Research Article

Feed Restriction in Kacang Goats: Major Impacts on Carcass Yield and Metabolic Gene Expression, but not Meat Fatty Acid Profile

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Abstract | Feed restriction is commonly implemented in smallholder goat systems; however, its effects on carcass, meat quality, and molecular aspects in Indonesian Kacang goats remain inadequately defined. Fifteen intact male Kacang goats were allocated to three dry-matter allowances over a period of 90 days: Higher (HR, 4% DM BW), Medium (MD, 3% DM BW), and Lower (LR, 2% DM BW). Data on slaughter traits, carcass and non-carcass components, primal cuts, meat proximate composition, and intramuscular fatty acid profile were collected. The expression levels of GHR, IGF1, FASN, and ACACA were quantified in the brain, liver, and longissimus dorsi using qPCR. Severe restriction (LR) significantly reduced slaughter weight, carcass weight and percentage, meat and bone yields, and various non-carcass components compared to high restriction (HR) and moderate restriction (MD), while MD generally preserved carcass performance akin to HR. Meat proximate composition and intramuscular fatty acid profile did not differ significantly among treatments. Showed a non-significant trend of higher expression in HR and MD groups compared to LR, whereas brain GHR appeared to be highest in LR. FASN and ACACA variability between tissues and treatments did not affect intramuscular fat levels or fatty acid classes. Severe feed limitation lowered carcass yield but not meat lipid quality in this 90-day experiment. A feeding level of 3% DM BW maintained carcass performance comparable to 4% DM BW, suggesting that moderate restriction may reduce feed allowance without compromising carcass yield within the conditions of this study.

Keywords | Carcass, Feed restriction, Gene expression, Intramuscular fat, Kacang goat

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INTRODUCTION

Indonesia is a vast archipelago nation characterized by agro-ecological zones that facilitate the presence of diverse local goat breeds (Ilham *et al*., 2023; Kusminanto *et al*., 2020; Susilorini *et al*., 2022). Kacang goats exhibit notable adaptability and demonstrate economic viability in lowland and marginal environments (Sutopo *et al*., 2018; Suyadi *et al*., 2019). Understanding the diversity of Indonesian Kacang goats in terms of morphology, genetics, and ecology is essential for conservation, the development of genetic improvement programs, and sustainable livestock farming (Putri et al., 2024; Pratiwi *et al*., 2024). The primary limitation for Kacang goats is the lack of feed

that meets their requirements, particularly in marginal regions (Beyleto and Hilmia, 2023). Higher feed levels and balanced rations, including protein supplements, enhance nutrient intake, digestibility, and growth, whereas feed restriction diminishes performance (Irawan *et al*., 2025; Luthfi *et al*., 2024; Nasich *et al*., 2019; Putri et al., 2024).

Feed restriction influences growth, body composition, and metabolic health in livestock, with effects mediated by alterations in gene expression in critical tissues (Costa *et al*., 2018; Hasan *et al*., 2023). The liver and brain exhibit simultaneous alterations in lipogenesis and energy metabolism pathways under feed limitation, marked by the downregulation of lipid synthesis genes and the overexpression of fatty acid oxidation genes (Hasan *et al*., 2023; Yang *et al*., 2016). The GH–IGF1 axis controls how ruminants grow, how their bodies work, and how well they can adapt to different diets (Zhong *et al*., 2012). The growth hormone receptor (GHR) in target tissues, predominantly in the liver but sometimes in muscle and other tissues, is what GH from the pituitary gland does to make IGF1. IGF1 is responsible for many of GH's anabolic and metabolic effects (Vázquez-borrego *et al*., 2021). The hypothalamus integrates dietary and metabolic information to regulate GH secretion via GHRH and somatostatin. Ghrelin, a gut hormone, also drives hypothalamus GH release (Donato and Kopchick, 2024; Lobiezz *et al*., 2000). Regulation in peripheral tissues (Liver, Muscle) growth hormone (GH) interacts with growth hormone receptors (GHR) in the liver, leading to the synthesis of insulin-like growth factor 1 (IGF1), which is then released into systemic circulation. Muscles and other tissues express GHR and produce IGF1 locally, thereby contributing to autocrine and paracrine regulation (Creyghton *et al*., 2004; Tse *et al*., 2006).

The expression patterns of GH, GHR, and IGF1 exhibit tissue-specific characteristics. Growth hormone (GH) expression is confined to the pituitary gland, whereas the liver serves as the principal site for growth hormone receptor (GHR) and insulin-like growth factor 1 (IGF1) expression, with hepatic IGF1 constituting the primary source for systemic circulation (Kobayashi *et al*., 2002; Radcliff *et al*., 2003; Zhong *et al*., 2012). Feed restriction has been shown to inhibit the expression of GHR and IGF1 in the liver, leading to a decrease in plasma IGF1 concentration. In skeletal muscle, the expression levels of GHR and IGF1 are lower than those in the liver (Ndandala *et al*., 2024; Tse *et al*., 2006). Additionally, muscle IGF1 expression exhibits greater stability in response to nutritional stress and typically increases following the refeeding phase. The brain network, specifically the hypothalamus, hippocampus, and choroid plexus, exhibits detectable expressions of GHR and IGF1 receptors, which demonstrates minimal sensitivity to nutritional deficiencies (Creyghton *et al*., 2004; Lobiezz *et al*., 2000). In goats, restricted feed intake or heat stress results in decreased expression of hepatic IGF1 and GHR (Firmenich *et al*., 2020; Madhusoodan *et al*., 2021).

Peripheral tissues exhibit significant and variable regulations of FASN and ACACA in response to nutritional stress. This suggests a metabolic transition away from direct enhancement as a compensatory mechanism. The brain remains unaffected by these changes, concentrating on the specific metabolic priorities of the tissues (Cardoso *et al*., 2020; Li *et al*., 2015). FASN and ACACA are expressed at high levels in the liver, adipose, and mammary tissues, and their expression levels change according to the dietary circumstances (Kusakabe *et al*., 2000). The expression of muscle tissue becomes more flexible, with higher levels of expression in some physiological situations and lower levels of expression when food is limited (Kang *et al*., 2015; Zhang *et al*., 2016). Brain expression is steadier and less affected by changes in diet, which suggests that muscle tissue has a higher metabolic priority (Clarke, 1993). Expression of Lipogenic Genes by Tissue Muscle Lipogenic gene downregulation (FASN, ACACB, FABP3) and fatty acid uptake/oxidation gene overexpression (LPL, FABP, GPR41, GPR43) (Costa *et al*., 2018; Kang *et al*., 2015).

Genes that regulate growth traits, carcass production, primal cuts yield, and lipogenesis in goat meat include GHR (growth hormone receptor), IGF1 (insulin-like growth factor 1), FASN (fatty acid synthase), and ACACA (acetyl-CoA carboxylase α) (Cai *et al*., 2024; Zhang *et al*., 2014, 2020). The expression of GHR, IGF1, FASN, and ACACA in meat goats shows a positive correlation with growth, carcass weight, and fat deposition. JAK2-STAT5 and PI3K/AKT pathways control GHR and IGF1, which in turn control lipogenesis and genes involved in the manufacture of fatty acids and cholesterol (Bhasker and Friedmann, 2008). SREBP-1 and LXRα govern transcription to regulate ACACA and FASN. These two proteins are needed to make new fatty acids and store triglycerides (Li *et al*., 2015; Zhu *et al*., 2014).

This study on small ruminants indicates that feed level and quality influence growth, carcass characteristics, and meat lipid composition, with nutrigenomic research highlighting GHR, IGF1, FASN, and ACACA as key regulators. Nevertheless, Kacang goats exhibit a deficiency in integrated data that connects graded feed restriction, carcass distribution, fatty acids, and tissue-specific gene expression.

MATERIALS AND METHODS

Experimental design, animals

This study was performed in the Faculty of Animal Science, Universitas Brawijaya, namely at the Sumber Sekar Field

Laboratory and the Biotechnology Laboratory. The feed test was performed *in vivo* with a completely randomized design (CRD). A cohort of 15 intact male Kacang goats was assigned to three feed restriction treatments: Higher (HR), Medium (MD), and Lower (LR), with 5 goats per treatment group. This research was performed over a 90-day period under conditions of feed restriction. Table 1 shows the results of the proximate analysis for the feed, which includes corn stover and concentrate, and Table 2 shows the formulation of the concentrate mix with HR at 4% (n= 5, dry matter 4% of body weight), MD at 3% (n= 5, dry matter 3% of body weight), and LR at 2% (n = 5, dry matter 2% of body weight).

Table 1: Chemical composition of individual feed ingredients.

Feed ingredient	Dry matter (%)	Ash (%)	Crude protein (%)	Crude fiber (%)	Crude fat (%)
Concentrate	89.29	9.69	13.73	22.96	4.64
Corn Stover	28.81	9.18	11.73	31.12	1.62

Table 2: Formulation of the concentrate mix.

Concentrate ingredient	Amount (kg)	Dry metter (%)	Crude protein (%)
Pollard	20	90.15	18.38
Copra meal	15	89.76	23.18
Cassava flour	30	87.42	3.4
Corn	8	90.15	9.51
Palm kernel meal	15	88.76	19.51
Molasses	8	77	3
Mineral premix	4	98,99	0
Total concentrate mix	100		

Animals and sampling methods

A total of 15 male Kacang goats that met the criteria of SNI 7352-2:2018 (two permanent incisors, age approximately 12–18 months) were used. The average initial body weight of the goats was 19.6 ± 2.8 kg. Animals were clinically healthy at the beginning of the study, dewormed, and adapted to the individual metabolic cages before the experimental feeding started. Goats are housed individually in separate pens. The goats were provided with a diet comprising 60% grass and 40% concentrate. Each goat was randomly assigned to one of the three feeding treatments Higher (HR), Medium (MD), and Lower (LR) ensuring a comparable distribution of initial body weight among treatments. The comprehensive expansion phase was executed utilizing an experimental methodology over a duration of 90 days. Feed was offered twice daily according to the assigned DM level, and fresh water was provided ad libitum.

All goats were slaughtered in accordance with halal practices following the completion of the ninety-day. Tissue samples were collected from three anatomically and functionally disparate sites (brain, liver, and longissimus dorsi muscle) following exsanguination. Approximately 250 mg of tissue was aseptically excised using a sterile scalpel or scissors. The initial fresh tissue specimens were swiftly chilled using liquid nitrogen to inhibit enzyme activity. Subsequently, to stabilize the nucleic acids, the fragments were transferred into 1.5 mL microtubes containing 300 µL of DNA/RNA shield (Zymo Research). The tubes are meticulously labeled with animal identification and tissue kind. The samples were initially held at 4°C during transport for short-term preservation, then subsequently transported to a -80°C freezer for long-term storage until RNA extraction.

RNA isolation and cDNA synthesis

The RNA extraction was conducted using the Zymo Research (USA) silica column-based kit, with minor alterations to the manufacturer's methodology. Upon thawing the frozen tissue preserved in DNA/RNA protection on ice, a sterile micropestle is employed to homogenize the tissue in a 1.5 milliliter tube until a uniform lysate is achieved. Following centrifugation of the homogenate for one minute at 12,000 × g, approximately 250 µL of the clear supernatant was transferred to a fresh microtube. The supernatant was mixed with RNA lysis buffer in a 1:1 ratio and gently vortexed for about one minute. Subsequently, the resultant 500 µL mixture was transferred to the initial spin column (yellow) and centrifuged for 30 seconds at 12,000×g. The eluate was gathered, combined with an equivalent volume of absolute ethanol, and progressively introduced to the second spin column (green). Centrifugation was conducted at 12,000 × g for 30 seconds, and the supernatant was removed following each spin. Following centrifugation, the column was rinsed with 400 µL of RNA Wash Buffer. Subsequently, DNase digestion was conducted on the column by introducing 5 µL of DNase I and 75 µL of DNA digestion buffer directly onto the membrane. The column was thereafter incubated for 15 minutes at ambient temperature. Subsequently, the column was rinsed with 400 µL of RNA Prep Buffer, followed by 700 µL of RNA Wash Buffer, and concluded with 400 µL of RNA Wash Buffer. 50 to 100 µL of DNase/RNase-free water was utilized to elute the RNA into a sterile tube. Spectrophotometry was employed to assess concentration and purity; only samples exhibiting an A260/A280 ratio of roughly 1.8–2.0 were utilized and thereafter stored at –80 °C. RNA subjected to DNase treatment was utilized for cDNA synthesis. This was accomplished via a commercially available reverse transcription kit including 4× DN Master Mix, gDNA remover, and 5× RT Master Mix II. Approximately 0.5–1.0 g of total RNA was denatured for 5 minutes at 65 °C and subsequently cooled on ice. Subsequently, 2 µL of 4× DN Master Mix was combined with the RNA and nuclease-free water to achieve a total volume of 8 µL.

Table 3: Sequences, amplicon size, and accession number of primers used in real-time qPCR.

Gene	Primer	Amplicon size (bp)	Acc. No
IGF1	F: 5'-GAGGCTGGAGATGTACTGTG-3'	208	HQ731040
	R: 5'-CGGAAGCAAGTCAGCAGATG-3'		
GHR	F: 5'-CGACATCCTAGTGAAATGGG-3'	186	EF559245
	R: 5'-GAGTATGAAGTGCGTGTGAG-3'		
FASN	F: 5'-GAAACCAGCTTTGCCAACTC-3'	161	DQ223929
	R: 5'-CCAATTTCCAGGAATCGACC-3'		
ACACA	F: 5'-GATTCAGATGCTCCTGGAAC-3'	125	DQ370054
	R: 5'-GATTGACATCAGAGTGGACC-3'		
GAPDH	F: 5'-GAGATCCTGCCAACATCAAG-3'	196	XM_005680968
	R: 5'-GTGGAGGGACTTATGACCAC-3'		
ACTB	F: 5'-CAAGTACTCCGTGTGGATTG-3'	145	JX046106
	R: 5'-CGGACTGTTAGTTGCGTTAC-3'		

Analysis of relative expression of target transcripts

Determining the relative trans the gene target was chosen based on the gene networks associated with lipid metabolism in reaction to feed limitation. Primers for GHR (growth hormone receptor), IGF1 (insulin-like growth factor 1), FASN (fatty acid synthase), and ACACA (acetyl-CoA carboxylase α), based on the corresponding Capra hircus gene coding sequences (CDS in GenBank) (Table 3). The PCR cycle initiates at 95°C for 15 minutes, succeeded by 40 cycles at 95°C for 15 seconds and 60°C for 1 minute. Primary specificity and primary dimer formation were assessed using melting curve analysis and by subjecting the amplification products to agarose gel electrophoresis to confirm the generation of a singular 125-208 bp amplicon per reaction.

Data analysis

Individual animals are considered the experimental units in all studies. We used one-way analysis of variance (ANOVA) to assess growth performance and carcass-related variables from the feed trial. These metrics include carcasss weight and percentage, non-carcass components, primal cuts yield, and Fatty Acid Composition. The independent variable is dietary intervention (HR, MD, LR). After identifying significant treatment effects ($P<0.05$), the averages were analyzed using appropriate post hoc tests (Duncan). The cycle threshold (Ct) values of the target genes (GHR, IGF1, ACACA, and FASN) were compared to stable housekeeping genes, such as ACTB or GAPDH (Table 3), to obtain ΔCt values. The 2-ΔCt method was used to determine relative expression levels, with one treatment group set as the reference standard. Before performing ANOVA, the ΔCt values or logarithmically transformed relative expression levels were evaluated for normality and homogeneity of variance. All statistical analyses were performed using R software (version 4.4.2; R Core Team, Vienna, Austria) within the Visual Studio Code environment.

RESULTS AND DISCUSSION

Effects of feed restriction on carcass, non-carcass, and commercial cuts

The carcass, meat, and bone percentages dropped from HR to MD and LR (Table 4). Meat and bone proportions were similar in HR and MD goats, however LR goats had significantly lower values ($P<0.05$). However, the meat-to-bone ratio was statistically stable and LR decreased slightly, showing that feed restriction within the range evaluated solely influenced carcass tissue amount rather than distribution. This pattern indicates that, in conditions of energy limitation, Kacang goats decrease total tissue accretion and carcass yield, while preserving a relatively stable carcass composition. Comparable findings have been observed in goats and sheep experiencing energy restriction, where carcass yield decreases while the proportional distribution of tissues remains largely intact (Bezerra *et al.*, 2013, 2017; Safari *et al.*, 2009). Feed restriction increases the muscle-to-fat ratio and results in a leaner carcass (Filho *et al.*, 2007). These results confirm nutritional partitioning in ruminants, where metabolizable energy is first used for maintenance and only surplus energy is used for carcass tissue growth. The growth and development of goats are influenced by their weight stage, tissues, organs, and the amount of feed consumed (Huang *et al.*, 2024). Ruminants, particularly meat goats, require dry matter for optimal growth and carcass quality (Gurung *et al.*, 2021).

The results obtained regarding non-carcass components (Table 4) indicated a significant depressive effect due to severe feed restriction. Similar patterns were noted in the skin, feet, liver, lungs, and digestive tract, where HR

and MD consistently exhibited higher weights, while LR goats showed significantly lower organ and tissue masses (P<0.05). This suggests that these non-carcass components are especially responsive to chronic energy deficiency. Prior research indicates that significant dietary energy restriction decreases visceral organ mass and overall metabolic activity in ruminants (Dupont *et al*., 2014; Keogh *et al*., 2016; Zhu *et al*., 2008).

Table 4: Carcass Yield and Non Carcass of goats with restricted feed.

Parameter	HR	MD	LR
Body weight (kg)	23.3 ± 2.14[a]	20.84 ± 1.11[a]	15.84 ± 1.50[a]
Carcass (%)	48.77 ± 3.10[a]	45.66 ± 2.00[a]	39.43 ± 2.94[b]
Meat (%)	33.22 ± 3.04[a]	31.25 ± 2.15[a]	25.44 ± 2.32[b]
Bone (%)	13.99 ± 1.56[a]	14.17 ± 2.01[a]	13.88 ± 0.99[b]
Meat bone ratio	2.41 ± 0.42[a]	2.24 ± 0.34[ab]	1.84 ± 0.20[a]
Weight of non-carcass components as a percentage of slaughter weight (%)			
Head	8.13 ± 0.[6]4a	7.62 ± 1.11[a]	8.06 ± 0.80[a]
Skin	8.54 ± 0.91[a]	7.83 ± 1.36[ab]	7.30 ± 0.51[a]
Feet	2.42 ± 0.09[a]	2.59 ± 0.39[a]	2.73 ± 0.26[a]
Liver	1.69 ± 0.20[a]	1.57 ± 0.11[a]	1.73 ± 0.40[a]
Kidney	0.30 ± 0.16[a]	0.24 ± 0.02[a]	0.30 ± 0.06[a]
Spleen	0.16 ± 0.04[a]	0.15 ± 0.04[a]	0.15 ± 0.04[a]
Heart	0.62 ± 0.24[a]	0.37 ± 0.04[b]	0.34 ± 0.01[b]
Lungs	1.11 ± 0.16[a]	1.27 ± 0.17[a]	1.19 ± 0.20[a]
Tail	0.16 ± 0.05[a]	0.13 ± 0.02[a]	0.14 ± 0.01[a]
Digestive	7.24 ± 0.51[a]	8.18 ± 0.67[ab]	9.11 ± 0.80[a]

HR: Higher ; MD: Medium; LR: Lower

Table 4 shows that feed restriction had a significant impact on carcass performance in Kacang goats. Animals receiving the highest feeding level (HR, 4% DM BW) exhibited the greatest carcass weight and percentages of meat and bone, while goats subjected to severe restriction (LR, 2% DM BW) displayed the lowest values (P<0.05). The medium level (MD, 3% DM BW) resulted in intermediate carcass weights and tissue percentages that were not significantly different from HR, indicating that moderate restriction did not adversely affect carcass deposition. A comparable trend was noted in the distribution of commercial cuts: the proportions of loin, leg, rib, forequarter, and neck–shoulder were greatest in HR goats, moderate in MD, and consistently lowest in LR. This suggests that severe restriction diminishes both total carcass yield and the relative contribution of high-value cuts (P < 0.05). The findings align with earlier studies on goats and lambs, indicating that restrictive feeding reduces carcass and primal cut weights at elevated levels of restriction (Filho *et al*., 2007; Yáñez *et al*., 2007). In contrast, a moderate restriction of about 20–30% below ad libitum has been shown to maintain favorable carcass traits and muscle quality in certain meat genotypes traits (Dos Santos *et al*., 2016; Ke *et al*., 2023). The response magnitude is influenced by the anatomical location of the cuts, duration of restriction, species, and genotype-specific adaptations (Lopes *et al*., 2014; Tilahun *et al*., 2014).

Table 5: Primal cuts yield characteristics of goats with restricted feed.

Primal cuts yield (%)	HR	MR	LR
Loin	3.22 ± 0.22[a]	3.10 ± 0.16a	2.86 ± 0.24b
Leg	13.12 ± 0.7[a]	12.85±0.39a	11.65±1.03b
Breast foreshank	13.15±1.01[a]	12.02±0.39a	10.76±0.86b
Neck shoulder	13.37±0.93[a]	12.40±1.05a	9.76 ± 0.75b
Rib	4.86 ± 0.51[a]	4.76 ± 0.38a	4.14 ± 0.33b
Meat loin	2.01 ± 0.22[a]	1.87 ± 0.14a	2.28 ± 1.85a
Meat leg	8.78 ± 0.95[a]	8.98 ± 0.33a	7.52 ± 0.90a
Meat breast foreshank	10.78±1.13[a]	9.45±0.83ab	7.89 ± 0.83b
Meat neck shoulder	6.83±1.13[a]	7.08 ± 0.83a	9.39 ± 0.83a
Meat rib	2.74 ± 0.74[a]	3.17 ± 0.35a	2.59 ± 0.56a
Bone loin	1.15 ± 0.05[a]	1.95 ± 1.64a	1.34 ± 0.14a
Bone leg	4.05 ± 1.56[a]	3.74 ± 0.30a	3.86 ± 0.37a
Bone breast foreshank	2.29 ± 0.14[b]	2.46±0.26ab	2.66 ± 0.17a
Bone neck shoulder	4.25 ± 1.54[a]	4.42±0.39a	4.41 ± 0.34a

HR: Higher ; MD: Medium; LR: Lower

Effect of feed restriction on meat fatty acid content

The results in Table 6 show that feed restriction did not significantly affect the proximate composition of the meat; the water, protein, fat, ash, carbohydrate, and crude fiber content in HR, MD, and LR showed the same superscript (a). Fat content varied between 5.61% and 6.17%, while protein content ranged from 19.65% to 20.36%, with no significant differences observed. Total fatty acids showed comparable values across treatments (71–77%), as did the proportions of saturated fatty acids (SFA) (36.7–39.2%), monounsaturated fatty acids (MUFA) (30.3–32.4%), polyunsaturated fatty acids (PUFA) (1.39–1.82%), and unsaturated fatty acids (UFA) (32.1–33.8%), all marked with "a". The only difference observed was in C17:0, which slightly increased in HR compared to MD and LR (P<0.05). The lipid profile of peanut meat showed stability at all levels of feed restriction evaluated in this study, showing no significant biological changes. Intramuscular fat (IMF) consistently declines with feed restriction, indicating diminished lipogenic activity and alterations in gene expression (Lin *et al*., 2017; Lu *et al*., 2021). Protein deposition may decline however, compensatory growth during refeeding can restore or elevate protein levels. Comparable results in swine and bovines corroborate this trend, indicating that restriction diminishes intramuscular

Table 6: Fatty acids concentration of goat meat.

Parameters	HR	MR	LR
Chemical composition			
Water Content	67.14 ± 3.66[a]	65.64 ± 4.64[a]	67.07 ± 3.03[a]
Protein Content	20.1 ± 2.17[a]	19.65 ± 2.56[a]	20.36 ± 1.76[a]
Fat Content	5.916 ± 1.24[a]	6.17 ± 1.63[a]	5.61 ± 1.25[a]
Ash Content	1.498 ± 0.95[a]	0.94 ± 0,38[a]	1.342 ± 0,70[a]
Carbohydrate	5.342 ± 5,20[a]	7.604 ± 4,56[a]	5.616 ± 1,98[a]
Fatty acid composition			
Butyc Acid C4:0	0.160 ± 0.08[a]	0.322 ± 0.28[a]	0.210 ± 0.07[a]
Capric Acid C10:0	0.743 ± 1.05[a]	1.762 ± 3.75[a]	0.110 ± 0.03[a]
Lauric Acid C12:20	1.070 ± 1.32[a]	0.696 ± 0.47[a]	0.626 ± 0.21[a]
Trideconic Acid C13:0	0.430 ± 0.85[a]	0.024 ± 0.01[a]	0.025 ± 0.01[a]
Myristic Acid C14:0	4.708 ± 2.52[a]	4.942 ± 1.56[a]	4.540 ± 0.84[a]
Myristoleic Acid C14:1	0.496 ± 0.53[a]	0.178 ± 0.23[a]	0.386 ± 0.27[a]
Pentadecanoic Acid C15:0	0.844 ± 0.81[a]	0.430 ± 0.23[ab]	0.198 ± 0.19[a]
Palmitic Acid C16:0	18.596 ± 3.29[a]	18.844 ± 1.33[a]	18.896 ± 1.63[a]
Palmitoleic_Acid_C16_1	1.984 ± 0.72[a]	1.360 ± 0.21[b]	1.446 ± 0.20[b]
Heptadecanoic Acid C17:0	1.386 ± 0.16[a]	1.006 ± 0.08[b]	1.018 ± 0.16[b]
Cis 10 Heptadecanoic Acid C17:1	0.540 ± 0.70[a]	0.412 ± 0.10[a]	0.366 ± 0.26[a]
Elaidic Acid C18 1n9t	1.476 ± 0.62[a]	1.984 ± 0.37[a]	1.624 ± 0.59[a]
Oleic Acid C18 1n9c	20.264 ± 8.07[a]	17.802 ± 2.26[a]	18.782 ± 2.61[a]
Linolelaidic Acid C18:2n9t	0.106 ± 0.03[a]	0.082 ± 0.02[a]	0.132 ± 0.05[a]
Linoleic Acid C18:2n9t	0.958 ± 1.00[a]	1.226 ± 1.26[a]	0.852 ± 0.76[a]
Arachidic Acid C20:0	0.174 ± 0.13[a]	0.158 ± 0.05[a]	0.282 ± 0.33[a]
Cis 11 Eicosenoic Acid C20:1	0.060 ± 0.02[a]	0.066 ± 0.05[a]	0.240 ± 0.34[a]
Total fatty acid	76.560±10.65[a]	71.960 ± 6.49[a]	70.976 ± 5.16[a]
SFA (%)	36.72 ± 7.92[a]	39.17 ± 6.96[a]	36.50 ± 3.76[a]
MUFA (%)	32.42 ± 11.59[a]	30.30 ± 4.22[a]	32.19 ± 4.50[a]
PUFA (%)	1.39 ± 1.32[a]	1.82 ± 1.76[a]	1.39 ± 1.08[a]
UFA (%)	33.81 ± 11.74[a]	32.12 ± 4.67[a]	33.57 ± 4.68[a]

HR: Higher; MD: Medium; LR: Lower; SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; UFA: unsaturated fatty acids

fat and protein, while refeeding facilitates recovery (Xie *et al*., 2023). Consistent energy restriction leads to a reduction in muscle fiber diameter and modifies the ultrastructure of the Longissimus dorsi muscle, indirectly affecting its proximate composition. Restrictions seldom result in substantial alterations in moisture, protein, fat, or ash levels (Lee *et al*., 2006; Pasteán *et al*., 2010; Sahlu *et al*., 2009). Severe or prolonged restrictions significantly impact fat levels. Intramuscular fat (IMF) consistently declines during feed restriction, indicating diminished lipogenic activity and alterations in gene expression (Brand *et al*., 2018; Lebret *et al*., 2007).

In this trial, feed restriction between 2% and 4% DM BW did not result in statistically significant differences in intramuscular fat content or in the proportions of SFA, MUFA, PUFA and UFA. Within the limited statistical power of a small-sample design, this finding suggests that carcass quantity in Kacang goats is more sensitive to the tested restriction range than the intramuscular fatty acid profile. However, given the small group size and the variability typically associated with fatty acid analysis, we cannot exclude the possibility of modest, biologically relevant changes that remained undetected (Type II error). Consequently, the apparent stability of the fatty acid profile in this study should be interpreted cautiously and viewed as hypothesis-generating rather than definitive proof that meat lipids are unaffected by feed restriction.

Previous work in pigs and cattle has frequently reported a decline in intramuscular fat (IMF) and changes in muscle ultrastructure under prolonged or severe energy restriction,

with partial or complete recovery during refeeding (Lebret *et al*., 2007; Brand *et al*., 2018; Xie *et al*., 2023). Similarly, studies in small ruminants have shown that moderate restriction seldom induces large shifts in moisture, protein, fat, or ash, whereas more drastic or long-term restriction can reduce fat content (Lee *et al*., 2006; Pasteán *et al*., 2010; Sahlu *et al*., 2009). The absence of major changes in proximate composition and fatty acid classes in the present trial may therefore reflect a combination of (i) the specific restriction range applied (2–4% DM BW), (ii) the 90-day time frame, and (iii) the relatively small sample size, which together may have limited our ability to detect subtle alterations in IMF and lipid class distribution.

Gene expression

The heatmap (Supplementary Figure 1) illustrates tissue-specific trends in gene expression in response to feed restriction at 4%, 3%, and 2% DM relative to body weight. The heatmap illustrates mean relative expression values ($2^{-\Delta\Delta Ct}$) for each gene-tissue combination using a standardized color scale; consequently, the color gradients indicate relative trends rather than statistically significant differences. Visual inspection indicates that IGF1 and GHR expression in the liver and muscle is elevated in HR and MD goats, while it is diminished in LR goats, reflecting the decreases in body weight and carcass percentage noted in the LR group. Nonetheless, these differences did not reach statistical significance ($P>0.05$), indicating that the observed patterns should be regarded as qualitative trends rather than conclusive effects. GHR expression in muscle was highest in HR and showed a numerical decrease in LR, indicating a possible downregulation of peripheral growth signalling along the somatotropic axis during energy restriction. In contrast, brain GHR expression tended to be highest in LR, although this difference was not statistically significant and should be viewed as a preliminary trend rather than a definitive indication of preserved central GH sensitivity (Du *et al*., 2018).

In the present study, feed restriction did not produce statistically significant changes in GHR or IGF1 mRNA expression in brain, liver or longissimus dorsi. Visual inspection of the data suggested that liver and muscle GHR/IGF1 expression tended to be numerically lower in LR goats than in HR and MD goats, in parallel with the observed reductions in carcass yield, whereas brain GHR appeared relatively less affected. Given the small group size and the lack of significant treatment effects, these patterns should be interpreted as qualitative and hypothesis-generating rather than as evidence for a true central–peripheral "disconnect" in the somatotropic axis. They are compatible with the idea that central and peripheral components of GH signalling may differ in their sensitivity to energy deficit, but our data do not provide direct functional evidence of central prioritisation, as we did not assess receptor activity, downstream signalling or tissue-specific hormone fluxes.

For the lipogenic genes, FASN and ACACA showed modest tissue- and treatment-related numerical variation, but these changes were not accompanied by detectable differences in intramuscular fat content or in the proportions of major fatty acid classes. This suggests a partial dissociation between mRNA abundance and the measured lipid traits under the present experimental conditions. While we initially referred to a "compensatory hepatic lipogenic response" in LR goats, we recognise that, under severe energy restriction, classical metabolic theory would predict a downregulation of lipogenesis rather than an increase, and our non-significant mRNA data are not sufficient to challenge this framework. A more cautious interpretation is that the small numerical differences observed in hepatic FASN and ACACA expression may reflect complex regulatory processes or random variation rather than a robust adaptive upregulation of lipogenesis, and they should therefore be viewed as preliminary and in need of confirmation.

This interpretation is hypothetical and requires validation through larger studies with more extensive sampling. The observed trends provide a basis for further investigation of GHR, IGF1, FASN, and ACACA as candidate genes associated with nutritional stress, carcass performance, and lipid metabolism in Kacang goats (Cai *et al*., 2024; Zhang *et al*., 2014). This theory remains hypothetical and necessitates larger studies with more extensive sampling for validation. The observed trends justify the need for additional research on the GHR, IGF1, FASN, and ACACA genes in Kacang goats. This association is attributed to nutritional stress, carcass performance, and lipid metabolism (Cai *et al*., 2024; Zhang *et al*., 2014). FASN and ACACA, two key lipogenic genes, showed tissue- and treatment-related variation in expression, but these changes did not translate into detectable differences in meat fat composition. ACACA expression in muscle tended to be higher in HR, whereas muscle FASN levels remained low and broadly comparable across groups. Both ACACA and FASN encode essential enzymes for de novo fatty acid synthesis and are known to influence intramuscular fat (IMF) and muscle lipid content (Kęsek-Woźniak *et al*., 2023; Li *et al*., 2015a, b).

Multiple mechanisms may explain the observed dissociation between hepatic and muscular gene expression and the stability of intramuscular fat and fatty acid profiles. One possibility is that post-transcriptional and post-translational regulation, along with substrate availability, mitigated the effects of mRNA changes on enzyme activity. Another possibility is that fat mobilization and deposition during restriction primarily occurred in non-intramuscular

depots, resulting in relatively conserved intramuscular fat (IMF). Previous studies on Taihang black and Yaoshan white goats have reported positive associations between elevated FASN and ACACA expression in the longissimus muscle and increased IMF content (Cai *et al*., 2024; Zhang *et al*., 2020).

The observed numerical decrease in IGF1 and GHR expression in the liver and muscle of LR goats parallels the reduction in carcass yield, but this pattern was not statistically significant and should therefore be interpreted as a qualitative trend rather than a definitive effect. The increase in GHR in the brain indicates a homeostatic mechanism that prioritizes nutrient allocation and hormonal signals to sustain central nervous system function. In contrast, alterations in FASN and ACACA expression were negligible and did not significantly affect intramuscular fat or the SFA–MUFA–PUFA profile.

CONCLUSION

This study suggests that Kacang goats with feed restriction exhibit greater sensitivity regarding carcass quantity compared to meat lipid quality. A feed allowance of 2% DM BW (LR) significantly decreased slaughter weight, carcass weight and percentage, meat and bone yields, as well as various non-carcass components, in comparison to allowances of 3% (MD) and 4% (HR). This suggests that severe restriction adversely affects tissue accretion and carcass yield. Under the present conditions, a feeding level of approximately 3% DM BW reduced feed allowance relative to 4% DM BW while preserving carcass performance, and therefore may be considered a practical moderate restriction strategy for Kacang goats.

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NOVELTY STATEMENT

This study presents the inaugural comprehensive evidence in Indonesian Kacang goats indicating that graded feed restriction (4%, 3%, and 2% dry matter relative to body weight for 90 days) significantly diminishes carcass yield and essential carcass and non-carcass components, whereas the proximate composition of meat and the intramuscular fatty acid profile remain predominantly unchanged. Additionally, this study used a tissue-specific molecular methodology to quantify the expression of GHR, IGF1, FASN, and ACACA in the brain, liver, and longissimus dorsi, uncovering qualitative tissue-dependent changes in response to dietary stress that are not reflected by lipid characteristics. These results demonstrate that a 3% dry matter body weight can sustain carcass performance similar to a 4% dry matter body weight under the investigated conditions, hence establishing foundational nutrigenomic-carcass linkages for Kacang goats.

AUTHOR'S CONTRIBUTION

Wike Andre Septian: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Visualization, Writing original draft.
Kuswati Kuswati: Methodology, Investigation, Supervision, Writing review & editing.
Muhaimin Rifa'i: Formal analysis, Data curation, Visualization, Writing review & editing.
Agus Susilo: Investigation, Resources, Project administration, Writing review & editing.
Tri Eko Susilorini: Supervision, Methodology, Writing review & editing.
Mashudi: Investigation, Resources, Writing review & editing.
Ari Ardiantoro: Investigation, Laboratory analysis (qPCR), Data curation, Writing review & editing.
Herlina Pratiwi: Investigation, Sample collection, Writing review & editing.
Rafika Febriani Putri: Investigation, Data curation, Writing review & editing.
Chairdin Dwi Nugraha: Methodology, Validation, Writing review & editing.
Irida Novianti: Laboratory analysis, Validation, Writing review & editing.
Ahmad Furqon: Methodology, Validation, Writing review & editing.
Suyadi: Conceptualization, Supervision, Writing review & editing.

Generative AI and AI-assisted technology statement

The authors claim that no generative AI technology or artificial intelligence was utilized to generate, analyze, or

interpret the research data. The sole application of generative AI technology was to assist with language editing, enhancing the book's readability, comprehensibility, and coherence. The authors bear complete responsibility for the integrity and accuracy of the work, having developed and validated all scientific material, data interpretations, and findings.

Ethical approval and animal welfare

The experimental method received approval from the Animal Care and Use Research Ethics Committee at Brawijaya University (No: 204-KEP-UB_2024). The manuscript includes the essential research details and methodology.

Conflict of interest

The authors have declared no conflict of interest.

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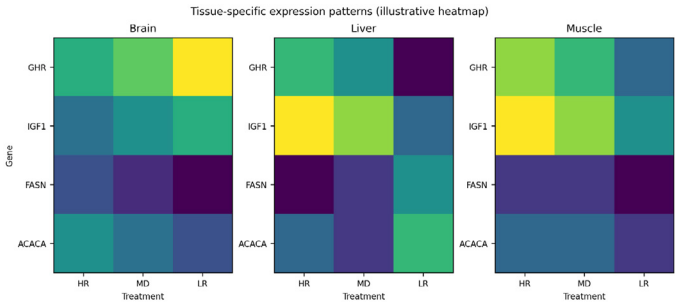

Supplementary Figure 1: Heatmap of tissue-specific expression patterns of GHR, IGF1, FASN and ACACA in the brain, liver and longissimus dorsi of Kacang goats under three feeding levels (HR = 4% DM BW, MD = 3% DM BW, LR = 2% DM BW). Each cell represents the mean relative expression for a given gene–tissue–treatment combination; darker shading indicates relatively higher expression, whereas lighter shading indicates relatively lower expression. The heatmap is provided as a qualitative illustration of gene expression trends only, and no statistically significant differences among feeding levels were detected for any gene–tissue combination.