Tropical Animal Health and Production (2022) 54: 42
https://doi.org/10.1007/s11250-022-03053-6

REGULAR ARTICLES

Performance and ruminal and intestinal morphometry of Santa Inês sheep submitted to feed restriction and refeeding

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Received: 19 July 2021 / Accepted: 4 January 2022 / Published online: 11 January 2022

Abstract
A study was carried out to evaluate the performance and ruminal and intestinal morphology of Santa Inês sheep subjected to feed restriction followed by refeeding. A total of 40 uncastrated lambs with an approximate age of 120 ± 15 days and mean body weight (BW) of 17.04 ± 1.18 kg were randomly divided into two groups of BW (20 and 25 kg of BW), which were subjected to different levels of feed restriction (0%, 25%, and 40% of feed restriction). For performance variables, six treatments were considered (0, 25%, and 40% of feed restriction for both groups (20 and 25 kg of BW)) and five treatments for morphometric variables (ad libitum, 25% and 40% for both groups (20 and 25 kg of BW)). All animals were slaughtered with 14 weeks of experimentation. During the feed restriction phase, the dry matter intake (DMI), feed efficiency (FE), and average daily gain (ADG) decreased ($P < 0.05$) as the level of restriction increased. During the refeeding phase, lambs with 20 kg of body weight subjected to restriction presented lower ($P < 0.05$) DMI in the ad libitum treatment. However, lambs with 25 kg of body weight under feed restriction presented DMI, FE, and ADG similar ($P > 0.05$) to the group ad libitum. The final body weight of restricted lambs after refeeding (both groups 20 and 25 kg of body weight) was lower ($P < 0.05$) than lambs feed ad libitum. In relation to morphology, restricted lambs showed greater height ruminal papillae and larger ($P < 0.05$) area of ruminal absorption and intestinal absorption, especially the lambs under treatment 40% of feed restriction. The feed restriction followed by refeeding in sheep provided partial compensatory gain, in addition, caused morphological changes in the rumen and intestine that allowed greater absorption and possibly compensatory gain in periods of greater refeeding.

Keywords Compensatory gain · Hair sheep · Histology · Performance · Small ruminants

Introduction

The sheep industry is a very important global activity, and in the Brazil, it is especially developed in the Northeast, which accounts for the largest proportion of the herd. Currently, there is a growing demand for sheep meat, both in quantity and in quality in the Brazilian market, being necessary to seek alternatives to improve the performance and carcass characteristics of the herds. This activity can generate a good profitability for the producer, as long as technologies adapted to the local conditions of production are adopted (Sotta et al. 2021).

Despite the growth in recent years of sheep farming in the Brazilian Northeast, the national sheep meat is not produced in sufficient quantity to serve the domestic market and does not have standardized quality to compete in the foreign market (Battagin et al. 2021). Thus, much of this deficit is supplied

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by meat imported from Mercosur and New Zealand countries (Suguisawa et al. 2009).

In order to meet this demand, the technique that has been most successful is the confinement, because it allows the producer to increase the density and productivity of farms. However, this production system has disadvantages, particularly related to animal feeding costs (Lopes and Magalhães 2005). As a result, various nutritional strategies are being used to reduce feeding costs without affecting the quality of the final product. One of these strategies is feed restriction followed by refeeding to produce compensatory gain (Abouheif 2013).

Sheep respond differently to refeeding when dietary restrictions are lifted. Compensatory gain was associated with higher feed intake (Kamalzadeh et al. 1997), better feed conversion (Homem Júnior et al. 2007; Shadnoush et al. 2011), greater feed efficiency (Abouheif et al. 2013), and greater weight gain (Abouheif et al. 2015), and mainly, with the best nutrient utilization due to the modifications in the size and morphology of the internal organs (Addah et al. 2017).

The organs and viscera, compared to other parts of the body, exhibit different growth rates and are primarily influenced by the chemical composition of the diet and its energy level (Kamalzadeh et al. 1998; Porto Filho et al. 2020). The gastrointestinal epithelium, for example, is responsible for many physiological functions, including digestion, absorption, transport, and metabolism of nutrients, with digestion and absorption being related to the development of rumen papillae and intestinal villi (Xu et al. 2009). According to Martens et al. (2012), sheep initially fed a low energy diet and subsequently with supplementation of the concentrate undergo changes in the ruminal epithelium, particularly in the size of the papillae, in adaptation to changes in rumen parameters such as pH, fatty acid concentration, and osmotic pressure. The epithelium of the small intestine can also change its structure according to the feed ingested, since it adapts to meet the nutritional requirements of the animal (Penner et al. 2011; Porto Filho et al. 2020). Despite these reports, there are few studies in the literature that demonstrate the effects of feed restriction and refeeding on the morphology of the digestive system. Our working hypothesis was that feed restriction and refeeding modify the ruminal and intestinal morphometry allowing a compensatory gain in Santa Inês sheep. Therefore, the aim of this study was to evaluate the performance and intestinal and ruminal morphometry of Santa Inês sheep submitted to feed restriction followed by refeeding.

Materials and methods

Location, animals, diets, and feeding regimes

The experiment was conducted in the Goat Production Sector of the Human Sciences, Social, and Agrarian Center of the Federal University of Paraiba (Universidade Federal da Paraíba-UFPB), located in the city of Bananeiras, State of Paraíba, Brejo Paraibano microregion. The local altitude is 552 m, lying between the geographic coordinates 6° 41′ 11″ south latitude and 35° 37′ 41″ west longitude of Greenwich, with a hot and humid climate. The temperature of the region varies between the maximum of 36 °C and the minimum of 18 °C with average annual precipitation of 1,200 mm (INMET 2018). The climate, according to the classification of Köppen, is type As1, hot and humid with autumn–winter rain.

A total of 40 Santa Inês lambs, aged approximately 120 ± 15 days and with mean body weight of 17.04 ± 1.18 kg, were used. The animals were identified with numbered collars, weighed, vaccinated against clostridiosis, and destemmed. For control of eimeriosis, sodium sulfaquinoxaline 25 g was used for 4 days. The treatments were distributed according to the feeding regime, with the purpose of evaluating the effect of feed restriction on performance and morphometry of rumen and delegated gut.

Each treatment consisted of four replicates (pens) with two lambs per pen that had dimensions of 3m^2 (1.5×2.0 m). The animals of the 1st and 4th treatments were fed ad libitum throughout the experiment; the animals of the 2nd and 3rd treatments were fed ad libitum up to 20 kg of weight, and then subjected to 25 and 40% restriction of the consumption for 35 days; and the 5th and 6th treatments were fed ad libitum up to 25 kg of weight, and then, they were submitted to the same restriction protocol of treatments 2 and 3. After the restriction, the animals returned to feed ad libitum. The refeeding time for groups 20 and 25 kg were 28 and 49 days, respectively.

A diet was formulated with a 30:70 forage:concentrate ratio, based on the recommendations of the National Research Council (NRC 2007), and the gain content consisted of 250 g/day. The forage was composed of sugar cane bagasse (*Saccharum officinarum* L.) and crushed in a crushing machine, reducing to smaller particles to facilitate the homogenization of the ingredients of the experimental diets.

Feeding regimes of the restricted groups were calculated by determining the average dry matter intake (DMI) of lambs ad libitum from the previous day, and multiplying the mean by 0.75 and 0.60 was determined the amount of feed to be offered to the lambs of the restriction groups 25 and 40% of ad libitum intake, respectively. Water was supplied ad libitum. The ingredients of the feed were pre-dried at 55 °C for 72 h and then ground with a Willey mill (Tecnal, Piracicaba City, São Paulo State, Brazil) with a 1-mm sieve, stored in air-tight plastic containers with lids (ASS®, Ribeirão Preto, São Paulo, Brazil), labeled, and subjected to further laboratory analysis to determine the chemical composition according AOAC (2012) to determine DM (method 967.03), ash (method 942.05), CP (method 981.10), and ether extract (method 920.29). To quantify the neutral detergent fiber (NDF) contents, the methodology of Van Soest et al. (1991) was used, with the modifications proposed in the Ankon device manual (Ankon Technology Corporation, Macedon, NY, USA). The percentages of the ingredients and composition of the ingredients used in the experimental diet formulation are shown in Table 1.

Animal performance

The weight control of the animals was performed weekly, in the morning, before the feeding, during the whole experimental period using a digital scale. The final body weight was obtained on the last day of the experiment. The average daily gain (ADG) was calculated using the initial and final body weight, as well as the feed efficiency (FE) was calculated with the data of the weights of these animals.

Sampling and analysis

After 14 experimental weeks, all animals were euthanized according to the guidelines of the National Council for the Control of Animal Experimentation using a compressed air gun. This was followed by the collection of rumen fragments (1 cm^2) and small intestine fragments (1 cm), which were then fixed in 10% formalin. Histological processing was performed in the Histology Laboratory of the Graduate Program in Animal Science of UFPB, following the standard histological processing protocol described by Ramos et al. (2011). Samples were cut (5 μm thick) from the paraffin blocks with a microtome and stained using hematoxylin and eosin.

Samples from eight animals per treatment were used for the morphometric analyses of the thickness of the intestinal mucosa and submucosa, papilla height, and rumen muscle layer thickness. Two images per animal were randomly chosen and scanned at 5 × magnification using an Olympus BX-60 microscope and a Zeiss AxioCam camera coupled to the digital image capturing program Motic Image Plus 2.0. From each image, three measurements were performed for a sample size of 48 per treatment.

Table 1 Proportion of ingredients and chemical composition of feed

Ingredients	($g\ kg^{-1}$) in DM
Sugarcane bagasse	300.0
Corn	520.0
Soybean meal	150.0
[1]Supplement mineral	15.0
Limestone	10.0
Ammonium chloride	5.0
Chemical composition	
Dry matter (%)	90.00
Crude protein (%)	17.55
Ethereal extract (%)	2.08
Neutral detergent fiber (%)	36.18
Fiber in acid detergent (%)	13.82
Metabolizable energy ME (kcal kg^{-1} DM)	3.80

[1]Supplement mineral (nutrient/kg supplement): vitamin A 135,000.00 U.I.; vitamin D3 68,000.00 U.I.; vitamin E 450.00 U.I.; calcium 240 g; phosphorus 71 g; potassium 28.2 g; sulfur 20 g; magnesium 20 g; copper 400 mg; cobalt 30 mg; chromium 10 mg; iron 2500 mg; iodine 40 mg; manganese 1350 mg; selenium 15 mg; zinc 1700 mg; maximum fluoride 710 mg. Solubility of phosphorus (P) in 2% citric acid (min.). [2]Free protein and ash

Statistical analysis

The experimental design was completely randomized with six or five treatments, the treatments ad libitum in the weights 20 and 25 kg formed by four animals and the others formed by eight animals totaling 40 animals. Six treatments were considered when the variables were of one of the specific periods (restriction phase and refeeding phase), in which the ad libitum treatment was separated in two (ad libitum of 20 kg and ad libitum of 25 kg). As for the variables of rumen and small intestine morphometry, five treatments were considered, with ad libitum treatment being only one. After obtaining the data, a database was edited for further statistical analysis.

The residues were plotted against the predicted values and were used to verify the model assumptions of homoscedasticity, independence, and normality of residuals (Shapiro–Wilk). A record was considered an outlier and removed from the database when the studentized residue was outside the ± 2.5 range.

The analysis of variance was made for all treatments (six treatments) as well as isolating treatments according to weight (three treatments for lambs of 20 kg and three treatments for lambs of 25 kg of body weight), according to the mathematical model described below:

$$yij = \mu + Ti + Wj + eij$$

where:

yij variable under study;
μ mean common to all observations;
Ti effect of treatments;
W*j* effect of weights;
eij random error associated with all observations.

The means of the variables were compared using the GLM procedure of the program Statistical Analyzes System (SAS, 2013), by the Tukey test at the 5% probability level.

Results

Performance during feed restriction and refeeding phase

During the restriction phase, the DMI decreased ($P < 0.05$) according to the increase in the level of restriction. Similarly, ADG and final body weight followed the same trend ($P < 0.05$) as DMI, since they are highly related (Table 2). The lambs that showed the greatest daily gains also presented higher ($P < 0.05$) feed efficiency (FE). Among the animals that started the feed restriction with 20 kg of body weight, there was no difference ($P > 0.05$) between the treatments ad libitum and 25% feed restriction for the feed efficiency, but there was a significant difference ($P < 0.05$) for the lambs subjected to 40% of feed restriction. Among lambs that started the restriction with 25 kg of body weight, the ad libitum treatment showed higher FE ($P < 0.05$) compared to under feed restriction.

In the refeeding phase, there was difference between treatments for DMI and initial and final body weight, with negative impact in lambs under feed restriction in both groups (20 and 25 kg of body weight) (Table 3). The exception was the lamb group of 25 kg with 40% of feed restriction, which presented similar DMI to the ad libitum treatment. There was no significant difference between the levels of feed restriction for DMI in both 20 and 25 kg of body weight. There was no difference between treatments for ADG and FE ($P > 0.05$). The treatments differed ($P < 0.05$) for final body weight, being lower for animals that had undergone previous restriction. The refeeding time was not sufficient for the lambs under feed restriction (25 and 40%) reestablish the weight of the ad libitum treatment.

Ruminal and intestinal morphometry

The villus:crypt ratio did not differ ($P > 0.05$) between treatments (Table 4). Lambs with highest morphological changes were those subjected to 40% of feed restriction. Regarding the rumen muscle layer height (RMLH), the values of the treatment under 40% of feed restriction, in both groups (20 and 25 kg), were higher ($P < 0.05$) when compared to ad libitum treatment. There was no difference ($P > 0.05$) between the lambs subjected to 25% of feed restriction and lambs feed ad libitum.

Ruminal papillae height (RPH) and weight range did not differ ($P > 0.05$) between ad libitum and feed restriction treatment in the lambs of 25 kg body weight. Higher ($P < 0.05$) ruminal papillae width (RPW) and ruminal absorption area (RAA) were observed in the lambs of 25 kg of body under feed restriction (Table 4).

Table 2 Performance of Santa Inês sheep during the feed restriction phase

Variables	Restriction level					Restriction level					
	Ad libitum	25%	40%	Mean ± SEM	P^1	Ad libitum	25%	40%	Mean ± SEM	P^2	P^3
	Body weight of 20 kg					Body weight of 25 kg					
IBW (kg)	20.45b	19.93b	19.57b	19.89 ± 1.18	0.4873	25.08a	25.20a	25.46a	25.28 ± 1.28	0.8630	0.0001
DMI (kg day^{-1})	0.92bA	0.69 dB	0.55eC	0.69 ± 0.01	0.0001	1.07aA	0.83cB	0.67dC	0.82 ± 0.03	0.0001	0.0001
DMI (% BW)	3.94aA	3.26bB	2.85cC	3.23 ± 0.22	0.0001	3.70aA	3.20bB	2.66cC	3.08 ± 0.21	0.0001	0.0001
ADG (g day^{-1})	215.71aA	132.32bB	65.31bC	125.19 ± 39.7	0.0001	235.00aA	107.86bB	63.27bB	118.20 ± 49.8	0.0002	0.0001
FE (%)	23.41aA	19.10abcAB	11.75bcB	17.30 ± 5.96	0.015	21.94abA	13.07abcB	9.45cB	13.60 ± 5.67	0.010	0.0969
FBW (kg)	28.00bcA	24.56cdB	21.59dC	24.06 ± 1.72	0.0001	33.30aA	28.98bB	27.39cbB	29.21 ± 2.21	0.0016	0.0001

SEM, standard error of the mean; *IBW*, initial body weight; *DMI*, dry matter intake/day; *DMI*, dry matter intake in percentage of body weight; *ADG*, average daily gain; *FE*, feed efficiency; *FBW*, final body weight; P^1, *P*-value for variables in lambs weighing 20 kg; P^2, *P*-value for variables in lambs weighing 25 kg; P^3, *P*-value for variables when comparing different body weights. Means followed by different uppercase letters on the same line differ statistically ($P < 0.05$) by the Tukey test for animals of different levels of restriction. Means followed by different lowercase letters on the same line differ statistically ($P < 0.05$) by the Tukey test for different body weights

Table 3 Performance of Santa Inês sheep during refeeding

Variables	Restriction level					Restriction level					P^3
	Ad libitum	25%	40%	Mean ± SEM	P^1	Ad libitum	25%	40%	Mean ± SEM	P^2	
	Body weight of 20 kg					Body weight of 25 kg					
IBW (kg)	28.00bcA	24.56cdB	21.59dC	24.06 ± 1.72	0.0001	33.30aA	28.98bB	27.39cbB	29.21 ± 2.21	0.0016	0.0001
DMI (kg day^{-1})	1.17abA	1.01cB	1.05bcB	1.06 ± 0.07	0.0101	1.22aA	1.08bcB	1.13abcAB	1.13 ± 0.06	0.0131	0.0002
DMI (% BW)	3.58	3.56	3.91	3.70 ± 0.27	0.0407	3.48	3.62	3.74	3.64 ± 0.31	0.4022	0.1252
ADG (g day^{-1})	207.29	206.25	237.50	219.63 ± 53.2	0.4751	211.11	264.20	260.65	250.82 ± 87.0	0.5944	0.5306
FE (%)	17.73	20.60	22.76	20.91 ± 4.94	0.275	17.64	24.73	23.14	22.45 ± 8.24	0.412	0.1498
FBW (kg)	37.95abA	33.75bcB	32.99cB	34.29 ± 2.41	0.0107	39.0aA	34.6bcB	34.43bcB	35.41 ± 2.54	0.0197	0.0020

SEM, standard error of the mean; *IBW*, initial body weight; *DMI*, dry matter intake/day; *DMI*, dry matter intake in percentage of body weight; *ADG*, average daily gain; *FE*, feed efficiency; *FBW*, final body weight; P^1, *P*-value for variables in lambs weighing 20 kg; P^2, *P*-value for variables in lambs weighing 25 kg; P^3, *P*-value for variables when comparing different body weights. Means followed by different uppercase letters on the same line differ statistically ($P < 0.05$) by the Tukey test for animals of different levels of restriction. Means followed by different lowercase letters on the same line differ statistically ($P < 0.05$) by the Tukey test for different body weights

Table 4 Morphometry of rumen and small intestine of Santa Inês lambs submitted to restriction and refeeding in the growth phase

Variables	Restriction level					Mean ± SEM	*P*-value
	Ad libitum	25%	40%	25%	40%		
		20 kg live weight		25 kg live weight			
Rumen muscle layer height (µm)	439c	460c	527ab	489bc	586a	490.63 ± 114.39	0.0001
Ruminal papillae height (µm)	955c	1127c	981c	1722a	1366b	1234.97 ± 321.40	0.0001
Ruminal papillae widht (µm)	156c	164c	140c	220b	394a	201.46 ± 44.84	0.0001
Ruminal absorption area (µm^2)	154538c	185521c	136207c	388871b	545678a	265,021.7 ± 121,067.8	0.0001
Intestinal mucosal height (µm)	238ab	256a	227b	244ab	262a	244.55 ± 44.19	0.003
Intestinal submucosa height (µm)	287b	327ab	358a	325ab	310ab	315.88 ± 95.55	0.001
Villus height (µm)	288ab	282b	319a	275b	317a	295.47 ± 77.30	0.001
Crypt depth (µm)	344b	405ab	429a	388ab	386ab	383.25 ± 167.54	0.011
Villus width (µm)	83.00b	92.80ab	100a	80.90b	90.57ab	88.42 ± 37.31	0.013
Villus:crypt ratio (µm)	0.89	0.76	0.88	0.76	0.90	0.85 ± 0.36	0.019
Intestinal absorption area (µm^2)	24036c	26266bc	31465a	22338c	29384ab	26,254.25 ± 13,559.39	0.0001

Means followed by different lowercase letters on the same line differ statistically ($P < 0.05$) by the Tukey test

Intestinal mucosal height (IMH) did not differ ($P > 0.05$) between treatments. However, there was a difference ($P < 0.05$) in intestinal submucosa height (ISMH), with reduction in the lambs of 20 kg subjected to 40% of feed restriction. The villus height (VH) differed ($P < 0.05$) between the levels of feed restriction in both groups of weight, being that the largest villi were found to lambs under 40% of feed restriction. For the variables crypt depth (CD) and villus width (VW), there was only a difference ($P < 0.05$) between treatments ad libitum and 40% of feed restriction in the lambs of 20 kg of body weight, with superior values for lambs under feed restriction (Table 4). The intestinal absorption area (IAA) increased for the lambs subjected to 40% of feed restrictions ($P < 0.05$).

Discussion

The decreases in ADG and FE and, consequently, in final body weight were commonly reported in several studies (Homem Júnior et al. 2007, 2010; Abouheif et al. 2013, 2015), being related that negative impacts are directly related to the nutritional plan imposed, resulting in an inadequate intake of nutrients (Cui et al. 2018), in which are necessary to sustain the rapid growth and development of animal. When feed intake is insufficient to cover their maintenance requirements, animals make use of body reserves, causing weight loss, and the magnitude of the reserve mobilization will depend on the severity and duration of the feed shortage (Pastén et al. 2010)**.**

During refeeding, the lambs that started the experiment with 20 of body weight under 25 and 40% of feed restriction and the lambs with 25 kg of body weight under 25% feed restriction presented lower intake compared to lambs feed ad libitum. This variation of results may be due to several factors, such as the high degree of feed restriction to which they were subjected in the restriction period, the length of stay under feed restriction, and the body weight or age of the animal.

Among the most important factors that influence the magnitude of compensatory growth are the age of the animal at the beginning of the restriction, the severity and duration of the nutritional restriction period, and the nature of feed restriction (Ryan et al. 1993; Puchala et al. 2011). For the animals that started the experiment with 25 kg body weight under 40% of feed restriction, there was no difference between treatments. Similar results were reported by Homem Júnior et al. (2007), who did not found difference on dry matter intake between animals under compensatory growing and normal growth. Homem Júnior et al. (2010) and Abouheif et al. (2013) observed that during the feeding period, the lambs that underwent feed restriction did not alter consumption, attributing this to diet. Differences in the severity, nature, and duration of the restriction period and the genetic potential of the animals contribute to discrepancies between research results using different feed regimes on gain and voluntary intake (Sainz et al. 1995).

There are conflicting results about daily weight gain after a period of feed restriction. Some authors (Homem Júnior et al. 2007; Abouheif et al. 2013, 2015) reported a significant increase in daily gain, while others (Mahouachi and Atti 2005) reported no significant difference. For the total compensatory gain, the lambs with 20 kg of body weight subjected to 25 and 40% of feed restriction should have presented a daily weight gain of 273 and 334 g day^{-1}, respectively, in the refeeding period. For the lambs with 25 kg of body weight and under 25 and 40% of feed restriction, the gain should be 358 and 415 g day^{-1}, respectively.

The compensatory gain cannot be attributed to DMI, since there was no difference between the restricted and ad libitum groups in both weight groups, but possibly due to the better feed efficiency of the feed restricted lambs (Yambayamba et al. 1996; Abouheif et al. 2015; Ma et al. 2017). These results are in agreement with those of Abouheif et al. (2013) and Homem Júnior et al. (2010), but different from those found by Greeff et al. (1986) and Homem Júnior et al. (2007), who reported that the rapid gain during refeeding was associated with increased feed intake, which did not occur in the present study. The inconsistency of the results can be explained by differences in restriction levels, diet composition, restriction and refeeding periods, and age at which animals were subjected to restriction (Hornick et al. 2000).

The trends of weight recovery after refeeding in growing Santa Ines lambs probably depend on the age/weight of lambs at the beginning of the restriction period. Almeida et al. (2011) evaluating Santa Inês lambs with different body weights (heavy lambs—56.8 and light lambs—33.5 kg) after compensatory gain observed that light lambs presented growth compensation after feed restriction, presenting final body composition similar to lambs feed ad libitum. On the other hand, heavy animals did not present compensatory gain. Based on this result, the authors suggested that the compensatory gain of lambs depends on the degree of maturity of the animals.

The RMLH in the lambs subjected to 40% of feed restriction was higher than that to other treatments. This fact is related to the physical stimulus caused in the rumen, with increased rumination rate and ruminal movements, which are used by ruminants under a feed restriction, being this the strategy used by the animals to obtain a compensatory gain. Morphometric differences in rumen epithelium of sheep were reported by other authors (Odongo et al. 2006; Wang et al. 2009; Zitnan et al. 2003), with significant increase in height of the rumen papillae in animals fed high concentrate diets. This fact is explained by the increase in the production of volatile fatty acids, mainly propionate and butyrate (Shen et al. 2004; Zitnan et al. 2005). These acids are responsible for the increase of mitotic indexes of ruminal cells, allowing a greater ruminal capacity to absorb nutrients from ruminal fermentation (Mentschel et al. 2001). This confirms that the feed restriction imposed on the animals altered the morphometry of the studied organs, improving the utilization of ingested feed.

The higher RPH lambs with 25 kg of body weight under feed restriction probably occurred by the refeeding time. The lambs that spent 28 days of refeeding increased their absorption area in an attempt to make better use of the feed during refeeding. On the other hand, the animals with 20 kg of body weight and subjected to restriction spent 49 days of refeeding for the return of the papillae. According to Martens et al. (2012), the size of the papillae decreases during a period of undernourishment and increases when the feed supply normalizes. However, this increase occurs slowly, reaching a maximum size around 50 to 60 days. This suggests that 25 kg body weight lambs previously feed restricted could spend more than 28 days in refeeding using this increase in the absorption area to convert volatile fatty acids (VFAs) to muscle.

In addition to refeeding, another explanation would be the increased availability of nutrients, due to the passage rate to be reduced in the rumen in animals that have been previously restricted, in an attempt to make better use of feed. According to Sun et al. (2011), RPH can also be influenced by age at weaning, quantity, type and energy content of the feed. It is known that the increase of concentrate leads to an increase in RPH (Odongo et al. 2006; Wang et al. 2009; Zitnan et al. 2003), which occurred in the refeeding.

Similarly to RPH, the ruminal absorption was influenced by feed restriction, since they are highly related. The increase in the availability of nutrients when the animals were refeeding may have influenced this morphological change, being that the higher the feed intake, the greater the amount of VFAs produced, consequently the greater the area of absorption of the VFAs. According to Costa et al. (2008), the increase of the epithelium was a reflection of the higher production and absorption of VFAs.

Lambs under feed restriction presented an increase in the intestinal submucosa. This increase was probably by stimulus of the glands to produce more mucus. Mucus is a water-insoluble glycoprotein with a protective function related basically to mechanical action. The goblet cells are secretory of these glycoproteins, which has the function of protecting the intestinal epithelium from the action of digestive enzymes and the abrasive effects of digesta (Maiorka 2004). In the present study, the feed restriction promoted a higher number and size of villi which depend on the number of cells that compose it. Thus, the greater the number of cells, the greater the size of the villi and, consequently, the greater the nutrient absorption area (Maiorka 2004).

Lambs with 20 kg of body weight under 40% of feed restriction had higher crypt depth, which is an indication of the compensatory capacity or hyperplasia of the epithelial cells due to a higher level of aggression to the morphological structure of the intestinal mucosa caused by restrictive diets (Arruda et al. 2008).

Despite the possible increase in the rate of epithelial desquamation, there was an increase of crypt and villus in consequence of adequate cell turnover rate and to guarantee replacement of cell loss of the apical region of the villi, allowing to infer that the higher the VH:CD ratio, the better the nutrient absorption and the lower the energy losses with cell renewal (Xu et al. 2009; Ma et al. 2017).

The higher intestinal absorption area in the lambs subjected to feed restriction is important by the better contact with feed in the refeeding and consequently the absorption and gain of weight (Wang et al. 2009). It is believed that when animals are submitted to feed restriction, the mucosa becomes thinner due to the high metabolic rate required by this epithelium, which has a high rate of renewal and maintenance (Boleli et al. 2002). Thus, refeeding with increased nutrient availability in the groups mentioned above led to an increase in intestinal absorption area due to the availability of nutrients in order to try a greater absorption from a larger area of contact with food. Nóbrega et al. (2014) working with Santa Inês sheep subjected to increasing levels of feed restriction followed by refeeding observed that the intestinal villi area increased, linearly, when the level of previous restriction was increased, probably in the attempt of increasing the absorption surface, since the small intestine seems to adapt to satisfy the nutritional needs of the animal. This work would address the need to increase nutrient demand (Zitnan et al. 2008), and compensate for the low intake of these elements by lambs during the previous restriction period, since a smaller area of villi would imply less enzymatic activity, digestibility, and nutrient absorption (Arruda et al. 2008). However, other studies must be carried out in order to verify that longer refeeding times after feed restriction can lead lambs to a full compensatory gain, considering the morphological changes found in the present study.

Conclusions

The feed restriction followed by refeeding in sheep was able to lead the animals to a partial compensatory gain. In addition, morphological changes in the rumen and intestine allowed greater absorption capacity. Further studies should be performed with longer refeeding time to test the compensatory gain.

Acknowledgements The authors would like to thank the Federal University of Campina Grande and Federal University of Paraíba for their technical assistance.

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Funding This study was supported by CNPq and CAPES.

Data availability Not applicable.

Code availability Not applicable.

Declarations

Ethics approval This study was approved by the Animal Ethics Committee of the Federal University of Paraiba (UFPB), Brazil (protocol no. 2305/14).

Conflict of interest The authors declare no competing interests.

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