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Effects of tail docking on the expression of genes related to lipid metabolism in Lanzhou fat-tailed sheep

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ABSTRACT. To evaluate stearoyl-CoA desaturase (*SCD*), hormone-sensitive lipase (*HSL*), lipoprotein lipase (*LPL*), and peroxisome proliferator-activated receptor (*PPARγ*) expression in Lanzhou fat-tailed sheep (with and without docked tails), 18 rams were randomly divided into two equal groups (docked group, LT; control group, LC). These data were also used to increase the understanding of sheep fat deposition and metabolism. All animals were harvested at the age of 18 months, and expression was determined for 10 tissues. The results indicated that the fat weight of each tissue in LT was higher than in LC ($P < 0.05$). *SCD* expression in semitendinosus, omentum majus fat (OF), subcutaneous fat, kidney fat (KF), and subcutaneous rump fat was higher in LT than in LC rams ($P < 0.05$). Trends ($P < 0.10$) associated with higher *HSL* expression of LC in comparison to that of LT rams in intestinal fat, OF, and KF tissues were detected. Numerically, *LPL* expression was the highest in KF, OF, and kidney tissues, but there were few differences ($P > 0.10$). *PPARγ* expression was greater in LT than in LC rams in liver tissues ($P < 0.05$),

but there were few differences in other tissues. No significant differences were found with regard to the regression analysis of expression and adipose tissue weights, but the two indices exhibited the same trend. The results indicated that changes in fatty deposits may be due to the common control of docking management and the minor effects associated with the regulation of *SCD*, *HSL*, *LPL*, and *PPARγ* expression.

Key words: Tail docking; Lanzhou fat-tailed sheep; Lipid metabolism; Gene expression

INTRODUCTION

Fat tissue is composed of adipocytes, and it functions as a primary site of energy storage and as an endocrine organ. The fat deposition in the tails of fat-tailed sheep has an important function, which allows the animals to adapt to nutritionally challenging environments. In actual production systems, tail docking and removal in rams seemed to aid the prevention of blowfly strike (Shutt et al., 1987), and it is generally considered good flock management (Kent et al., 1995). Additionally, considering the preferences of consumers and processors for animals with less fat, docking can reduce the total carcass fat of fat-tailed sheep (Muammer et al., 2010). Lanzhou fat-tailed sheep are located primarily in Lanzhou City, Gansu Province. The fat tail of this breed normally reaches the hock, and it is approximately 25 cm in width. The percentage of tail fat in the Lanzhou fat-tailed sheep carcass is approximately 11.46% (Ding et al., 1986).

There are numerous studies on the effects of tail docking on the production, reproductive traits, and physiological functions of fat-tailed sheep, and several studies examine the genes that effect meat traits, fatty acid composition of muscles, and carcass traits (Marai et al., 1987; Al Jassim et al., 2002; Sarvar et al., 2009; Muammer TK et al., 2010; Sun et al., 2014). However, research evaluating the impact of tail docking on the expression of genes related to lipid metabolism has not been widely reported. There is a need to evaluate the impact of tail docking on the expression of genes related to fat metabolism and deposition in order to better understand the genetics of fat metabolism and related effects on product quality. Consequently, the objectives of this experiment were: 1) to evaluate gene expression levels for stearoyl-CoA desaturase (*SCD*), hormone-sensitive lipase (*HSL*), lipoprotein lipase (*LPL*), and peroxisome proliferator-activated receptor (*PPARγ*) in Lanzhou fat-tailed sheep with and without docked tails, and 2) to analyze the relation of fat weight and gene expression levels in different tissues after tail docking.

MATERIAL AND METHODS

Animals and experimental design

Sheep used in this study were three-month old Lanzhou fat-tailed ram lambs produced by the Gansu Huajia Animal Husbandry Company in Dingxi City, Gansu Province. All 18 lambs were healthy, and development was consistent with age. The rams were randomly divided into two groups with nine rams per group. One group was docked surgically (LT), and the second group was left undocked as a control (LC). Management and rations were the same for each group throughout the trial. The sheep were harvested by exsanguination at the age of 18 months. Samples of RNA

from liver (LV), kidney (KD), semitendinosus (ST), longissimus dorsi (LD), and six adipose tissues (subcutaneous fat, SF; intestinal fat, IF; omentum majus fat, OF; kidney fat, KF; subcutaneous rump fat, BF; and tail head fat, TF) were collected. Tissue samples were immediately flash frozen in liquid nitrogen and stored at -80ºC until subsequent RNA analyses.

Fat weight

After harvesting, the five adipose tissues (SF, IF, OF, KF, and BF) were excised from the carcass and weighed on an electronic platform scale (Kaifeng, Jinhua, Zhejiang, China).

Quantitative real-time PCR

Total RNA of each tissue was isolated using Trizol (Invitrogen, Carlsbad, CA, USA) according to the manufacturer instructions, and the RNA was subsequently reverse-transcribed into cDNA using the GoScript™ Reverse Transcription System (Promega, Madison, WI, USA). Specific primers for sheep *SCD*, *HSL*, *LPL*, and *PPARγ* were used for expression analyses (Table 1). This experiment was conducted using GoTaq® qPCR Master Mix (Promega) and a LightCycler 480 Real Time PCR (Roche, Basel, Switzerland). Amplification was carried out as follows: one cycle at 95°C for 2 min; 40 cycles at 95°C for 15 s per cycle with annealing at 60°C for 1 min. There were three replicates for each sample. The mRNA quantities of the target genes were normalized to that of the reference gene (*beta actin*).

Table 1. Parameters of gene-specific primers for stearoyl-CoA desaturase (*SCD*), hormone-sensitive lipase (*HSL*), lipoprotein lipase (*LPL*), and peroxisome proliferator-activated receptor (*PPARγ*), and *beta actin.*

Gene name	GenBank accession No.	Primer sequence	Annealing temperature (°C)
SCD	NM_001009254.1	5'-TTCTCTTTCTCCTCATTGCCCC-3'	60
		5'-TCGGCTTTGGAAGCTGGAA-3'	
HSL	NM_001128154.1	5'-GGGAGCACTACAAACGCAACG-3'	60
		5'-TGAATGATCCGCTCAAACTCG-3'	
LPL	NM_001009394.1	5'-TACCCTAACGGAGGCACTTTCC-3'	54
		5'-TGCAATCACACGGAGAGCTTC-3'	
PPARγ	NM_001100921.1	5'-CATTTCTGCTCCGCACTAC-3'	60
		5'-GGAACCCTGACGCTTT-3'	
beta actin	NM_001009784.1	5'-GGCAGGTCATCACCATCGG-3'	60
		5'-CAGCACCGTGTTGGCGTAG-3'	

Statistical analysis

The SAS software (Cary, NC, USA) was used to analyze the fat weights using a completely randomized design. The tail treatment was analyzed as a fixed factor (LT, LC), and variation among rams within the tail treatment was considered experimental error. *SCD*, *HSL*, *LPL*, and *PPARγ* gene expression in LV, KD, ST, LD, SF, IF, OF, KF, BF, and TF tissues was calculated using the comparative threshold cycle (CT) value and the $2^{-\Delta\Delta CT}$ method. These data were then analyzed using a completely randomized design with a fixed treatment of intact tail versus docked tail, and the data were analyzed using the PROC MULTTEST program (SAS®, Cary, NC, USA). Data were analyzed as untransformed and log base 2 transformed data, and hypothesis tests were

conducted using the false discovery rate methodology to control for error rates (Benjamini and Hochberg, 1995). Gene expression was also adjusted to an average tissue weight using the PROC MIXED software (SAS®) for relevant tissues (e.g., gene expression levels for subcutaneous fat adjusted to a mean subcutaneous fat weight). Both untransformed and log base 2 transformed gene expression data were analyzed using analysis of covariance where the linear model included treatment effects (intact versus docked tails). Moreover, the covariate of tissue weight was nested in the tail treatment to ascertain if the relationship between gene expression and tissue weight was similar in both treatment groups. Hypothesis tests concerning the covariates were conducted using *t* statistics at significance level of $P < 0.05$, and $P < 0.10$ was considered a trend.

RESULTS

Fat weights of different tissues

The effects of docking on the fat weight of different tissues are summarized in Table 2. The fat weights of each LT tissue were higher than those observed in LC sheep. No significant differences were detected between LT and LC sheep in adipose tissues. However, the total weights of OF and IF were different between docked and intact sheep ($P < 0.05$). The internal fat (INF) and BF weights of LT were also higher than those of LC sheep ($P < 0.05$). However, the total fat (TTF) of LT rams was lower than that of LC rams ($P < 0.05$) due to the additional tail fat of the LC rams.

Table 2. Effect of docking on the distribution of the fat in Lanzhou fat-tailed sheep (kg).

Treat	KF	SF	OF	IF	OF and IF	INF	BF	TTF
Cut	0.44 ± 0.15^{A}	2.17 ± 0.73^{A}	1.21 ± 0.45^{A}	0.54 ± 0.19^{A}	1.75 ± 0.46^{A}	2.19 ± 0.47^{A}	0.58 ± 0.22^{A}	4.94 ± 1.45^{B}
Not	0.35 ± 0.19^{A}	1.82 ± 0.6^{A}	0.82 ± 0.47^{A}	0.38 ± 0.20^{A}	1.2 ± 0.39^{B}	1.55 ± 0.68^{B}	0.33 ± 0.25^{B}	6.72 ± 1.54^{A}

KF = kidney fat; SF = subcutaneous fat; OF = omentum majus fat; IF = intestinal fat; INF = internal fat; BF = buttocks fat; TTF = total fat. ^{A,B}Different subscripts in the same column indicate significant differences between the two treatments ($P < 0.05$).

Analysis of gene expression levels

SCD, *HSL*, *LPL,* and PPARγ expression in each tissue of LC and LT rams, analyzed using real-time PCR, is shown in Figures 1-4. *SCD* expression was numerically greatest in BF, and values were greater in SF and TF tissues than in other tissues in LT and LC rams. Moreover, expression in adipose depots was generally greater than that in muscle and internal organ tissues. *SCD* expression levels of LT rams in ST, OF, SF, KF, BF, and TF were greater ($P < 0.05$) than of LC rams, while gene expression levels in LV, KD, IF, and LD were similar between the two tail treatments (Figure 1).

HSL expression in all fat tissues was greater than that in muscles, and there was little *HSL* expression in LV and KD tissues. There were trends ($P < 0.10$) associated with greater expression in LC rams for IF, OF, and KF tissues compared to that in LT rams, but there was little evidence of tail treatment differences associated with gene expression in other tissues (Figure 2).

Moreover, there was little evidence of tail treatment differences in *LPL* expression in any of the tissues ($P > 0.10$), but *LPL* expression levels were highest in KF, OF, and KD tissues. Similar to other genes, *LPL* expression was numerically greater in adipose depots than in muscle, and LT rams had higher *LPL* expression in all the tissues compared to LC rams, with the exception of LD tissue (Figure 3).

PPARγ expression was greater in LT rams than in LC rams in LV ($P < 0.05$), but there was little evidence of tail treatment differences in other tissues. Numerically, the expression levels were higher in adipose depots than in muscle and internal organs, and *PPARγ* expression was numerically highest in BF, TF and OF tissues. Estimates of *PPARγ* expression in LV, OF, KF, BF, and IF were numerically greater in LT than in LC rams, and values were numerically lesser in KD, ST, LD, SF, and TF in LT than in LC rams (Figure 4).

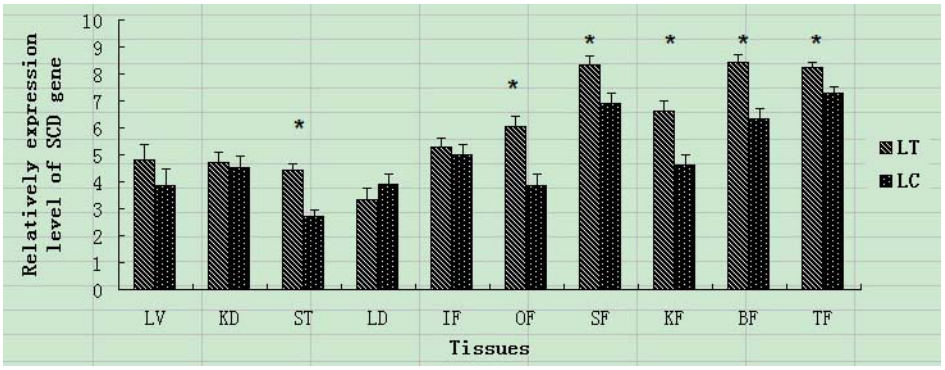

Figure 1. Stearoyl-CoA desaturase (*SCD*) expression in each Lanzhou fat-tailed sheep tissue. LV = liver; KD = kidney; ST = semitendinosus; LD = longissimus dorsi; IF = intestinal fat; OF = omentum majus fat; SF = subcutaneous fat; KF = kidney fat; BF = buttocks fat; TF = tail head fat. *Significant differences detected between the gene expression of LT and LC rams in the same tissues ($P < 0.05$).

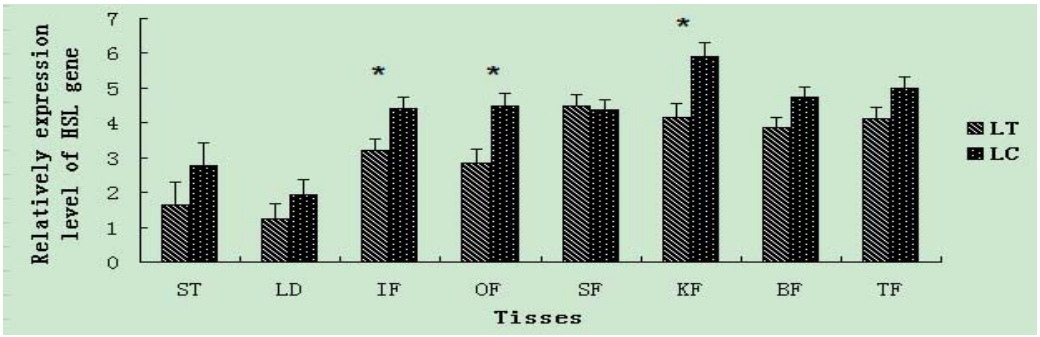

Figure 2. Hormone-sensitive lipase (*HSL*) expression in each Lanzhou fat-tailed sheep tissue. ST = semitendinosus; LD = longissimus dorsi; IF = intestinal fat; OF = omentum majus fat; SF = subcutaneous fat; KF = kidney fat; BF = buttocks fat; TF = tail head fat. *Significant differences detected between the gene expression of LT and LC rams in the same tissues ($P < 0.05$).

Relationship between gene expression levels and fat weight

In general, there was little evidence of a relationship between gene expression and adipose tissue weight for the target genes and adipose tissues. However, there was some evidence indicating that the relationship differed for all tissues and tail treatments associated with the four genes. The regression equations between gene expression and tissue fat weights for the four genes, specific adipose tissues, and tail treatments are given in Table 3. Regression equations

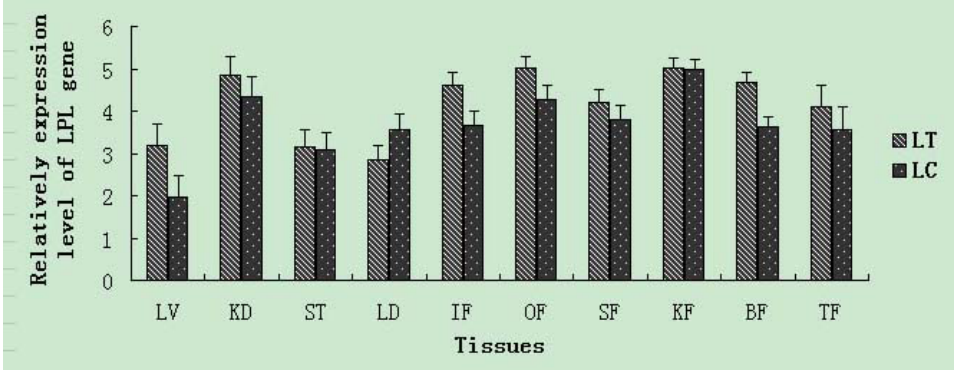

Figure 3. Lipoprotein lipase (*LPL*) expression in each Lanzhou fat-tailed sheep tissue. LV = liver; KD = kidney; ST = semitendinosus; LD = longissimus dorsi; IF = intestinal fat; OF = omentum majus fat; SF = subcutaneous fat; KF = kidney fat; BF = buttocks fat; TF = tail head fat. *Significant differences detected between the gene expression of LT and LC rams in the same tissues ($P < 0.05$).

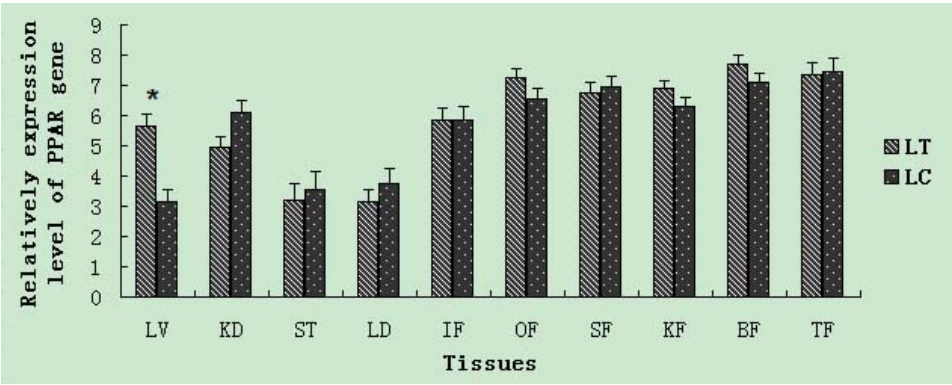

Figure 4. Peroxisome proliferator-activated receptor (*PPARγ*) expression in each Lanzhou fat-tailed sheep tissue. LV = liver; KD = kidney; ST = semitendinosus; LD = longissimus dorsi; IF = intestinal fat; OF = omentum majus fat; SF = subcutaneous fat; KF = kidney fat; BF = buttocks fat; TF = tail head fat. *Significant differences detected between the gene expression of LT and LC rams in the same tissues ($P < 0.05$).

were included where there were weak trends and significant regression coefficients. *SCD* data suggested that increases in KF weight were associated with increased gene activity in intact-tailed rams ($P < 0.05$). Moreover, *HSL* data also indicated that increased BF weight was associated with decreased gene activity in rams with intact tails ($P = 0.05$). Regarding *LPL*, increased KF was associated with increased gene activity in lambs with docked tails ($P = 0.05$), and there were trends that suggested that increases in SF and BF weights in rams with intact tails were associated with increased gene activity ($P \leq 0.10$). In *PPARγ*, evidence suggested that increases in BF weight ($P < 0.05$) in intact-tailed rams were associated with increased gene activity, and KF weight ($P < 0.10$) was associated with decreased gene activity in KD. Heterogeneities in these regression coefficients indicated that the relationship between fat weights and gene activity could depend on both fat deposits and tail treatment.

Table 3. Correlation between gene expression and fat weight.

Gene	Expression in each tissue	Treat	WT	Regression equation	Pr
SCD	SF	Cut	SF	y = 0.706x + 6.799	0.148
	KD	Cut	KF	y = 4.13x + 6.537	0.123
	KD	Not	KF	y = 3.353x + 5.917	0.044
HSL	BF	Not	BF	y = -4.995x + 6.389	0.052
	SF	Not	SF	y = -0.624x + 5.604	0.177
LPL	BF	Not	BF	y = 3.840x + 2.347	0.103
	SF	Not	SF	y = 0.915x + 5.951	0.073
	KF	Cut	KF	y = 3.015x + 6.363	0.052
PPARγ	BF	Not	BF	y = 6.294x + 5.025	0.017
	KD	Not	KF	y = -6.234x + 7.229	0.089

KD = kidney; SF = subcutaneous fat; KF = kidney fat; BF = buttocks fat.

DISCUSSION

Tail docking in Lanzhou fat-tailed sheep appears to increase internal fat deposition associated with kidney, intestine, and omentum majus tissues. There is also some evidence of increased subcutaneous fat in docked tailed sheep over the buttocks. The research of O'Donovan et al. (1973) on Turkish Tuj rams revealed that nearly 50% of fat originally deposited in the tail migrated to subcutaneous, intermuscular, and INF in docked lambs, which is consistent with the current research. Al Jassim et al. (2002) also concluded that docked lambs had more fat deposition in omental, pelvic, and kidney than undocked lambs under high energy feeding levels. Apparently, tail docking interferes with fat deposition mechanisms, resulting in higher deposition in fat depots other than the tail. However, TIF weight was less in rams with docked tails than in rams with undocked tails. These results implied that fat deposition was not only diverted, but it was also blocked to an extent. Moreover, the results highlighted Lanzhou fat-tailed sheep breed characteristics, namely the super fat deposition capability of the tail. Genes related to lipid metabolism play an important role in the processes of fat cell differentiation, fat deposition, and mobilization. In this study, gene expression was altered by tail treatment, which is consistent with the observations associated with differential fat deposition.

SCD is a rate-limiting enzyme that regulates the biosynthetic process of obtaining monounsaturated fatty acids from saturated fatty acids. *SCD* is located in the endoplasmic reticulum, and it plays an important role in fat metabolism (Kaestner et al., 1989; Mele et al., 2007). The results of this study demonstrated that the *SCD* expression levels were higher in adipose depots than in muscle and internal organs, and the highest expression levels were detected in SF, BF, and TF. Liu (2014) found a similar result in that *SCD* expression levels of Lanzhou fat-tailed sheep were higher in subcutaneous fat than other tissues. A dramatic increase in *SCD* expression favors fat accumulation, which causes obesity and insulin resistance, whereas substantial inhibition of *SCD* expression may promote fat catabolism (Liu et al., 2011). In this study, *SCD* mRNA expression levels of rams with docked tails were higher in ST, OF, SF, KF, BF, and TF tissues ($P < 0.05$) than in rams with intact tails. The results possibly indicate that fat accumulation increased in each tissue after tail docking, which is consistent with the fat weight results.

HSL is predominately expressed in white and brown adipose tissue, and it is thought to

play a crucial role in the hydrolyzing of triglycerides deposited in adipose tissue (Langin et al., 1993; Haemmerle et al., 2002). Previous research (Xu, 2010; Zang, 2011) showed that *HSL* expression levels in Lanzhou fat-tailed sheep differed in tissues, and the *HSL* expression level was highest and lowest in KF and muscle tissues, respectively. Furthermore, *HSL* is scarcely expressed in visceral tissues, and a similar result was revealed in this study. This result may be related to the fat metabolism of ruminants, mainly associated with adipose tissue and intramuscular fat deposition. *HSL* deficiency in mice causes the accumulation of diglycerides in adipose tissue, skeletal muscle, and testis (Haemmerle et al., 2002). Research on pig muscles (Chen et al., 2003) showed that intramuscular fat content decreased with increased *HSL* expression levels. The results of this study indicated that the *HSL* expression of each tissue in controlled rams was higher than that in docking rams. The results indicated a trend ($P < 0.10$) associated with the higher expression in IF, OF, and KF of LC compared to that of LT rams. Previous studies indicated that increases in *HSL* expression could depress the accumulation of triglycerols in adipose cells (Mary et al., 1993; Sztalryd et al., 1995), which was also demonstrated in skeletal muscle (Hansson et al., 2005). Most LC ram tissues with lower fat weight had the greatest *HSL* mRNA expression. This result is consistent with previous research in that the difference in *HSL* expression in LT and LC Lanzhou fat-tailed sheep might be largely caused by docking.

LPL is generally accepted as the rate-limiting enzyme that hydrolyzes triglycerides (Weinstock et al., 1997; Wang and Eckel, 2009), and it is predominantly found in muscle and adipose tissues. Moreover, *LPL* can control the distribution of triacylglycersols between muscles and adipose tissues (Hocquette et al., 1998). Previous research on sheep (Barber et al., 2000) showed that the *LPL* expression level was highest in omental depots and perirenal depots, and the levels were significantly higher than popliteal and flank depots. Liu (2014) found the same results in Lanzhou fat-tailed sheep. In this study, the *LPL* expression level was highest in KF, followed by OF and KD, and the expression levels were all higher in adipose depots than in muscle. This result was consistent with previous research results. *LPL* expression in adipose tissues of docking tail rams was higher than that found in the control specimens. Previous research results led to the conclusion that there was a correlation between increase *LPL* activity and lipid storage in white adipose tissue (Chen et al., 2004). Furthermore, there was an upregulation of *LPL* expression in tailless rams than in tailed rams, which would result from increased fat deposition. The fat weight results of each tissue confirmed this conclusion. Research on swine (Gao et al., 2004) revealed that *LPL* expression increases in muscle were accompanied by increases in intramuscular fat content, and Qiao et al. (2007) found similar results. The *LPL* expression of ST was slightly higher in LT than LC rams, which indicated that the intramuscular fat content of ST was higher in LT than LC rams, and this was supported by the intramuscular fat content results of ST.

PPARγ is a member of ligand-activated nuclear transcription factor family, and it belongs to the nuclear receptor superfamily. It regulates gene expression that is correlated with fat metabolism, and it plays an important role in lipid metabolism (Schoonjans et al., 1996; Qi et al., 2000; Lee et al., 2003). Previous research indicated that *PPARγ* exhibited differential expression in adipose tissue, internal organs, muscles, and other tissues of pigs, sheep, and cattle, and the highest *PPARγ* expression levels were detected in adipose tissues (Wang et al., 2008; Lin et al., 2012; Zhang et al., 2014). The same results were obtained in this study. PPARγ was expressed in each tissue, and the expression levels were higher in adipose tissues than in muscle and internal organs. Lin et al. (2012) researched Guangling large-tailed sheep, and found that the *PPARγ* expression level in adipose tissue of TF was higher than that of KF, IF, and OF. Guangling large-tailed sheep have a

long, fat tails where a large amount of fat stored is stored, and *PPARγ* expression was higher in the tail. In this study, Lanzhou fat-tailed sheep had the highest *PPARγ* expression levels in BF, TF, and OF, which was similar to previous results. *PPARγ* expression was upregulated in LV, OF, KF, BF, and IF, and it was downregulated in KD, ST, and LD after docking ($P < 0.05$). Therefore, the results suggest that *PPARγ* could promote the deposition of fatty acids in adipose tissue. Furthermore, there may be some resistance in KD, ST, and LD after docking, which could lead to decreased *PPARγ* expression levels.

Lanzhou fat-tailed sheep have long, fat tails where fat is specifically deposited. In this study, the results suggested that the docking of Lanzhou fat-tailed sheep tails could distribute portions of the fat to other organs, and it could also influence the expression of some related genes. However, there was no general correlation between gene expression levels and fat weight. Further molecular research may be required to further study the regulation of fat deposition.

Conflicts of interest

The authors declare no conflict of interest

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