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An Novel SNP in *LPL* Gene Exon 8 Associated with Meat Quality Traits in Ducks

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ABSTRACT

Lipoprotein lipase (LPL) plays a crucial role in the metabolism and transport of lipids. The polymorphism of the *LPL* gene exon 8 and associations with duck meat quality traits were investigated using PCR-SSCP analysis and DNA sequencing. A novel silent mutation 1251 T>C was first identified located in exon 8 of the *LPL* gene. Two alleles (T and C) and three genotypes designed as TT, TC and CC were detected in the PCR products. The T allele and TT genotype were dominant in the five breeds. The 1251 T>C locus belonged to moderately informative polymorphism except for the Yinjiang ducks. The genotype distribution of the Xingyi, Jinding and Cherry Valley populations deviated from Hardy–Weinberg equilibrium but not the Sansui and Yinjiang populations. The 1251 T>C locus was significantly associated with meat quality traits except for pH, water holding capacity, intramuscular fat, C14:1, and C15:0. Significant additive effects were detected for C12:0, C14:0, C16:0, C16:1, C17:0, C18:2, C20:1, C20:3, PUFA and EFA, significant dominance effects for shear value, C14:0, C17:0, C18:0, C18:1, C18:3, C20:0, C20:1, C20:2, C20:4 and UFA. The results suggested that the 1251C>G polymorphism might be useful genetic markers in duck breeding to improve the content of beneficial fatty acids.

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Authors' Contribution

YYZ conceived and designed the study, and wrote the article. WGL carried out the experimental work. DDW analyzed the data of the study.

Key words

Duck, *LPL* gene, SNP, meat quality traits.

INTRODUCTION

In avian species, excessive accumulation of lipids in subcutaneous and abdominal adipose tissues is a major concern for producers, because most of accumulative fat are lost during evisceration of the carcass or processing of the meat, which results in lower meat yields (Fesler and Peterson, 2013). Any attempt to modify these metabolic processes must take into consideration the specific features of lipid metabolism in birds. The synthesis of fatty acids in poulty takes place mainly in the liver, adipose tissue growth and subsequent fattening depend on the availability of plasma triglycerides, which are transported as components of lipoproteins (Braun and Severson, 1992). Lipids and especially triglycerides may be stored in adipocytes, hepatocytes and growing oocytes. Lipid storage in oocytes is associated with vitellogenesis and further development of the embryo, but the fatty acid synthesis does not occur in the ovary (Sato and Akiba, 2002). In growing birds, VLDL is the major transporter of triglycerides, and attempts to reduce excessive fatness in poultry have involved the control of VLDL metabolism (Hermier, 1997).

Lipoprotein lipase (LPL) is a central enzyme responsible for the hydrolysis of triglycerides in very low-density lipoproteins (VLDLs) and chylomicrons producing intermediate-density lipoproteins (IDLs) and chylomicron remnants, respectively (Li *et al.*, 2014). LPL is synthesized by many tissues, including adipose tissue, islets, macrophages, and cardiac and skeletal muscle, and provides energy in the form of fatty acids and monoacylglycerol to the capillary lumen of many tissues for utilisation by GPIHBP1, a GPI-anchored protein of endothelial cells (Young *et al*., 2011). An absence of GPIHBP1 abolishes the entry of LPL into capillaries, causing severe chylomicronemia and an accumulation of catalytically active LPL in the interstitial spaces (Voss *et al*., 2011). LPL is also involved in promoting the cellular uptake of free fatty acids, cholesterol-rich lipoproteins, and chylomicron remnants while ApoC-II acts as a cofactor of LPL (Tian *et al*., 2012). Based on the role of LPL, LPL plays as a critical role in regulation of lipids deposition and transport, energy balance, body weight and growth traits for development as determined in farm animal (Du and Huang, 2007). *LPL* gene mutation may affect the LPL activity, and results in lipid metabolism disorder, which attracted much attentions on the association of polymorphism and economic traits in poultry. *LPL* gene comprises 9 introns and 10 exons in poultry, fish, primate, rodent, and mammal. Many studies have been performed on the effect of polymorphisms of the *LPL* gene on animal growth, carcass, fatty acid composition, and meat quality traits (Wang *et al*., 2012; Rahalkar *et al*., 2009). However, few studies have been reported on polymorphism of the *LPL* gene in duck. The

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exon 8 of *LPL* gene is the key sequence for coding the catalytic center of lipoprotein lipase (Li *et al.*, 2014). Therefore, the aim of this study was to detect single nucleotide polymorphisms (SNPs) of 165 bp fragment containing exon 8 of *LPL* gene in ducks and explore their possible associations with meat quality traits.

MATERIALS AND METHODS

Sample collection and preparation

Xingyi duck is a Chinese indigenous breed of eggs-meat dual purpose type, which was continuous selected by College of Animal Science, Guizhou University, Guiyang, Guizhou, P.R. China. About 150 Xingyi ducks were randomly selected from the population of commercial generation in the same farm and used in the association study at 70 days of age. All of individuals were maintained in a semi-open house and subjected to conventional management conditions and fed commercial corn–soybean diets that met NRC requirements. Three Chinese indigenous breed of Sansui (130 ducks) (SS), Yinjiang (97 ducks) (YJ), Jinding (110 ducks) (JD) and a introduced duck variety of Cherry Valley (100 ducks) (CV) were also included in the genotyping analysis. All birds were handled and treated according to the animal care and used the Departmental Ethics Committee for Research on Animals (DECRA), under the DECRA reference number R11/37.

Genomic DNA from birds was extracted from blood samples using the TIANamp Blood DNA Midi kit (Tiangen Biotech, Beijing, China). Meat quality traits, included pH-value, shear value ($kg.cm^{-2}$), water holding capacity (WHC) (%), intramuscular fat (IMF) (%), and fatty acid composition of breast muscle of each individual of Xingyi duck, were measured as described by Poławska *et al*. (2012) and Han *et al*. (2013).

Primer design and PCR amplification

Based on the duck *LPL* gene sequence (GenBank Accession No: FJ185781), primer pair was designed to amplify a 165 bp fragment of exon 8 of the duck *LPL* gene using the software Oligo 6.0. The primer sequences were as follows: forward 5'-AAC AAG ACC TTC TCC TTC CTG-3' and reverse 5'-TTT CTG AGT TTC GCC TGA C-3'. Polymerase chain reaction (PCR) was performed by mixing 8μL of 2×*HiFi*-PCR Master (*Pfu*) (Sangon Bioteck, Shanghai, China), 9 μL of dd H_2O, 1 μL of each primer (10 μM), and 1 μL of genomic DNA (100 ng) in a 20 μL volume, and running according to the following program: 95°C for 10 min, 30 cycles of 94°C for 30 s, 60°C for 30 s, and 72°C for 30 s and final extension at 72°C for 2 min. The PCR products were electrophoresed on 1% agarose gel.

Polymorphism screening and sequencing

All DNA samples of Xingyi, Sansui, Yinjiang, Jinding, and Cherry Valley ducks were used to PCR-SSCP. Aliquots of 5 μL of the PCR products were mixed with 5 μL of the denaturing solution (95 % formamide, 0.025 % bromophenol blue, 0.025 % xylene–cyanole and 25 mM EDTA), heated for 15 min at 98°C and then rapidly chilled on ice. Denatured DNA was subjected to 10% acrylamide: bisacrylamide (29:1) gels analysis, which was run with 1× TBE buffer for 10 h at 130 voltage constantly. The gel was stained with 0.1 % silver nitrate and visualized with 2% NaOH solution, and record the genotype of each sample. The PCR fragments from different PCR–SSCP patterns in different populations were sequenced using the forward and reverse primers commercially.

Statistical analysis

Sequences were edited and aligned using DNAMAN and AlignIRversion 2.0 program. Genotypic frequencies, allelic frequencies, heterozygosity(H), polymorphism information content (PIC), and Hardy–Weinberg equilibrium were estimated for each breed by using POPGENE version 1.32. The associations of LPL exon 8 genotypes with meat quality traits were analyzed in Xingyi duck populations using the general linear model of SAS (SAS Institute Inc). The estimated genotype values were compared by Duncan's Multiple Range Test of SAS. The statistical model was shown as following: $Y = \mu + G + e$, where Y is the dependent variable (analyzed traits), μ is the overall mean, G is the genotype of different variation for the *LPL* gene exon 8 (fixed effect), and e is the random error. The additive effect of the DNA polymorphisms was estimated as the difference between the solutions of means of the two homozygous genotypes divided by two and the dominance effect was estimated by subtracting the average of solutions of homozygous genotypes from the solution of the heterozygous genotype according to Zhu and Jiang (2014) and Falconer and Mackay (1996).

RESULTS AND DISCUSSION

Polymorphism identification and detection

An amplification of 165 bp fragment of *LPL* gene for all the genomic DNA samples was successfully amplified. The SSCP results indicated that exon 8 of the duck *LPL* gene showed three polymorphism patterns of TT, TC and CC in five duck populations (Fig.1). Three PCR fragments from different SSCP patterns in different populations were two-way direct sequenced. Comparisons among sequencing results showed that an alteration in exon 8: 1251 T>C silent mutation (ss

831878774) was firstly identified (Fig.2).

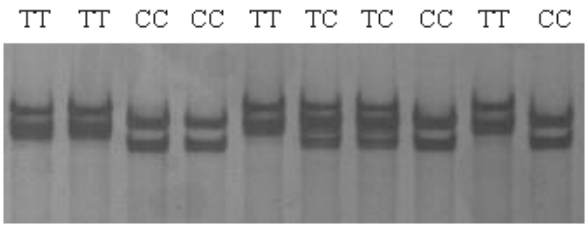

Fig.1 PCR-SSCP band pattern

Genotype and allele frequencies

The allele and genotype frequencies of the 1251 T>C polymorphism of *LPL* gene exon 8 were detected in five duck populations with counts of genotypes listed in Table I. The T allele and TT genotype were dominant in the five breeds, respectively. The 1251 T>C locus belonged to moderately informative polymorphism (0.25 PIC>0.5) except for the Yinjiang ducks as described by Botstein *et al*. (1980). The moderately informative and highly informative content were advantageous in group differentiation of breeding but not slightly informative content. The genotype distribution of the Xingyi, Jinding and Cherry Valley populations deviated from Hardy–Weinberg equilibrium (P<0.05 or 0.01) but not the Sansui and Yinjiang populations. One explanation could be that the Xingyi, Jinding and Cherry Valley populations suffered intensive selection during long-term commercial breeding. In selected populations, deviations of genotype frequencies from Hardy–Weinberg equilibrium should be expected for loci with impact on traits under selection (Groeneveld *et al*., 2010).

Association of exon 8 polymorphism with meat quality traits

Many of the biological aspects of LPL, including lipoprotein metabolism, fattening and reproduction have been implicated in animal (Mead *et al*., 2002). Regulation of LPL appears to be very complex and responds to dietary or hormonal changes and environmental conditions being clearly tissue-specific (Sato *et al*., 2010). In our study, association of the 1251C>G (ss 831878774) locus of *LPL* gene with Xingyi duck meat quality traits were showed in Table I. The results showed that the 1251 T>C locus was significantly associated with meat quality traits except for pH, water holding capacity, intramuscular fat, C14:1, and C15:0. There were significant differences between genotypes TT and TC for shear value, C14:0, C16:0, C17:0, C18:0, C18:1, C18:3, C20:0, C20:1, C20:2, C20:3, C20:4 and unsaturated fatty acid, between TT and CC for C12:0, C14:0, C16:0, C16:1, C17:0, C18:2, C20:1, C20:3, polyunsaturated fatty acid and essential fatty acid, between CC and TC for C16:0. For the 1251C>G locus of *LPL*, significant additive effects were detected for C12:0, C14:0, C16:0, C16:1, C17:0, C18:2, C20:1, C20:3, polyunsaturated fatty acid and essential fatty acid at P<0.05 or 0.01, significant dominance effects were detected for shear value, C14:0, C17:0, C18:0, C18:1, C18:3, C20:0, C20:1, C20:2, C20:4 and unsaturated fatty acid at P<0.05 or 0.01.

Comparatively, Ding *et al*. (2012) reported that the nucleotide polymorphism (SNP)-C→T (nt19913) in exon 7 of the *LPL* gene caused responsible for a Phe-to-Ser substitution, which was a significant effect on live-weight, average daily weight gain and carcass weight in yak (*Bos grunniens*) steers. Oh *et al*. (2013) reported that three polymorphic SNPs (c.322G>A, c.329A>T and c.1591G>A) were associated with fatty acid composition in Korean cattle. Liu *et al*. (2006) and Cooper *et al*. (1992) reported that 23 SNPs were detected in the 5´ flanking and coding regions of chicken *LPL* gene, and them results indicated that, in the 5´flanking region, the loci d and e significantly affected thickness of subcutaneous fat, abdominal fat weight and subcutaneous fat, while in the coding region, synonymous mutation in exon 8 was significantly associated with intermuscular fat width, however, the non-synonymous mutations in exon 7 and exon 9 did not show statistically significant effects on fat deposition traits. Results of Wu *et al*. (2008) indicated that a synonymous alteration in exon 7 of the *LPL* gene (c.91C>T; EU834120 and EU834121) was associated with abdominal fat weight and percentage of abdominal fat weight of native Peking duck and with percentage of subcutaneous fat plus skin weight and abdominal fat weight of Cherry Valley Peking duck. Our results showed that the fatty acid composition with TT genotype and T allele of the 1251 T>C locus may be beneficial for meat flavor and human health. The 1251C>G polymorphism could be used as a important selection marker in duck breeding to improve the content of beneficial fatty acids. In avian species, the fatty acid composition has emerged as an economically relevant trait due to increasing consumer awareness of the health implications of fat intake associated with red meat consumption (Wang *et al*., 2009). Accumulated evidence suggested that the type of dietary fatty acid composition has a more profound impact on human health than the amount of fat in the diet (Kerr *et al*., 2014). It was well established that the intake of saturated fatty acids (SFA) was positively correlated with atherosclerosis and other cardiovascular diseases, whereas polyunsaturated fatty acids (PUFA) and rumenic acid can have health benefits. Recent studies showed that some PUFA such as C18:1, C16:1, C20:3, have a series of potential health benefits (Aldai *et al*., 2008; Özparlak,

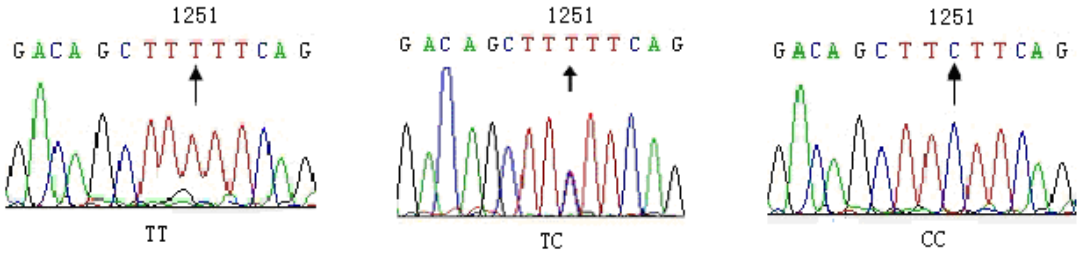

Fig. 2. Sequencing map with different genotypes

Table I.- Characteristics of the 1251 C>G locus of LPL gene in five duck populations.

Breeds	Genotypic frequencies			Allelic frequencies		H	PIC	χ^2(Hardy–Weinberg Equilibrium)
	TT	TC	CC	T	C			
XY	0.7067	0.1866	0.1067	0.8000	0.2000	0.3200	0.2688	10.30**
SS	0.4706	0.3333	0.1961	0.6373	0.3627	0.4622	0.3553	4.03
YJ	0.8182	0.1636	0.0182	0.9000	0.1000	0.1800	0.1638	0.46
JD	0.6909	0.1818	0.1273	0.7818	0.2182	0.3412	0.2830	8.97*
CV	0.4727	0.2364	0.2909	0.5909	0.4091	0.4834	0.3665	12.89**

Note: XY, Xingyi duck; SS, Sansui duck; YJ, Yinjiang duck; JD, Jinding duck; CV, Cherry Valley duck; H, Heterozygosity; PIC, polymorphism information content.
χ^2-test=Hardy-Weinberg equilibrium, $\chi 2_{0.01(2)}$=9.21, $\chi 2_{0.05(2)}$=5.99, **P*<0.05, ***P*<0.01

Table II.- Least-square means and estimated effects of 1251 T>C locus of *LPL* gene on meat quality in Xingyi duck.

Traits	Genotypes			Additive effect	P-value	Dominance effect	P-value
	TT(106)	TC(28)	CC(16)				
pH	6.03±0.02	6.067±0.055	6.029±0.060	0.001±0.035	0.978	0.037±0.118	0.856
WHC	16.52±0.57	18.985±1.266	17.712±1.379	-0.594±0.175	0.621	1.867±0.572	0.122
SV	2.16±0.06^a	1.795±0.133^b	1.875±0.145^{ab}	0.142±0.057	0.056	-0.222±0.169	0.044*
IMF	7.93±0.24	8.950±0.554	8.672±0.574	-0.371±0.110	0.285	1.648±0.431	0.234
C12:0	0.04±0.001^a	0.043±0.003^{ab}	0.051±0.003^b	-0.005±0.008	0.038*	-0.004±0.023	0.886
C14:0	0.47±0.01^a	0.530±0.027^b	0.539±0.026^b	-0.037±0.024	0.040*	0.028±0.077	0.116
C14:1	0.03±0.001	0.025±0.003	0.033±0.003	-0.002±0.008	0.272	-0.006±0.024	0.079
C15:0	0.08±0.001	0.079±0.003	0.081±0.003	-0.003±0.008	0.273	0.001±0.024	0.528
C16:0	26.75±0.14^a	26.751±0.325^a	27.726±0.316^b	-0.489±0.084	0.006**	-0.486±0.272	0.560
C16:1	1.97±0.08^a	2.478±0.177^b	2.613±0.172^b	-0.319±0.061	0.010*	0.184±0.197	0.057
C17:0	0.22±0.005^a	0.190±0.012^b	0.188±0.011^b	0.014±0.016	0.021*	-0.012±0.039	0.019*
C18:0	13.65±0.35^a	10.897±0.812^b	12.339±0.791^{ab}	0.653±0.131	0.163	-2.096±0.429	0.011*
C18:1	35.97±0.45^a	39.028±1.171^b	37.030±1.140^{ab}	-0.531±0.161	0.326	2.529±0.474	0.016*
C18:2	18.88±0.2^a	18.266±0.464^{ab}	17.606±0.452^b	0.637±0.101	0.016*	0.023±0.288	0.322
C18:3	0.21±0.008^a	0.159±0.018^b	0.171±0.017^{ab}	0.019±0.019	0.119	-0.031±0.059	0.030*
C20:0	0.57±0.01^a	0.644±0.034^b	0.621±0.033^{ab}	-0.028±0.027	0.166	0.051±0.082	0.044*
C20:1	0.30±0.01^a	0.233±0.025^b	0.241±0.024^b	0.030±0.023	0.019*	-0.038±0.066	0.019*
C20:2	0.23±0.007^a	0.195±0.016^b	0.219±0.016^{ab}	0.006±0.019	0.408	-0.030±0.055	0.013*
C20:3	0.15±0.007^a	0.105±0.016^b	0.105±0.016^b	0.020±0.019	0.040*	-0.020±0.059	0.060
C20:4	0.52±0.02^a	0.376±0.045^b	0.442±0.043^{ab}	0.039±0.032	0.054	-0.105±0.082	0.005**
UFA	58.19±0.37^a	60.777±0.865^b	58.506±0.841^{ab}	-0.159±0.138	0.729	2.430±0.461	0.009**
PUFA	20.01±0.23^a	19.123±0.554^{ab}	18.552±0.538^b	0.730±0.112	0.016*	-0.159±0.324	0.175
EFA	19.63±0.23^a	18.822±0.533^{ab}	18.225±0.518^b	0.704±0.111	0.016*	-0.107±0.312	0.211

Note: WHC-water holding capacity; SV-shear value (kg.cm^{-1}), IMF- intramuscular fat, UFA- unsaturated fatty acid, PUFA-polyunsaturated fatty acid, EFA- essential fatty acid. Data are least square means ± standard errors; Values with different superscript letters (a, b) are significantly different (Duncan's Multiple Range Test, P<0.05) in genotypes TT, TC, and CC. * show the level of 0.05, ** show the level of 0.01.

2013). Increasing the concentrations of beneficial fatty acids of poulty would add values to the birds products. However, meat quality traits are complex quantitative traits involving multiple genes, loci and interactions. Hence, it cannot be ruled out that the identified genetic-traits associations could be caused by SNPs in linkage with the *LPL* exon 8 and not by the *LPL* gene expression itself. Whether the TT genotype and T allele of the 1251C>G mutation can contribute to the improved the content of beneficial fatty acids still requires further physiological and biochemical evidence.

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Conflict of interest declaration

Authors have declared no conflict of interest.

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