Q = quadratic effect of slaughter weight; Sex × SW = interaction of sex × slaughter weight.

[2]Intake = ratio of iNDF:NDF ingested (offered diet – orts).

[3]Colon represents the colon and rectum.

Table 5. Mean retention time (MRT) of particulate and solute marker in different gastrointestinal tract (GIT) segments of goats of different sexes and slaughtered at 3 different target weights (initial, intermediate, and final), estimated by indigestible NDF (iNDF) for particulate matter and by Cr-EDTA for solute marker

	Initial			Intermediate			Final				*P*-value[1]			
Item	Females	Castrated males	Intact males	Females	Castrated males	Intact males	Females	Castrated males	Intact males	SEM	Sex	SW_L	SW_Q	Sex × SW
MRT by iNDF, h														
Reticulorumen	42.0	33.2	31.6	36.3	43.6	38.1	36.6	38.3	32.6	3.99	0.33	0.94	0.21	0.36
Omasum	1.3	1.1	1.0	0.8[b]	1.8[a]	1.6[a]	1.8	1.9	1.6	0.23	0.26	<0.01	0.85	0.01
Abomasum	8.3	5.3	5.6	4.0	5.2	3.7	3.0	3.8	2.1	0.74	0.08	<0.01	0.50	0.09
Small intestine	1.3	1.1	1.4	1.1	1.1	1.2	1.1	1.0	1.1	0.14	0.23	0.17	0.71	0.90
Cecum	2.2	1.3	1.8	1.4	2.4	1.3	1.5	1.4	1.3	0.33	0.62	0.15	0.61	0.07
Colon[2]	8.4[a]	5.2[b]	6.4[ab]	4.6[b]	8.8[a]	10.8[a]	10.1[a]	7.2[ab]	6.6[b]	0.91	0.58	0.09	0.35	<0.01
GIT[3]	68.0[a]	44.9[b]	47.0[b]	47.9	59.7	56.5	49.5	53.6	43.8	5.78	0.47	0.37	0.39	0.04
MRT by Cr-EDTA, h														
Reticulorumen	2.3	3.7	3.3	3.9	4.1	4.3	5.9	5.4	4.3	0.62	0.65	<0.01	0.90	0.28
Omasum	0.04	0.09	0.10	0.07	0.11	0.15	0.17	0.17	0.12	0.024	0.26	<0.01	0.87	0.14
Abomasum	0.5	0.5	0.6	0.5	0.7	0.4	0.5	0.5	0.4	0.09	0.30	0.36	0.55	0.32
Small intestine	1.0	1.3	1.0	0.8	1.0	1.1	1.0	1.0	1.1	0.13	0.40	0.67	0.16	0.43
Cecum	1.1	1.0	1.2	1.1[ab]	1.4[a]	0.6[b]	1.4[a]	0.8[b]	0.9[b]	0.17	0.08	0.27	0.74	0.02
Colon[2]	4.2	3.8	3.9	3.1[b]	4.5[a]	4.2[ab]	5.9[a]	4.2[b]	4.1[b]	0.45	0.61	0.06	0.18	0.02
GIT[3]	9.1	9.7	10.5	8.7[b]	11.6[a]	10.0[ab]	14.5[a]	11.3[b]	10.4[b]	0.71	0.44	<0.01	0.08	<0.01

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

[1]Main effects and interaction of sex × slaughter weight. SW_L = linear effect of slaughter weight; SW_Q = quadratic effect of slaughter weight; Sex × SW = interaction of sex × slaughter weight.

[2]Colon represents the colon and rectum.

[3]Total GIT is the sum of wet weight of reticulorumen, omasum, abomasum, small intestine, cecum, and colon tissues.

occurs just before feeding and declines for approximately 5 to 7 h thereafter, before gradually increasing again (Palmonari et al., 2010). Additionally, it is important to consider that after the animal is slaughtered, the rumen fermentation continues without absorption of VFA, which would lead to an increased VFA concentration in the reticulorumen and, consequently, a decreased pH.

Fiber Digestion

The ratio of iNDF:NDF in digesta can be used to determine the contribution of different segments of the GIT to digestion of fiber (Walz et al., 2004; Ahvenjärvi et al., 2010). An increase in iNDF:NDF ratio for ingested diet with increasing slaughter weight was observed in this study. A possible explanation can be related to a decrease of feed selectivity with increasing BW. Studies comparing different herbivorous species (Clauss et al., 2010; Müller et al., 2013; Steuer et al., 2014) showed that the degree of selectivity usually declines with increasing BW (i.e., smaller herbivores have narrower mouths and so can select higher-quality food compared with the large herbivores). For instance, the animals at initial and intermediate slaughter weight in this study had lower ratio of iNDF:NDF for ingested diet than the offered diet (0.27 and 0.29 vs. 0.31, respectively). Therefore, animals at initial and intermediate slaughter weight may have selected for higher-quality diet parts, which would lead to better quality of ingested diet compared with animals at final slaughter weight.

Walz et al. (2004) found a progressive decrease in potentially digestible NDF relative to iNDF through different segments of the ruminant GIT with the exception of the small intestine. Additionally, it has been shown that additional cell wall digestion occurs in the omasum (Ahvenjärvi et al., 2000; Walz et al., 2004; Huhtanen et al., 2010), an effect also observed in this study. However, the observed ratio of iNDF:NDF in the abomasal digesta at initial slaughter weight in the present study may be unrepresentative because the ratios of iNDF:NDF in the cecum and colon were lower than the observed values in the abomasum (Walz et al., 2004; Leite et al., 2015). For instance, a similar ratio of iNDF:NDF in the abomasum and cecum is expected, and a greater ratio is expected in the colon compared with that in the abomasum. Therefore, to calculate the proportion of NDF digested, no fiber digestion was considered to occur between the omasum and cecum. The proportion of NDF digested in the forestomach across different slaughter weight groups in this study was about 91%, which is similar to the value for cattle obtained from meta-analysis by Huhtanen et al. (2010).

Demment and Van Soest (1985) argued that large herbivores animals should have greater capacity to retain feed for longer times and digest it more extensively than small herbivores. However, Müller et al. (2013) analyzed large interspecies data sets of feeding trials on captive herbivores and concluded that larger herbivore species could eat more food than smaller species in relation to metabolic requirements but larger species had no digestive advantage. Furthermore, the increased ratio of iNDF:NDF for the reticulorumen and colon with increasing slaughter weight may be a consequence of decreased selectivity with increasing weight, as supported by the greater ratio of iNDF:NDF observed for ingested diet in the present study. Additionally, Clauss et al. (2013), comparing different species of herbivores, stated that increasing BW did not improve digestibility.

Estimates of Mean Retention Time of Particulate and Solute Marker

Studies using the flux/compartmental pool method with iNDF as the internal marker can give more biologically relevant predictions (Krizsan et al., 2010). Furthermore, a negative relationship between DMI and MRT has been reported (Colucci et al., 1990; Huhtanen and Kukkonen, 1995; Dias et al., 2011). No alteration in MRT in the reticulorumen with increasing slaughter weight was observed in this study. The similar iNDF intake (% BW) could explain the observed similarities of particle MRT in the reticulorumen.

This study showed that the particulate matter MRT in the reticulorumen represented 70% of total GIT retention time in Saanen goats. This value is similar to 72% observed for dairy cows (Ahvenjärvi et al., 2010) and 71% for goats (Walz et al., 2004), respectively. Previous studies have also indicated that the reticulorumen is the major site of feed MRT in cattle (Ellis et al., 1994; Huhtanen and Vanhatalo, 1997). Additionally, Huhtanen et al. (2010) stated that the contribution of the hindgut to total NDF digestion should be slightly lower in duodenal compared with omasal sampling because of additional fiber digestion occurring in the omasum (Ahvenjärvi et al., 2001).

The GIT development is characterized by increases in mass, volume, and surface area (Baldwin, 1999). Furthermore, tissue growth is followed by a differentiation, which results in physical changes including an increase or decrease in the GIT segments (% BW). The increased wet weight of omasum tissue and decreased wet weight of abomasum tissue (% BW) may have contributed to the increased and decreased MRT through the omasum and abomasum, respectively, in this study, although the iNDF intake (% BW) was similar among slaughter weights.

Studies have shown a negative relationship between DMI and reticulorumen MRT of solute marker (Grovum

and Williams, 1977; Colucci et al., 1990). Müller et al. (2013) confirmed that the DM concentration of GIT contents decreases with increasing BW in herbivores and stated that it is to compensate for the less favorable volume:surface area ratio in the GIT. It could lead to an increase of liquid fraction MRT, which it is in agreement with the results of the present study.

This study revealed a decreased selectivity with increasing BW, as supported by a greater ratio of iNDF:NDF for ingested diet. Increasing BW lead to neither a longer particle MRT in the reticulorumen nor a digestive advantage. The results also indicated that, on average, 91% of fiber digestion occurred in the forestomachs of the goats.

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