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Impact of Feeding Systems on Performance, Blood Parameters, Carcass Traits, Meat Quality, and Gene Expressions of Lambs

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Abstract: The aim of this study was to investigate the effects of feeding systems on the growth performance of Santa Inês x Dorper lambs, meat quality, fatty acid profile, and gene expression. Thirty lambs at an initial body weight of 22.6 ± 2.59 kg were randomly assigned to one of three feed systems: a grazing system with 1.2% body weight concentrate supplementation (GS); a feedlot system with 28% forage and 72% concentrate (FFC); or feedlot with 85% whole corn grain and 15% pellets (FHG). The lambs were slaughtered after 60 days of experiment. Average daily gain, glucose, and insulin concentration were higher for lambs on FHC than lambs on a GS feeding system. The fatty acid profile in the meat of the lambs fed GS showed a higher proportion of c9t11-C18:2, C20:5, C22:5, and C22:6 compared with FFC and FHC ($p < 0.05$). Meat tenderness was lower for lambs under FFC treatment compared with GS and FHG. FHG treatment provides better performance and higher deposition of lipid content in meat compared with GS and FHG. The expression of the genes SCD-1, SREBP1-c, and EVOL6 was greater in lambs undergoing GS and FHC treatments compared with FFC. Results of this research showed a reduced performance of grazing lambs compared with the feedlot system; however, it enhanced the fatty acid profile with increased levels of polyunsaturated acids and reduced n6/n3 ratio.

Keywords: grain fed; grass fed; fatty acids; lipid metabolism; pasture; feedlot; whole grain

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1. Introduction

Nutritional strategies have been proposed to enhance the profitability and productivity of sheep systems. Pasture and feedlot are traditional management systems applied in livestock to promote greater growth rates and market-targeted fat deposition. The type of forage and grain has been shown to affect meat quality, mainly sensory characteristics, and the concentration of polyunsaturated fatty acids in the meat of lambs [1–3]. Pasture systems are richer in polyunsaturated fatty acids, which are beneficial for human health, while grain systems are known to enhance daily weight gain [4]. Overall, strategies combining feed management and nutrition aim to produce meat with better sensory acceptability and increased polyunsaturated fatty acids, which promote better human health [5].

Lamb meat from grass-fed systems contains a lower concentration of saturated fatty acids and a higher proportion of mono and polyunsaturated fatty acids, especially alphalinolenic (ALA), eicosapentaenoic (EPA), docosahexaenoic (DHA), conjugated linoleic acid (CLA), and lower n6/n3 ratio, which are beneficial to human health [2,5,6]. These fatty acids are well known to promote better nutritional value to meat, have anticarcinogenic properties, and reduce the incidence of coronary heart disease in humans [6,7].

Although meat from grass-fed lamb provides a better fatty acid profile for human consumption, from the point of view of productivity and feed efficiency, finishing lambs in feedlots is more efficient. Feedlot diets are rich in grains and high in energy; there are diets with forage and diets without forage based on whole corn grains and protein pellets [8]. These diets provide rapid growth and greater deposition of fat in the carcass [4,8].

Carcass fat deposition is a trait commercially important to the industry and target markets. Adipose tissue accumulation occurs when lipogenesis is higher than lipolysis, and these processes are controlled by some key hormones, transcription factors and enzyme-coding genes [9]. Fatty acids from meat can be controlled even more using specific factors, such as genes related to lipid metabolism [10].

Steroid-binding protein transcription factor (SREBP-1c) plays a central role in energy homeostasis, promoting lipogenesis and adipogenesis [11,12]. SREBP-1c activates the transcription of genes such as acetyl-CoA carboxylase (ACACA), fatty acid synthase (FASN), elongases (ELOVL), stearoyl-CoAdesaturase (SCD-1), and other genes that participate in bioenergetics, adipogenesis, lipolysis, and synthesis of new fatty acids and triglycerides [13–15]. Previous studies have reported gene expression related to fat metabolism in lambs [16,17]; however, there is a lack of information on gene expression due to the effects of different feeding systems.

The aim of this study was to evaluate growth performance, blood parameters, carcass traits, meat quality, and gene expression related to lipid metabolism in the *Longissimus lumborum* muscle of lambs under three different feeding systems: GS, grazing with supplement (*Cynodon* spp. cv Tifton—85 with supplement); FFC, feedlot with forage (72% concentrate; 28% *Cynodon* spp. cv Tifton—85 hay); or FHC, feedlot whole grain without forage (85% whole-grain corn; 15% pellets).

2. Materials and Methods

Experimental procedures used in this study were approved by the Ethics and Animal Welfare Committee of the Federal University of Lavras (UFLA), Brazil (protocol No. 063/16). Meat sensory analysis was approved by the Ethics Committee on Research with Human Beings of UFLA (process No. 2.984.593. CAAE No. 99920918.7.0000.5148), following the Resolution of the National Health Council 196/96 [18].

This study was carried out in the Sheep Farm Facility of the Department of Animal Science of the Federal University of Lavras, MG, Brazil (21°13′38″ S, wet subtropical mesothermal Cwa from dry winter). There was an average rainfall and temperature of 110.33 mm and 22.4 °C, respectively, during the experiment, from February to April 2017.

2.1. Animals and Feeding Systems

Thirty male lambs (½Santa Inês ½Dorper) at an average body weight of 22.6 ± 2.59 kg (mean ± SD) and age of 70.0 ± 10 days (mean ± SD) were used. Previously, at 60 days of age, the lambs were weaned and were fed an initial diet (70% ground corn, 15% soybean meal, 5% vitamin mineral premix, and 10% cane molasses) and Tifton pasture. Prior to the experiment period, the lambs were prescribed 1 mL/10 kg of 5% levamisole hydrochloride (Ripercol® L, Zoetis Indústria de Produtos Veterinários Ltd.a., Campinas, SP, Brazil) for deworming. The experiment was a randomized design with three treatments and 10 animals in each treatment group. Data were collected for a period of 60 days. Experimental feeding systems consisted of GS grazing with supplementation (n = 10): *Cynodon* spp. cv Tifton—85 pasture plus 1.2% body weight concentrate supplementation; FFC conventional feedlot (n = 10): a diet containing 72% concentrate and 28% *Cynodon* spp. cv Tifton—85 hay; and FHG high grain feedlot (n = 10): a diet containing 85% whole-grain corn and 15% pellets (Premix Mineral Confipeso Alto Grão, Presence-Nutrição Animal, Paulínia, SP, Brazil). Data provided for FFC treatment have been used as a control treatment in Dias Junior et al. [17] in another context of analysis.

The ingredients, chemical composition and fatty acid profile of the diets are listed in Table 1. The diets for FFC and GS feeding systems were formulated to meet the nutritional requirements of lambs with 30 kg live weight and ADG of 300 g/day [19]. The supplement provided to the lambs on the GS feeding system was calculated for 1.2% body weight.

Lambs from FFC and FHC treatments were kept in individual 1.3 m^2 pens with free access to feed and water. The lambs were fed twice a day, at 8:00 a.m. and 4:00 p.m., ad libitum. The feeding offered, and the orts were recorded daily, calculated for a daily surplus of 15% ad libitum.

Table 1. Ingredients, chemical composition, and fatty acid profile (g/kg dry matter) of the experimental diets.

Ingredients, g/kg of Dry Matter	Feeding System		
	GS	FFC	FHG
Tifton—85 hay (*Cynodon* spp.)	-	279	-
Pasture Tifton 85	611	-	-
Soybean meal	334	400	-
Ground corn	41	297	85
Mineral premix	11	22	-
Dicalcium phosphate	2	2	
Pellets	-	-	15
Chemical composition, g/kg of dry matter			
Dry matter	562	926	893
Crude protein	216	217	130
Ether extract	14	21	39
Neutral detergent fiber	455	215	124
Minerals	60	50	46
Non-fibrous carbohydrate	291	392	660
Metabolizable energy, Mcal/kg *	26	27	25
Fatty acids, g/kg of dry matter			
C14:0	11	18	1
C16:0	50	29	22
c9-C16:1	7	2	2
C18:0	9	33	22
c9-C18:1	101	261	320
C18:2 n6	320	415	5
C18:3 n3	213	2	2

GS: Grazing supplemented (*Cynodon* spp. cv Tifton—85 pasture ad libitum and supplement in the proportion of 1.2% body weight); FFC: Feedlot with forage (72% concentrate; 28% *Cynodon* spp. cv Tifton—85 hay); FHG: Feedlot whole grain without forage (85% whole-grain corn; 15% pellets). * Metabolizable energy estimated by Cannas et al. [20].

The GS lambs grazed from 7 a.m. to 6 p.m. and were kept overnight in individual 1.3 m^2 pens with free access to water. The supplement was individually provided during the overnight period at 1.2% body weight, with an average value of 0.365 kg of supplement throughout the experimental period. Daily in the morning, the orts of the supplements were collected, weighed, and sampled per animal to determine the individual animal intake. The GS lambs rotationally grazed a total area of 9000 m^2, subdivided into five paddocks of 1800 m^2 composed of Tifton-85 (*Cynodon* spp.). Each paddock contains a water trough and shed area with a polyethylene fabric of 20 m^2 in each paddock to provide 80% shade. The stocking rate was fixed, and the grazing cycle was 35 days, with 7 of occupation and 28 of rest. Pasture composition was, on average, 30.98 g/kg of dry matter, 12.57 g/kg of crude protein, 1.4 g/kg of ether extract, and 74.75 g/kg of neutral detergent fiber (NDF).

Pasture sampling was performed manually, simulating the grazing of the animals on the first, third, and seventh day of grazing of each paddock, always in the morning, until a sample of approximately 400 g of forage for each experimental group was obtained. The morphological characteristics at the time of entry and exit are shown in Table 2. Pasture samples were dried in a forced ventilation oven at 65 °C for 72 h for pre-drying. Then, the samples were ground using a 1 mm sieve for the bromatological analyses and 5 mm for the degradability test.

Table 2. Pasture characterization—mean of morphological constituents of pasture and height of the forage (*Cynodon* spp.) at the time of entry and exit of the animals to the paddock.

Pasture Constituents (%)	Entry	Exit
Leaf	52.95	46.66
Thatch	23.53	26.86
Senescent material	11.76	13.03
Other forages and weeds	11.76	13.45
Height, cm	25.50	15.50

Pasture intake was evaluated from the 23rd to the 30th day and from the 53rd to the 60th day of the experiment using titanium dioxide (TiO_2) as an external indicator, according to Willians et al. [21], cited by Silva and Queiroz [22]. Pasture intake was evaluated for twelve days (seven days of adaptation followed by five days of feces and feeding sampling). In addition, 4 g of TiO_2 was provided via the esophagus, 2 g at 7 a.m., and 2 g at 6 p.m. Fecal samples were collected from each animal in the morning and afternoon, summing ten samples per animal during each evaluation period, which were composed per animal in each period. The composed were stored at −18 °C, then dried at 65 °C, and ground using a 1 mm sieve mill for subsequent analysis. The concentration of TiO_2 in the feces was determined [23].

To determine indigestible neutral detergent fiber (NDFi), five bags of textile non-textile (TNT) per sample, containing 0.5 g forage and feces, were previously dried, weighed, and incubated for 264 h in the rumen of a cannulated cow [3,24]. Bags were removed, cleaned with water, dried at 65 °C and boiled for 1 h in a neutral detergent solution. Then, it was washed with hot water and acetone, dried and weighed [25]. The remaining residue was recorded as NDFi. The production of fecal dry matter was determined using the following formula: Fecal production = intake of the indicator (kg)/concentration of the indicator in feces (%), which allowed to obtain pasture intake as DMIpasture (kg/day) = (fecal production × NDFifeces)/NDFipasture.

The diets of the FFC and FHC treatments, the supplement of GS treatment, and the orts were sampled every day and combined every 15 days to obtain a fortnightly sample per experimental unit. The samples were stored at −18 °C. Dry matter of feed, orts, and pasture was determined according to the method of the Association of Official Analytical Chemists [26]. All samples were ground with a Wiley mill (Marconi, Piracicaba, São Paulo, Brazil) to pass a 1 mm screen. Ash was obtained by incinerating the sample in a muffle furnace at 550 °C for 4 h [26], and ether extract (EE) was measured according to AOAC International [27]. Crude protein (CP) was determined using micro-Kjeldahl analysis [28]. The ash-free neutral detergent fiber was determined by Van Soest et al. [25]. Non-fibrous carbohydrate fraction determined as non-fibrous carbohydrate = 100 − (crude protein + ether extract + ash + neutral detergent fiber). Metabolizable energy intake was determined by Cannas et al. [20].

2.2. Performance and Digestibility

Body weight was recorded fortnightly after 16 h of fasting during the 60 days of the experimental period to determine average daily gain and feed efficiency. Feed efficiency was calculated as the average dry matter intake divided by the average daily gain, both in kg/day.

The nutrient intake and dry matter intake of the FFC and FHC treatments and the supplement intake of GS were measured daily (Dry matter intake = feed offered − orts). Pasture intake was measured using indigestible neutral detergent fiber (NDFi) as an internal marker [29].

The apparent digestibility coefficient was calculated for dry matter, crude protein, ether extract, neutral detergent fiber, total digestible nutrients, and non-fibrous carbohydrates according to the digestibility formula: (Feed nutrient − Fecal nutrient)/Feed nutrient. The total digestible nutrient content was determined according to the following equation: Total

digestible nutrient = crude protein digestible + (ether extract digestible × 2.25) + non-fibrous carbohydrate digestible + neutral detergent fiber digestible [30].

2.3. Blood Biochemical Analysis

At 58 days of the experiment, blood samples were collected minutes before the first feeding of the day. Blood samples were collected by performing jugular venipuncture using 10 mL vacutainer tubes with sodium fluoride + EDTA. Immediately after collection, the samples were centrifuged (1500× *g*, room temperature for 10 min) and frozen and stored at −20 °C in 1.5 mL plastic tubes until laboratory analysis. The colorimetry technique was applied using a 96-well plate spectrophotometer reader (Multskan GO, Thermo Scientific, Waltham, MA, USA). Glucose (Bioclin Glucose Monoreagent, Belo Horizonte, Brazil), cholesterol (Bioclin Cholesterol Monoreagent, Belo Horizonte, Brazil), insulin (DRG ELISA D-35039, DRG Instruments, Marburg, Germany), and triglycerides (Bioclin Triglicerides Monoreagente, Belo Horizonte, Brazil) were quantified using commercial kits.

2.4. Slaughter and Carcass Sampling

At the end of the feeding trial (60 days), the animals were individually weighed in the morning, and pre-slaughter live weight was determined. The lambs were transported to a commercial abattoir located 128 km from the experimental facility. The lambs underwent 16 h of fasting for solids and ad libitum access to water. Muscle samples (5 g) were taken approximately seven minutes after bleeding, between the 12th and 13th ribs (right side), placed in cryogenic tubes, transported in liquid nitrogen, and stored at −80 °C for gene expression analysis. Hot carcass weight was recorded immediately after evisceration and skin removal. Non-carcass components and internal fat (mesenteric and visceral fat) were weighed using a scale with 0.100 kg accuracy (Filizola, Campo Grande, MS, Brazil).

pH was measured pre-rigor (right carcass side between the 12th and 13th ribs) using a pH meter TESTO-205 (Testo, Campinas, Brazil). The pH meter was calibrated at room temperature on pH 7.0 and 4.0 with standard buffers (Testo buffer, Campinas, Brazil).

Carcasses were hung at 4 °C for 24 h in the slaughterhouse. Carcasses were transferred to the university laboratory in a refrigerated truck. Cold carcass weight was recorded, and a second measure of pH was undertaken (post-rigor). Subcutaneous fat thickness was recorded by making two incisions through the fat along lines extending over the greatest depth of the muscle between the 12th and 13th ribs [31] using a digital caliper (Battery, model SR44) on the left side of the carcass. Acetate paper was placed on the LL muscle to record muscle area using ImageJ software, https://imagej.net/software/imagej/ (accessed on 13 June 2024) (National Institutes of Health, Bethesda, MD, USA). After deboning, the left and right sides of the LL muscle were wrapped in aluminum foil, vacuum-packed, and stored at −20 °C for further analysis.

2.5. Meat Quality

The frozen longissimus muscle (left side) was divided into six steaks of 2.5 cm thickness each, labeled, vacuum-packed, and held at −20 °C. The steaks were allocated in each analysis in the anterior–posterior direction: qualitative analyses (three steaks), thiobarbituric acid reactive substances (TBARSs) (one steak), proximate composition (one steak), and fatty acid analysis (one steak). Thawing loss was determined using three steaks that were thawed for 12 h at 2 °C. Following this, color measurements were taken after opening the vacuum bag and 30 min of blooming. A Minolta CR700 Chroma Meter (Konica Minolta, Osaka, Japan) was used set on illuminant A and a 10° standard observer. The displays per steak were undertaken to record lightness (L^*), redness (a^*), and yellowness (b^*). Meat color parameters were averaged from nine readings per animal.

Water-holding capacity was determined using the Hamm and Deatherage [32] method and expressed as the ratio Ap/Ae [33].

Three 2.5 cm steaks were used to determine cooking loss. Meat samples were randomly placed in polyethylene bags and cooked in a water bath set at 98 ± 1 °C (aimed at 71 °C

internal temperature using a digital thermometer [34]). Meat samples were weighed after 2 h of cooling at room temperature. Cooking loss was determined in percentage as the weight difference before and after cooking. For shear force analysis, each steak used for cooking loss analysis was subdivided into three subsamples (1 cm^2) cut in parallel to the direction of the muscle fibers (removing connective tissue and fat). A texturometer (Modle TA-TX2, Stable Micro Systems Ltd., Godalming, Surrey, UK) attached to a Warner–Bratzler slide was used and calibrated using a weight of 2 kg with an adjusted speed of 200 mm/min. The maximum positive peak values were recorded as kgf/cm^2.

LL muscle (100 g) was trimmed of external fat and connective tissue for proximate analysis. A multiprocessor (Philips RI7630, Itapevi, Brazil) was used to homogeneously ground the samples. Crude protein, fat, moisture, and ash were determined with a near-infrared method [35] using a FoodScanTM device (FOSS, Hillerod, Denmark).

2.6. Sensory Analysis

After thawing and trimming, longissimus muscles were weighed, and salt was added (1%) for sensory analysis. A grill (SFSE Croydon) was set at 250 °C, and the samples were cooked to an internal temperature of 70 °C using a digital thermometer. After cooking, the muscle was cut into cubes of 12–15 g [36]. A total of 55 panelists (25 men and 30 women ranging from 18 to 60 years old) evaluated the samples on a white plastic plate, coded with three random digits in an individual chamber. Panelist assessment was carried out in one day. Sensory evaluation was undertaken as described previously [37] using appearance, flavor, tenderness, and overall liking as sensory parameters on a hedonic scale of nine points [37].

2.7. Fatty Acids and Enzyme Activity

For fatty acid analysis, extraction [38], hydrolysis, and methylation [39] were performed as previously reported. A gas chromatograph fitted with a 100 m Supelco SP 2560 capillary column (0.25 mm and 0.2 µm film thickness) was used as described previously [17]. Carrier gas helium flow of 1.8 mL per minute, set at 45 mL per minute for make-up gas (N_2), 40 mL per minute for hydrogen, and 450 mL per minute for synthetic flame gas. The oven temperature was set at 70 °C for 4 min, increased to 170 °C at a rate of 13 °C for 1 min, subsequently increased to 250 °C at a rate of 35 °C for 1 min, and maintained at 250 °C for 5 min. The percentage of fatty acid in total lipids (fatty acids methyl ether—FAME) was obtained by individual area of fatty acid × 100/total area of fatty acid. Estimates of Δ9-desaturase and elongase enzyme activity were determined as described by Malau-Aduli et al. [40] and Kelsey et al. [41]. The overall desaturase index was calculated as follows: $\Delta 9 - \text{overall} = \Delta 9 - 14 + \Delta 9 - 16 + \Delta 9 - 18$, as modified by Archibeque et al. [42].

2.8. Gene Expression Analysis

Reference and target primers design were carried out by the sequences registered and published in the public database of Genbank (NCBI platform—National Center for Biotechnology Information). Open Reading Frames (OFRs) of the selected sequences were obtained using the NCBI ORFinder tool and associated with the coded protein bank using the translate tool (ExPASY protein bank). Oligo PerfectTM Designer software (https://www.thermofisher.com/pl/en/home/life-science/oligonucleotides-primers-probes-genes/custom-dna-oligos/oligo-design-tools.html, accessed on 13 June 2024) was used considering the sequences obtained from Genbank. Primer's information is detailed in Dias Junior et al. [17].

Total RNA extraction from LL muscle is detailed described in Dias Junior et al. [17]. Relative gene expression was based on the corrected cycle threshold values for the amplification efficiency of each primer pair [43].

2.9. Statistical Analysis

Statistical analysis was performed using the GLM procedure of SAS (SAS Version 9.1, SAS Institute, Cary, NC, USA). Experimental diets were used as a fixed effect and the initial weight as a covariate. Only meat sensory analysis was considered a randomized block design, with each panel member representing one block (block effect was considered random). The MIXED procedure of SAS was used to verify the effect of the experimental diets (fixed effect) on acceptability, and the score of each panel member was considered as a repeated measure. The comparison between the mean of the different parameters evaluated was made using the *t*-test, with a difference considered significant when $p < 0.05$.

3. Results

3.1. Nutrient Intake, Digestibility, and Performance

The intake of dry matter, crude protein, ether extract, and non-fibrous carbohydrates was higher in FFC than FHG and GS ($p < 0.0001$), subsequently (Table 3). GS treatment showed the greatest neutral detergent fiber intake ($p < 0.0001$), and FFC and FHG showed superior total digestible nutrient intake compared with GS ($p < 0.0001$).

Table 3. Intake and digestibility of nutrients, average daily gain, and feed efficiency of lambs under three feeding systems.

Parameter	Feeding System			SEM	*p* Value
	GS	FFC	FHG		
Intake, kg/day					
Dry matter	0.76 ^{c}	1.17 ^{a}	0.90 ^{b}	0.048	0.0001
Crude protein	0.15 ^{c}	0.28 ^{a}	0.22 ^{b}	0.007	0.0001
Neutral detergent fiber	0.38 ^{a}	0.23 ^{b}	0.12 ^{c}	0.007	0.0001
Ether extract	0.01 ^{c}	0.02 ^{b}	0.03 ^{a}	0.001	0.0001
Non-fibrous carbohydrate	0.15 ^{c}	0.44 ^{b}	0.54 ^{a}	0.023	0.0001
Total digestible nutrient	0.53 ^{b}	0.80 ^{a}	0.75 ^{a}	0.032	0.0001
Digestibility coefficient					
Dry matter	0.63 ^{b}	0.75 ^{a}	0.77 ^{a}	0.013	0.0478
Crude protein	0.73 ^{b}	0.80 ^{a}	0.79 ^{a}	0.010	0.0001
Neutral detergent fiber	0.69 ^{a}	0.46 ^{b}	0.39 ^{c}	0.017	0.0001
Ether extract	0.62 ^{b}	0.70 ^{a}	0.72 ^{a}	0.014	0.0001
Non-fibrous carbohydrate	0.68 ^{c}	0.77 ^{b}	0.84 ^{a}	0.013	0.0001
Total digestible nutrient	0.71 ^{b}	0.82 ^{a}	0.84 ^{a}	0.012	0.0001
Performance					
Average daily gain, kg/day	0.182 ^{b}	0.222 ^{b}	0.311 ^{a}	0.015	0.0001
Feed efficiency	0.342 ^{b}	0.279 ^{b}	0.426 ^{a}	0.023	0.0006

GS: Grazing supplemented (*Cynodon* spp. cv Tifton—85 pasture ad libitum and supplement in the proportion of 1.2% body weight); FFC: Feedlot with forage (72% concentrate; 28% *Cynodon* spp. cv Tifton—85 hay); FHG: Feedlot whole grain without forage (85% whole-grain corn; 15% pellets). SEM: Standard error of the mean. Mean in the same row with different superscripts differ significantly ($p < 0.05$).

The apparent digestibility coefficients for dry matter, crude protein, ether extract, and total digestible nutrients were lower in GS compared with FFC and FHG ($p < 0.05$). GS showed the greatest digestibility of neutral detergent fiber and the lowest for non-fibrous carbohydrates ($p < 0.0001$).

Average daily gain and feed efficiency were greater for lambs raised under FHG compared with GS and FFC ($p < 0.0001$).

3.2. Blood Biochemical Parameters

The concentration of cholesterol and triglycerides was not affected by the feeding system ($p > 0.05$); however, glucose and insulin were lower in lambs raised under GS compared with FFC and FHG ($p < 0.001$) (Table 4).

Table 4. Blood biochemical parameters (mg/dL) of lambs under three feeding systems.

Parameter	Feeding System			SEM	*p* Value
	GS	FFC	FHG		
Cholesterol	133.28	137.83	162.34	12.340	0.2202
Glucose	59.29 ^{c}	73.18 ^{b}	89.49 ^{a}	3.641	0.0001
Triglycerides	71.46	65.99	66.95	4.611	0.6736
Insulin	55.33 ^{b}	90.54 ^{a}	104.82 ^{a}	8.722	0.0019

GS: Grazing supplemented (*Cynodon* spp. cv Tifton—85 pasture ad libitum and supplement in the proportion of 1.2% body weight); FFC: Feedlot with forage (72% concentrate; 28% *Cynodon* spp. cv Tifton—85 hay); FHG: Feedlot whole grain without forage (85% whole-grain corn; 15% pellets). SEM: Standard error of the mean. Mean in the same row with different superscripts differ significantly ($p < 0.05$).

3.3. Carcass and Meat Quality Parameters

The pre-slaughter live weight of lambs raised under FFC was greater than FHG but lower than GS ($p < 0.01$) (Table 5). Lambs raised under FHG had lower weights of non-carcass components, but in proportion, they were greater ($p < 0.01$). Hot carcass weight was not affected by the feeding system ($p > 0.05$), but cold carcass weight was lower under GS compared with FFC and FHG ($p < 0.05$). Loin muscle area and subcutaneous fat thickness were inferior for GS lambs compared with FFC and FHG ($p < 0.01$). Internal fat (mesenteric + visceral fat) was greater in lambs raised under FFC compared with GS but lower than FHG ($p = 0.0016$). Carcass pH (hot and cold) was not affected by the feeding system ($p > 0.05$).

Table 5. Carcass characteristics of lambs under three feeding systems.

Parameter	Feeding System			SEM	*p* Value
	GS	FFC	FHG		
Pre-slaughter live weight, kg	33.46 ^{c}	38.53 ^{b}	43.17 ^{a}	0.860	0.0001
Non-carcass components, kg	15.40 ^{b}	16.13 ^{ab}	17.75 ^{a}	0.480	0.0061
Non-carcass components, %	46.64 ^{a}	41.97 ^{b}	41.53 ^{b}	1.219	0.011
Hot carcass weight, kg	15.79 ^{b}	19.40 ^{a}	20.81 ^{a}	0.443	0.0001
Hot carcass yield, %	47.25	50.28	48.24	1.035	0.1308
Cold carcass weight, kg	15.35 ^{b}	18.91 ^{a}	20.30 ^{a}	0.464	0.0001
Cold carcass yield, %	45.98	48.97	47.04	1.089	0.1703
Loin muscle area, cm^2	13.75 ^{b}	17.53 ^{a}	18.01 ^{a}	0.697	0.0004
Subcutaneous fat thickness, mm	1.51 ^{b}	3.32 ^{a}	3.34 ^{a}	0.346	0.0068
pH hot carcass	6.94	6.75	6.78	0.085	0.2598
pH cold carcass	5.74	5.90	5.93	0.106	0.3948
Internal fat	0.73 ^{c}	0.97 ^{b}	1.38 ^{a}	0.110	0.0016

GS: Grazing supplemented (*Cynodon* spp. cv Tifton—85 pasture ad libitum and supplement in the proportion of 1.2% body weight); FFC: Feedlot with forage (72% concentrate; 28% *Cynodon* spp. cv Tifton—85 hay); FHG: Feedlot whole grain without forage (85% whole-grain corn; 15% pellets). SEM: Standard error of the mean. Mean in the same row with different superscripts differ significantly ($p < 0.05$).

*L** was lower on the longissimus muscle of GS lambs compared with FFC and FHG ($p = 0.0043$), and no effect was observed on *a** and *b** values ($p > 0.05$) (Table 6). The feeding system did not affect thawing loss, cooking loss, shear force, and water-holding capacity ($p > 0.05$).

The proximate composition of the meat did not differ in crude protein and ash content ($p > 0.05$), whereas the lipid content in the meat was higher in FHC lambs compared with GS ($p = 0.0269$), and the moisture content was higher in FHG lambs compared with GS ($p = 0.0464$).

Table 6. Parameters of meat quality and chemical composition of lambs under three feeding systems.

Parameter	Feeding System			SEM	*p* Value
	GS	FFC	FHG		
*L**	38.07 [b]	41.28 [a]	41.99 [a]	0.802	0.0043
*a**	14.78	15.28	14.78	0.647	0.8188
*b**	10.68	9.83	10.45	0.617	0.6111
Thawing loss, %	5.37	4.39	5.09	0.343	0.1388
Cooking loss, %	14.19	12.74	14.18	1.388	0.7015
Shear force, kgf/cm^2	3.44	3.59	3.27	0.182	0.469
Water-holding capacity	0.15	0.18	0.17	0.011	0.283
Moisture, %	74.57 [a]	73.88 [ab]	73.29 [b]	0.343	0.0464
Crude protein, %	21.61	21.40	21.70	0.256	0.7057
Fat, %	2.19 [b]	2.52 [ab]	3.44 [a]	0.316	0.0269
Ash, %	1.62	2.18	1.88	0.200	0.1581

GS: Grazing supplemented (*Cynodon* spp. cv Tifton—85 pasture ad libitum and supplement in the proportion of 1.2% body weight); FFC: Feedlot with forage (72% concentrate; 28% *Cynodon* spp. cv Tifton—85 hay); FHG: Feedlot whole grain without forage (85% whole-grain corn; 15% pellets). SEM: Standard error of the mean. Mean in the same row with different superscripts differ significantly ($p < 0.05$).

3.4. Sensory Analysis

Appearance and overall liking of the meat were not affected by the feeding system ($p > 0.05$) (Table 7). Consumers scored higher for the flavor of meat from lambs raised under GS compared with FFC and FHG ($p = 0.0023$), but scored meat tenderness lower in lambs raised under FFC compared with GS and FHG ($p = 0.0246$).

Table 7. Sensory analysis of muscle Longissimus lumborum muscle of lambs under three feeding systems.

Parameter	Feeding System			SEM	*p* Value
	GS	FFC	FHG		
Appearance	5.87	6.02	6.20	0.231	0.6699
Flavor	7.20 [a]	6.47 [b]	6.18 [b]	0.239	0.0023
Tenderness	7.05 [a]	6.70 [b]	7.46 [a]	0.19	0.0246
Overall liking	6.73	6.18	6.67	0.229	0.1111

GS: Grazing supplemented (*Cynodon* spp. cv Tifton—85 pasture ad libitum and supplement in the proportion of 1.2% body weight); FFC: Feedlot with forage (72% concentrate; 28% *Cynodon* spp. cv Tifton—85 hay); FHG: Feedlot whole grain without forage (85% whole-grain corn; 15% pellets). SEM: Standard error of the mean. Mean in the same row with different superscripts differ significantly ($p < 0.05$).

3.5. Fatty Acids

Fatty acids were affected by feeding systems; the main and most beneficial enhancement was observed in the meat of lambs raised under GS. C16:0 and c9-C18:1 were inferior to GS compared with FFC and FHG ($p < 0.01$), and the sum of SFA tended to be inferior as well ($p = 0.0570$) (Table 8). The PUFAs C20:4 (arachidonic), C20:5 (EPA), C22:5 (DPA), and C22:6 (DPA), as well as CLA c9 t11-C18:2 (CLA) and the sum of n3 and n6 and the sum of PUFAs, were higher for GS compared with FFC and FHG ($p < 0.01$). The same pattern was observed in the elongase activity estimate ($p = 0.0131$). Lambs raised under FFC had greater levels of MUFA and Δ 9–18 compared with GS but lower levels than FHG ($p < 0.01$).

Table 8. Fatty acid composition (% of total fatty acid) of the Longissimus lumborum muscle of lambs under three feeding systems.

Fatty Acid, % FAME	Feeding System			SEM	*p* Value
	GS	FFC	FHG		
C10:0	0.15	0.14	0.14	0.020	0.9416
C14:0	2.63	2.44	2.41	0.232	0.6418

Table 8. *Cont.*

Fatty Acid, % FAME	Feeding System			SEM	*p* Value
	GS	FFC	FHG		
C16:0	20.60 ^{b}	23.88 ^{a}	23.14 ^{a}	0.547	0.0006
C18:0	16.20 ^{a}	13.92 ^{b}	10.62 ^{c}	0.549	0.0001
c9-C16:1 n7	1.79	1.89	2.49	0.217	0.0676
t11 C18:1	3.61 ^{b}	2.47 ^{b}	5.36 ^{a}	0.356	0.0001
c11-C18:1	1.67	1.77	1.92	0.138	0.468
c9-c18:1	34.98 ^{b}	41.47 ^{a}	40.52 ^{a}	0.836	0.0001
C18:2 n6	0.05	0.04	0.04	0.005	0.8816
C20:4 n6	3.00 ^{a}	1.70 ^{b}	1.12 ^{b}	0.374	0.0046
C18:3 n3	0.12	0.09	0.10	0.008	0.0735
C20:5 (EPA)	0.31 ^{a}	0.09 ^{b}	0.04 ^{b}	0.037	0.0001
C22:5 (DPA)	0.65 ^{a}	0.28 ^{b}	0.14 ^{b}	0.071	0.0001
C22:6 (DHA)	0.17 ^{a}	0.07 ^{b}	0.03 ^{b}	0.021	0.0002
c9 t11-C18:2 (CLA)	0.82 ^{a}	0.49 ^{b}	0.33 ^{c}	0.043	0.0001
Σ n3	0.60 ^{a}	0.25 ^{b}	0.18 ^{b}	0.056	0.0001
Σ n6	3.279 ^{a}	2.00 ^{b}	1.26 ^{b}	0.404	0.0051
n6/n3	5.09 ^{b}	7.59 ^{a}	7.18 ^{a}	0.606	0.0159
Σ SFA	42.82	43.03	39.82	1.001	0.0570
Σ MUFA	44.30 ^{c}	49.33 ^{b}	52.58 ^{a}	0.878	0.0001
Σ PUFA	12.01 ^{a}	7.25 ^{b}	7.11 ^{b}	1.127	0.0057
Δ 9–14	6.80	4.33	4.70	1.137	0.2693
Δ 9–16	7.94	7.25	9.68	0.818	0.1152
Δ 9–18	68.33 ^{c}	74.84 ^{b}	79.25 ^{a}	0.875	0.0001
Δ 9 Overall	48.33 ^{b}	51.91 ^{b}	54.37 ^{a}	0.776	0.0001
Elongase	69.60 ^{a}	68.25 ^{ab}	66.57 ^{b}	0.669	0.0131

GS: Grazing supplemented (*Cynodon* spp. cv Tifton—85 pasture ad libitum and supplement in the proportion of 1.2% body weight); FFC: Feedlot with forage (72% concentrate; 28% *Cynodon* spp. cv Tifton—85 hay); FHG: Feedlot whole grain without forage (85% whole-grain corn; 15% pellets). SEM: Standard error of the mean. Σ n3: sum omega 3 fatty acids. Σ n6: sum omega 6 fatty acids. n6/n3: omega6/omega3. Σ SFA: sum saturated fatty acids. Σ MUFA: sum monounsaturated fatty acids. Σ PUFA: sum of polyunsaturated fatty acids. Mean in the same row with different superscripts differ significantly ($p < 0.05$).

3.6. Gene Expression

The expression of the SCD-1 gene was lower in lambs under FFC treatment compared with GS and FHC ($p = 0.0375$) (Figure 1). The feeding system did not affect the expression of the PPARα gene ($p > 0.05$). The SREBP-1c gene was more expressed in GS compared with FFC but less than FHC ($p < 0.0001$). ELOV6 gene expression was higher in lambs under GS compared with FFC and FHC ($p = 0.0114$).

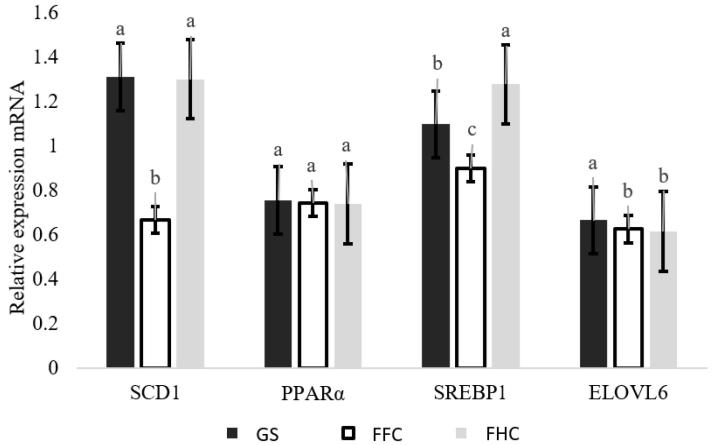

Figure 1. Relative expression of the Sterol regulatory element-binding proteins (SREBP-1), peroxisome proliferator-activated receptor alpha (PPAR-α), Stearoyl-CoA desaturase (SCD1) and Elongase 6 (ELOVL6)

genes in the Longissimus lumborum muscle of lambs under three feeding systems. GS: Grazing supplemented (*Cynodon* spp. cv Tifton—85 pasture ad libitum and supplement in the proportion of 1.2% body weight); FFC: Feedlot with forage (72% concentrate; 28% *Cynodon* spp. cv Tifton—85 hay); FHG: Feedlot whole grain without forage (85% whole-grain corn; 15% pellets). SEM: Standard error of the mean. Mean in the same row with different superscripts differ significantly ($p < 0.05$).

4. Discussion

Dry matter intake was lower in lambs under GS, as ruminants often reduce dry matter intake when dietary energy density decreases [44,45]. Also, the neutral detergent fiber in the GS diet contributes to the reduction in feed intake [46,47]. Lambs under FHC showed intermediary dry matter intake, which is associated with physiological, physical, or psychogenic mechanisms [48]. The physiological mechanism could be observed when high-energy diets, such as FHC, were provided in this study. Consequently, lambs from the FHC treatment had the highest intake of non-fibrous carbohydrates and total digestible nutrients, which are inherent to the diet.

A lower digestibility of dry matter for GS treatment was expected due to its higher fiber content. De Paula Carlis et al. [47] observed similar results when studying increased levels of neutral detergent fiber in feedlot lambs. This result is due to the replacement of corn with hay, whereas corn has greater digestion potential compared with hay [19]. The total digestible nutrients of corn (820 g/kg) are 1.4 times higher than the total digestible nutrients of coast cross hay (500 g/kg) [49,50], and it explains the higher digestibility of total digestible nutrients for lambs raised under FFC and FHC.

Neutral detergent fiber digestibility was higher in lambs raised under GS due to a higher proportion of this nutrient in the pasture and its higher intake. Pereira et al. [51] observed a similar result in lambs under feedlot-fed diets differing in fiber levels. The intake of neutral detergent fiber from forage is probably favored for maintaining rumen pH in the optimal range for the growth of fibrolytic bacteria. The favorable environment may have stimulated the increase in the population of these bacteria, which resulted in the greater digestibility of neutral detergent fiber [52].

The higher intake and digestibility of non-fibrous carbohydrates and total digestible nutrients in the FHC treatment may explain a greater weight gain in those lambs. As suggested by De Paula Carlis et al. [47], these are conditions that promote a greater production of short-chain fatty acids in the rumen and, consequently, a better performance. An increase in short-chain fatty acids reflects an increase in the amount of metabolizable energy for weight gain [53], which culminated in a greater average daily gain for lambs raised under FHC. Feed intake is associated with a higher weight gain and feed efficiency improvement to FHC treatment. Similar results of increased feed efficiency for sheep consuming high-grain diets are reported in the literature [8,54].

The highest glucose concentration in lambs raised under FHC and the lowest under GS is associated with the type of fermented carbohydrate in the diet. Diets with higher proportions of non-fibrous carbohydrates, especially starch, provide greater production and absorption of propionate, which is the main precursor of gluconeogenesis in ruminants [55] and may lead to an increased concentration of glucose in the plasma. [56] reported that an increase in glucose concentration is directly related to an increase in propionate production. In addition, the results of insulin concentration can be associated with the results of glucose concentration. Insulin is an anabolic hormone essential in maintaining glucose homeostasis. It is secreted by pancreatic islet β-cells in response to increased concentrations of circulating glucose and amino acids [57]. The higher glucose input from gluconeogenesis in lambs raised under FHC and FFC stimulated the production and release of insulin to maintain glucose homeostasis. A higher concentration of insulin and glucose in ruminants is associated with a higher fat deposit, as insulin stimulates the uptake and use of glucose

by cells [58]. In ruminants, blood is not a site of synthesis or storage of excess energy, as these processes occur in the adipose tissues.

The lower hot and cold carcass weight in lambs raised under GS is explained by a lower intake and digestibility of dry matter, resulting in lower average daily gain and live weight in GS lambs. Lambs raised under FFC showed lower live weight compared with FHC, but their hot and cold carcass weight were similar. This is associated with a higher amount of internal fat in FHC lambs.

Subcutaneous fat thickness was lower for lambs raised under GS, which is related to a lower insulin concentration, an anabolic hormone that stimulates lipogenesis [58]. Lambs raised under FHC and FFC showed higher concentrations of insulin, which stimulated the lipogenesis process, reflecting higher saturated fatty acids. Loin muscle area was superior in lambs raised under FHC and FFC, which is related to carcass weight, whereas loin muscle area reflects the degree of muscularity of the carcasses [59]

*L** was higher in meat from lambs raised under FHC and FFC, which is associated with a greater deposition of intramuscular fat. According to Realini et al. [60], fat is the chemical component of meat that has the highest luminosity. These effects on luminosity were also reported by Brito et al. [61] and Holman et al. [62].

Water loss from thawing or cooking is directly related to the water-holding capacity, which may influence shear force values. In the present study, water-holding capacity and shear force were similar between feeding systems and had characteristic values of meat considered tender by consumers. Protein and mineral contents in the meat were similar in the feeding systems. However, the fat proportion of the meat was higher in lambs raised under FHC. These results are related to the increased intake and digestibility of total digestible nutrients and a higher concentration of glucose and insulin, resulting in greater lipogenesis and hypertrophy of adipocytes. Moisture content was negatively correlated with the fat results, and it agrees with data published by D'Alessandro et al. [63], as the lipid meat content is inversely associated with the moisture content.

Meat quality is an important factor for product acceptance. It is closely related to several aspects, including sensory characteristics. Meat from lambs raised under GS showed better flavor than the other treatments. This result is related to a lower fat content in the meat of these animals. Bravo-Lamas et al. [64] found that meat from animals consuming high-grain diets had a lower intensity of species-specific flavor due to a lower proportion of C18:3 n3, which is associated with a strong flavor of sheep meat. However, the contribution of C18:3 n3 in the amount of total fatty acids is low, and in the present study, there was no greater deposition of C18:3 in the meat of lambs raised under GS.

Meat texture is one of the main attributes of meat acceptance [65]. This attribute showed a significant difference between feeding systems, and more tender meat was observed in lambs under FFC. This result agrees with Muela et al. [66] and Sañudo et al. [1], who reported that grazing lambs tended to have tougher meat than lambs finished in confinement. In the present study, lamb meat from the GS e FHC treatments showed a similar texture. This may be associated with the age at which the animals were slaughtered since the age of slaughter has a strong impact on the quality of lamb meat [67].

Overall liking was not affected by the feeding system, and sensory analysis indicated a moderate to high acceptance of the lamb meat of all three groups. Commercially, moderate acceptance demonstrates consumption and recommendation of the product [68].

The highest concentration of C18:0 in lambs raised under GS is explained by the greater extent of biohydrogenation in the rumen and the greater relative expression of the ELOVL6 gene in the muscle LL of GS lambs (Figure 1). A longer feed retention time in the rumen allows complete biohydrogenation to form the final product C18:0 [69], favoring its deposition in the meat. The ELOVL6 is the main enzyme responsible for the elongation process of fatty acids in ruminants [70], and it showed higher expression in the LL of GS lambs, which is consistent with the higher proportion of C18:0. A higher C18:0 content accompanied by the reduction in the C16:0 present in muscle of animals from GS is

beneficial; C16:0 is associated with cardiovascular diseases, while C18:0 may have a neutral or protective effect against cardiovascular diseases [71].

The highest concentration of c9-C18:1 in FHC agrees with the expression of the SCD-1 gene. The SCD-1 has desaturation activity between carbons 9 and 10, converting C18:0 into c9-C18:1 [72]. According to Campbell et al. [73] and Smith et al. [74], more energetic diets stimulate lipogenesis, promoting a greater activity of the enzyme stearoyl-CoA desaturase (SCD-1). The gene expression results corroborate with a higher desaturase activity on the C18:0 fatty acid. These results are also associated with the desaturation index (Δ9 total), and the FHC treatment showed the highest value of this index.

Although FHC showed higher amounts of t11-C18:1, this did not result in a higher proportion of c9t11-C18:2 (conjugated linoleic acid, CLA) as expected since t11-C18:1 is a precursor of c9t11-C18:2. During endogenous synthesis, the desaturation of t11-C18:1 occurs through the action of the enzyme Δ9 desaturase, converting it into c9t11-C18:2. On the other hand, a higher proportion of c9t11-C18:2 was observed under GS due to a higher proportion of C18:3 n3 and C18:2 n6 in lambs raised under GS. The increase in c9t11-C18:2 is associated with positive effects on human health due to anticarcinogenic, antioxidant, antidiabetic, and immunostimulatory actions [75], and it was associated with an increase in C18:0 and a reduction in C16:0 in the LL of GS lambs, increasing the quality of the final product and making it healthier for human consumption.

There was no effect of the feeding system on PUFA C18:3 n3 or C18:2 n6, though the n6/n3 ratio was the lowest in GS lambs. Even so, at 5.093, it was still higher than the recommended 4:1 ratio for promoting a human health benefit while being far lower than the 10:1 ratio that causes damage to health (n6/n3) [76].

C20:4 (arachidonic acid) is an intermediate in the metabolism of C18:2 n6 and C18:3 n3. Lambs raised under GS showed a higher sum of these precursors of C20:4, which resulted in a greater deposition in the meat (Table 8).

Fatty acids of the n3 series, C20:5 n3 (eicosapentaenoic acid, EPA), C22:5 n3 (docosapentaenoic acid, DPA), and C22:6 n3 (docosahexanoic, DHA), which have anticarcinogenic and anti-inflammatory actions and act in the development and protection of the nervous system [77], showed the highest values in lambs raised under GS. Lambs managed in the pasture have higher proportions of the fatty acids EPA, DHA, and DPA due to the action of elongases and desaturases, which act in the biosynthesis of long-chain fatty acids from C18:3 n3 present in pastures. This result is associated with the gene expression of ELOVL6 (Figure 1), which was higher in lambs raised under GS.

The expression of PPARα transcription factor mRNA was similar among feeding systems. The activation of the PPARα starts in response to the need for energy, resulting in the catabolism of fatty acids [9,78]. In the present study, the absence of differences between the different feeding systems indicates that none of the treatments required the mobilization of fat for energy, corroborating the results found for triglycerides.

A higher SCD-1 gene expression in lambs raised under GS and FHC corroborates the higher proportion of c9-C18:1 under FHC and c9-t11-C18:2 under GS. SCD-1 gene expression is related to the activity of the stearoyl-CoA desaturase enzyme; this enzyme's main products are c9-C18:1 and c9-t11-C18:2 [72], corroborating the results for these fatty acids.

The results obtained for SREBP-1c and SCD-1 for lambs raised under FHC were associated with a higher insulin concentration, thereby stimulating the SREBP-1c transcription factor. According to Ricoult et al. [12], the greatest stimulus to produce the transcription factor SREBP-1c is the concentration of insulin in the bloodstream. The intermediate values for SREBP-1c transcription factors in lambs raised under GS may be related to a higher proportion of acetate, the main short-chain fatty acids produced from the fermentation of neutral detergent fiber [25], which was present in high concentrations in GS treatment. After absorption, acetate is distributed to peripheral tissues, where it is converted into acetyl-CoA through the action of the enzyme acetyl-CoA synthetase, which is encoded by SREBP-1c [79].

Lambs raised under GS showed a higher expression of the ELOVL6 gene, which acts in the process of the elongation of fatty acid chains [80]. The ELOVL6 gene encodes the enzyme that catalyzes the elongation of palmitic acid (C16:0) to stearic acid (C18:0) [81]. In the present study, C18:0 was higher in lambs raised under GS, corroborating the higher ELOVL6 expression and higher elongase activity index.

5. Conclusions

The results indicated no major differences in carcass characteristics and parameters of meat quality between lambs raised under feedlot and high-grain systems; however, the high-grain system showed superiority in feed efficiency and glucose concentration. Nonetheless, the results of this study confirm that grazing lambs under supplementation increases the expression of the gene ELOVL6 and enhances meat flavor and the concentration of PUFA, which are important to human health. Differences between the feeding systems can be used by producers to determine target markets. More research is needed to overcome the challenges and limitations of experimental grazing research, e.g., replication groups and a larger number of animals, and assess the economic profitability among the different systems.

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Data Availability Statement: Data will be made available at a reasonable request to the last author, I.F.F.G.

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