# Effects of Muscle Fatty Acids on Meat Quality in Ruminants and Their Regulatory Factors: Post-print

**Authors:** Li Xiaoya, Tang Defu, Li Fadi, Li Fei

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## Abstract

The content and composition of fatty acids in muscle tissue affect meat quality and consumer health to a certain extent. Meat products from ruminant animals represent a major source of health-promoting conjugated linoleic acid. Therefore, elucidating the formation mechanisms and regulatory approaches of muscle fatty acids in ruminant animals is essential. This paper primarily reviews the regulatory factors of muscle fatty acids in ruminant animals and their effects on meat flavor, oxidative stability, and meat color, aiming to provide a reference for improving muscle fatty acid profiles in ruminant animals.

## Full Text

### Effects of Muscle Fatty Acids on Meat Quality and Their Regulatory Factors in Ruminants

**LI Xiaoya[1], TANG Defu[2], LI Fadi[1,3], LI Fei[1]***

(1. State Key Laboratory of Grassland Agro-ecosystems, College of Pastoral Agriculture Science and Technology, Lanzhou University, Lanzhou 730020, China; 2. College of Animal Science and Technology, Gansu Agricultural University, Lanzhou 730070, China; 3. Gansu Biotechnology Engineering Laboratory for Meat Sheep Breeding, Minqin 733300, China)

**Abstract:** Muscle fatty acid content and composition significantly influence meat quality and consumer health. Ruminant meat products represent the primary source of health-promoting conjugated linoleic acid (CLA). Therefore, elucidating the formation mechanisms and regulatory approaches for muscle fatty acids in ruminants is essential. This review synthesizes current knowledge on how muscle fatty acids affect meat flavor, oxidative stability, and color, while

examining the key regulatory factors governing fatty acid profiles in ruminants, with the aim of providing insights for improving muscle fatty acid composition.

**Keywords:** ruminant; muscle fatty acid; meat quality; regulatory factor

With rising living standards, consumers increasingly demand higher meat quality, seeking not only superior taste and tenderness but also health benefits. Ruminant meat products are favored for their low cholesterol, low fat content, and rich nutritional profile. Muscle fatty acid deposition is influenced by multiple factors including nutrition, breed, age, sex, and genetics. Research indicates that fatty acid content and composition serve as important indicators of meat quality, as they constitute key precursors for meat flavor and directly impact human health. Consequently, investigating the formation mechanisms and influencing factors of muscle fatty acids holds significant importance for meat quality improvement. This paper focuses on the effects of muscle fatty acids on meat quality and their regulatory factors in ruminants.

## 1 Effects of Fatty Acids on Meat Quality

Meat quality encompasses various parameters, including physical characteristics such as color and water-holding capacity, chemical properties like antioxidant capacity, and sensory attributes including flavor and juiciness. Fatty acids primarily influence meat quality through their effects on flavor and oxidative stability.

### 1.1 Fatty Acids and Flavor

Meat flavor can be categorized into two types: a general meaty aroma common to all species, and a species-specific distinctive flavor. Research demonstrates that the Maillard reaction between amino acids and carbonyl compounds produces the typical aroma of cooked meat, while the degradation of fat into various short-chain fatty acids—such as caproic acid (C6:0) and caprylic acid (C8:0)—constitutes the primary source of species-specific flavors. Studies have identified a significant positive correlation between palmitoleic acid (C16:1) content and meat flavor in Mongolian sheep. In free-ranging Sunit sheep, higher oleic acid (C18:1) content and an elevated oleic-to-linoleic acid ratio (C18:1:C18:2) correlate with richer, more delicious mutton flavor. Conversely, stearic acid (C18:0) content associates with mutton odor intensity, particularly when high levels in subcutaneous fat exacerbate the characteristic smell. Research on Merino sheep similarly indicates that increased C18:0 content tends to enhance off-flavors, reducing consumer acceptance. During processing, linolenic acid (C18:3) in lamb generates derivatives such as 2-pentene, significantly intensifying fishy odors. Furthermore, short-chain saturated fatty acids (SCFA) in sheep body fat show a significant positive correlation with mutton odor; elevated levels of capric acid (C10:0) and butyric acid (C4:0) markedly intensify the characteristic smell. In summary, C16:1, C18:1, and linoleic acid (C18:2) substantially contribute to desirable meat flavor, while C18:0, C18:3, C10:0, and C4:0 significantly correlate

with off-flavors. Therefore, modifying muscle fatty acid content and composition represents an important strategy for regulating mutton flavor.

### 1.2 Fatty Acids and Oxidative Stability

Under normal physiological conditions, the redox system in livestock maintains dynamic equilibrium, protecting against free radical damage. However, post-slaughter, this balance is disrupted, shifting toward oxidation. Lipid oxidation is primarily influenced by the content of readily oxidizable polyunsaturated fatty acids (PUFA) in muscle. Studies show that beef antioxidant stability, shelf life, and color lightness decrease significantly with increased $\omega$-3 PUFA content, ultimately affecting consumer acceptance. Different PUFA types exhibit varying antioxidant capacities, with $\omega$-3 PUFA demonstrating greater antioxidant potential than $\omega$-6 PUFA, thereby extending meat shelf life. Additionally, medium-long chain unsaturated fatty acids (C8–C17) and branched-chain fatty acids (BCFA) have relatively low melting points, and increased levels of these fatty acids can significantly improve meat juiciness and overall palatability. Saturated fatty acids (SFA) are characterized by higher melting points, greater density, and lower oxidation susceptibility compared to unsaturated fatty acids (UFA). Consequently, higher SFA content may enhance muscle antioxidant capacity and facilitate long-term meat storage. However, elevated levels of most SFAs, including lauric acid (C12:0), myristic acid (C14:0), and palmitic acid (C16:0), adversely affect human health by increasing low-density lipoprotein and blood cholesterol levels, thereby raising the risk of cardiovascular diseases such as atherosclerosis and coronary heart disease. Research suggests that the optimal dietary ratio of saturated to monounsaturated to polyunsaturated fatty acids (SFA:MUFA:PUFA) for human health is 1:1:1, indicating that an appropriate balance between SFA and UFA is more beneficial for human health.

## 2 Regulatory Factors of Muscle Fatty Acids

### 2.1 Gene Regulation

Genetic influences on intramuscular fat deposition can be divided into positive and negative regulation. As essential components of fat, fatty acids are directly affected by the synthesis and catabolism of adipocytes, which determines their content and composition in muscle.

**2.1.1 Genes Upregulating Intramuscular Fat Deposition** Lipoprotein lipase (LPL) is a rate-limiting enzyme in triglyceride metabolism that plays a crucial role in regulating adipocyte maturation and differentiation. Fatty acid synthase (FAS) is a key enzyme in fatty acid synthesis, primarily catalyzing saturated fatty acid production. Studies demonstrate that LPL and FAS expression promotes intramuscular fat deposition in various muscle sites of Hu sheep. Acetyl-CoA carboxylase (ACC) exists as two isoforms in ruminants: ACC-$\alpha$ (ACACA) is the rate-limiting enzyme for long-chain fatty acid (LCFA) syn-

thesis, catalyzing the conversion of acetyl-CoA to malonyl-CoA, while ACC-$\beta$ (ACACB) primarily promotes malonyl-CoA generation and regulates mitochondrial fatty acid oxidation. Research indicates that ACC influences C16:0 and LCFA synthesis, and its expression level shows a significant positive correlation with intramuscular fat deposition. Therefore, LPL, FAS, and ACC upregulate intramuscular fat deposition.

**2.1.2 Genes Downregulating Intramuscular Fat Deposition** Carnitine palmitoyltransferase 1 (CPT1) is a key enzyme controlling LCFA oxidation, participating in fatty acid $\beta$-oxidation and accelerating tissue fat degradation, thereby significantly reducing fat deposition. Preadipocyte factor 1 (Pref-1) is highly expressed in preadipocytes and decreases during adipocyte differentiation, becoming absent in mature adipocytes; consequently, downregulating Pref-1 expression significantly enhances adipocyte differentiation. Hormone-sensitive lipase (HSL) catalyzes triglyceride hydrolysis to diglycerides and subsequently to monoglycerides, serving as a rate-limiting enzyme in fat degradation. HSL also hydrolyzes monoglycerides to free fatty acids (FFA), making it a key enzyme regulating adipose tissue lipolysis. Studies show that Pref-1 and HSL expression levels negatively correlate with intramuscular fat deposition and decrease with increasing body weight in Sunit lambs. Leptin significantly reduces fat deposition by stimulating fat oxidation and decomposition in tissues, while the leptin receptor (OBR) is a transmembrane protein with high affinity for leptin. Uncoupling protein 3 (UCP3) is a proton transporter located in the mitochondrial inner membrane, and increased UCP3 in muscle significantly enhances fat oxidation levels. Research indicates that OBR and UCP3 expression downregulates intramuscular fat deposition in Hu sheep. Peroxisome proliferator-activated receptor $\gamma$ (PPAR$\gamma$) is an important factor promoting adipocyte differentiation and fat metabolism, while adipocyte determination and differentiation factor I (ADD ) is a crucial transcription factor for fat synthesis-related genes. Studies reveal that PPAR$\gamma$ and ADD expression levels show significant negative correlation with intramuscular fat deposition in lambs. In summary, CPT1, HSL, Pref-1, OBR, UCP3, PPAR$\gamma$, and ADD downregulate intramuscular fat deposition.

**2.1.3 Fatty Acid Desaturase (FAD) Genes** FAD catalyzes the formation of C=C bonds at specific positions of fatty acyl chains through C–C dehydrogenation, serving as a key enzyme in PUFA synthesis. The FAD gene family comprises numerous subtypes. Fatty acid desaturase 1 (FADS1) and fatty acid desaturase 2 (FADS2) control $\Delta$5 and $\Delta$6 desaturase activities, respectively, which represent the capacity to elongate C18:2 and C18:3 into their long-chain PUFA derivatives. Moreover, grazing can significantly increase $\Delta$5 and $\Delta$6 desaturase activities. Fatty acyl desaturase 2 (Fad2) primarily regulates $\Delta$4 desaturase activity, which represents the conversion capacity from C22:5 to C22:6. Therefore, FADS1, FADS2, and Fad2 control the elongation of C18:2, C18:3, and C22:5 into long-chain PUFAs by regulating $\Delta$5, $\Delta$6, and $\Delta$4 desaturase activities, respectively. Stearoyl-CoA desaturase (SCD) is the key enzyme for

endogenous CLA synthesis in ruminant meat products. Studies demonstrate that CLA content in lamb meat increases significantly with elevated SCD expression, and SCD can serve as a candidate gene for fatty acid genetic variation. In summary, FADS1, FADS2, Fad2, and SCD are enzyme genes responsible for muscle fatty acid desaturation.

### 2.2 Nutritional Regulation

**2.2.1 Dietary Manipulation** Diet represents an important pathway for regulating muscle fatty acids. Dietary supplementation with linseed significantly increases muscle content of $\omega$-3 PUFA, $\omega$-6 PUFA, and CLA, with 10% linseed supplementation producing lamb meat with CLA and PUFA levels more aligned with human health standards. Furthermore, combined supplementation of linseed and vitamin E significantly reduces the $\omega$-3 PUFA:$\omega$-6 PUFA ratio, thereby improving lamb meat quality. Research shows that dietary isoflavone and CLA supplementation significantly increases SCD activity in muscle, while $\alpha$-tocopherol supplementation significantly elevates C18:1 content, with both approaches ultimately increasing CLA content in lamb meat. Catechin and mulberry leaf supplementation inhibit rumen microbial hydrogenation of PUFA, significantly increasing PUFA content in lamb meat. Dietary tannins affect the rumen microbial hydrogenation step converting C18:1 to C18:0, thereby significantly increasing muscle C18:1 content. Additionally, dietary oils influence muscle fatty acids. Studies indicate that fish oil and sunflower oil supplementation both significantly increase muscle CLA content, possibly due to reduced numbers of *Clostridium proteoclasticum* under these conditions, leading to increased production of vaccenic acid (TVA), a CLA precursor. In summary, different diets may influence muscle fatty acid content and composition by altering SCD activity, modifying microbial hydrogenation steps, and changing microbial populations.

**2.2.2 Grazing Management** Grazing enables ruminants to access diverse forage types, thereby affecting muscle fatty acid content and composition, making it an effective regulatory approach. Research demonstrates that grazing improves muscle fatty acid profiles to better align with human dietary standards. Compared to indoor feeding, grazing significantly increases muscle CLA and $\omega$-3 PUFA content, likely because forage contains more PUFA and SCD than concentrates, and because forage is more readily digestible with shorter rumen retention time, reducing microbial hydrogenation time for PUFA and increasing rumen-bypass PUFA. Moreover, increasing grazing intensity and duration can optimize the $\omega$-3 PUFA:$\omega$-6 PUFA ratio for human health. Studies show that forage species and proportions during grazing significantly affect muscle content of monounsaturated fatty acids (MUFA), PUFA, C18:1, C18:2, and C18:3, with legume-based diets significantly improving lamb nutritional value. Comparative studies between organic and conventional pasture grazing reveal that organic systems produce more health-beneficial fatty acids such as $\omega$-3 PUFA, docosapentaenoic acid (DPA), and docosahexaenoic acid (DHA), presumably

because organic pastures contain more PUFA and superior forage quality, generating more health-promoting fatty acids. In summary, grazing enhances PUFA content through two main mechanisms: (1) increased fresh forage intake provides more ω-3 PUFA substrate for rumen hydrogenation, and (2) higher SCD activity in forage significantly increases muscle PUFA, especially CLA content.

### 2.3 Animal Factors

**2.3.1 Breed** Research indicates that under identical indoor feeding conditions, Tan sheep exhibit significantly higher total essential fatty acid (EFA) content and DPA and DHA levels compared to Small-tailed Han sheep. Additionally, Large-tailed Han sheep show significantly higher C18:0 content in tail fat than Small-tailed Han sheep. Studies on major local sheep breeds in southern Xinjiang reveal substantial differences in PUFA:SFA ratios: Duolang sheep (0.072) > Hetian sheep (0.064) > Karakul sheep (0.053) > Kirgiz sheep (0.046). Overall, genetic background differences contribute to variations in fatty acid content among sheep breeds.

**2.3.2 Sex** Sex primarily influences fatty acid composition in intermuscular fat. Studies show that ram muscle contains significantly higher PUFA content but lower SFA and C16:0 levels compared to ewes. Castration serves as an effective method for improving meat quality, with castrated bulls exhibiting significantly higher C16:0 and C18:1 content than intact bulls. This effect may involve two mechanisms: (1) meat quality regulation by androgens, with reduced androgen secretion after castration, and (2) castration significantly increasing muscle C18:1 content and altering fatty acid composition, though the specific regulatory mechanisms require further investigation.

**2.3.3 Age** Postnatal tissue development follows the sequence of bone, muscle, and fat, establishing a relationship between fatty acids and age. Research shows that lamb muscle contains significantly higher PUFA and MUFA content than adult sheep, while adult sheep have higher SFA content, particularly C18:0 which correlates with mutton odor intensity. Additionally, BCFA content serves as an important indicator for distinguishing lamb from mutton, with 4-methyloctanoic acid, 4-methylnonanoic acid, and 4-ethyloctanoic acid generally increasing with age and intensifying mutton odor when present at high levels. Consequently, lamb meat has relatively lower odor intensity. In summary, lamb muscle is rich in UFA, and odor-related fatty acid content increases proportionally with animal age.

## Conclusion

In conclusion, modifying muscle fatty acid content and composition can effectively regulate ruminant meat quality attributes including flavor, oxidative stability, and color. However, limited research has addressed the effects of fatty acids on water-holding capacity, cooking loss, pH, and changes in fatty acid

content and composition during meat processing, with the latter representing a particularly noteworthy research direction. Ruminant muscle fatty acids are influenced by numerous factors including nutritional regulation, genetics, breed, sex, and age. In practical production, nutritional factors should be fully utilized to regulate muscle fatty acids and improve their content and composition. Furthermore, the regulatory mechanisms of genes involved in fat deposition require further elucidation, and additional FAD genes that promote elongation of fatty acids into long-chain PUFAs need to be identified.

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*Note: Figure translations are in progress. See original paper for figures.*