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Association of the *LXRα* gene with meat quality traits in White Muscovy ducks*

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Liver X receptor alpha (*LXRα*) is a nuclear receptor that plays a crucial role in regulating the expression of genes involved in lipid metabolism. The objectives of this study were to detect polymorphism of the *LXRα* gene and investigate its association with meat quality traits in the White Muscovy duck (n=230). One 53 G>A single nucleotide polymorphism (SNP) and one 1483 T>- insertion/deletion were first identified in 5'-UTR and 3'-UTR, respectively. 53 G>A and 1483 T>- were genotyped and analyzed using the PCR-SSCP method. There were two alleles and three genotypes in each locus. Association analysis revealed that the 53 G>A genotypes were significantly associated with intramuscular fat (IMF), contents of polyunsaturated (PUFA) and unsaturated fatty acids (UFA) (P<0.05). The 1483 T>- genotypes were significantly related (P<0.05) to water holding capacity. Interactions of 53 G>A and 1483 T>- *loci* of the *LXRα* gene were significantly associated with shear force, IMF, UFA, PUFA and essential fatty acids (EFA) (P<0.05). These results suggested that the 53 G>A and 1483 T>- mutations of the *LXRα* gene are potential gene markers for White Muscovy meat quality. Therefore, they may be used in the marker-assisted selection (MAS) in breeding work on Muscovy ducks.

KEY WORDS: liver X receptor alpha gene / meat quality / polymorphism / single nucleotide / White Muscovy

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Meat quality traits, which are under the control of multiple genes, are economically important traits in poultry industry. Selection of animals with higher meat quality is of great significance for breeders and consumers [Wood *et al*. 2008]. Identification of chromosome regions containing candidate genes affecting meat quality traits is possible thanks to today's availability of neutral polymorphisms scattered throughout the genome. The candidate gene approach may provide a more direct understanding of the genetic background of the expression of quantitative differences between individuals and reveal genomic regions and specific markers that are associated with traits [Wang *et al*. 2013]. The combination of traditional breeding methods and modern molecular biology technology may be preferred for meat quality genetic improvement of the livestock and poultry species in the future [Davis and Hetzel 2000, Groeneveld *et al*. 2010].

The LXRs are members of the nuclear receptor super family and can be activated by oxysterols and related intermediates in the cholesterol synthetic pathway [Willy *et al*. 1995, Marion *et al*. 2011]. The pivotal role of the LXRs in the metabolic conversion of cholesterol to bile acids has been well established. The LXR subfamily consists of two isoforms, *LXRα* (NR1H3) and LXRβ (NR1H2), that are highly related and share ~78% identity of their amino and acid sequences in both DNA and ligand-binding domains [Wójcicka *et al*. 2007]. *LXRα* is highly expressed in the liver, and at lower levels in the intestine, macrophages, adipose tissue, lung, adrenal glands and kidney tissue, while LXRβ is ubiquitously expressed. Upon ligand induced activation both isoforms form obligate heterodimers with the retinoid X receptor (RXR) and regulate gene expression through binding to LXR response elements (LXREs) in the promoter regions of the target genes [Fiévet and Staels 2009]. Analysis of gene expression in *LXRα* and *LXRβ* deficient mice confirmed that LXR regulates a number of target genes involved in both cholesterol and fatty acid metabolism in the liver, macrophages, and the intestine [Zhang *et al*. 2012]. LXRE consists of two idealized hexanucleotide sequences (AGGTCA) separated by four bases (DR-4 element) [Wagner *et al*. 2003]. LXR/RXR is the so-called "permissive heterodimer" that may be activated by the ligands for either partner in an independent manner. LXR recruits complexes of corepressors that are exchanged with coactivators upon receptor activation in the absence of ligands [Howell *et al*. 2009]. The observation that *LXRα* was responsive to fatty acids and expressed in metabolic tissues suggested that it also plays a general role in lipid metabolism [Baranowski 2008]. Adipose tissue is the main storage site for fat in the body and plays a crucial role in overall lipid handling. Both *LXRα* and *LXRβ* are expressed and activated by endogenous and synthetic ligands, which lead to lipid accumulation into adipocytes. This indicates an important regulatory role of the LXRs in several metabolic signalling pathways in the adipose tissue, such as glucose uptake and de novo fatty acid synthesis. Several studies have demonstrated that expression of the *LXRα* (but not *LXRβ*) is controlled by an autoregulatory mechanism [Laffitte *et al*. 2001, Ulvena *et al*. 2005]. The *LXRα* autoregulatory loop is generally thought to be specific to human cells, since it was not observed in murine macrophages or

preadipocytes [Li *et al*. 2002]. Transcriptional activity of the *LXRα* is also regulated posttranslationally by the protein kinase A that phosphorylates receptor protein at two sites, thereby impairing its dimerization and DNA-binding [Kase *et al*. 2007]. Polyunsaturated fatty acids (PUFA) were reported to be competitive LXR antagonists in various cell lines [Ou *et al*. 2001, Yoshikawa *et al*. 2002]. The porcine *LXRα* gene is located within the genomic region of QTLs in chromosome 2 for loin eye area and intramuscular fat content (IMF) [Malek *et al*. 2001]. The chicken *LXRα* gene is located in the genomic region of QTLs in chromosome 5 for IMF in breast muscles [Nassar *et al*. 2012]. Recent researches also demonstrated that the *LXRα* gene had important effects on mammalian carcass weight, growth and meat quality [Hoashi *et al*. 2008, Huang *et al*. 2010, Han *et al*. 2013].

The purpose of this study was to detect the SNPs of *LXRα* and investigate its association with the White Muscovy meat quality traits, which may give an insight into the genetic mechanism of this economic character and be helpful in improving the economic traits in ducks.

Material and methods

Samples and data collection

Blood samples were collected from 230 healthy female ducks (aged 10 weeks) that belonged to the commercial group of the White Muscovy duck from France. All birds were maintained in a semi-open house and subjected to conventional management conditions, fed commercial corn-soybean diets that met the NRC requirements and were slaughtered with appropriate humane methods at 70 days of age. Ethical clearance had been obtained from the Departmental Ethics Committee for Research on Animals (DECRA), under the DECRA reference number R11/37.

The meat quality traits, including pH value, water holding capacity (%), shear value ($kg \cdot cm^{-1}$), IMF (%), UFA (%), PUFA (%), and EFA (%) of the breast muscle of each duck were measured within 48 h post mortem as described by Aldai *et al.* [2008] and Huang *et al.* [2007].

DNA extraction

Genomic DNA was isolated from blood samples using the standard phenol-chloroform method and stored at -20° for use. DNA concentration and quality were measured with the ND-100 spectrophotometer (Nano-Drop, USA) and the concentrations were adjusted to a range from 100 to 200 ng/μL.

Primer sequences

Based upon the *Cairina moschata LXRα* gene sequences (Accession no. GU132847), six pairs of primers (L1-L6, Tab. 1) were designed using the Oligo 6.0 program to amplify the duck *LXRα* gene.

Table 1. Information on primers used in current study

Primers	Primer sequence (5'→3')	Position/Product size (bp)	Tm (°C)
L1	F: CCTGCTGCTCCTTACTCTGC R: AGTGAAAGCCCTTCCTCCTC	1-156/156	60
L2	F: CAAAGATGCTGGGAAATGAA R: ACATGTCCATCTCACACTTGC	228-392/165	58
L3	F: CAAGGGTGCCCAGTATGTCT R: CGTCCTCCTGTTTCTTCAGC	340-512/173	60
L4	F: CCGGCTAAAGAAGCTGAAGA R: TTTGAGCCTGTCTGTGAACG	481-661/181	55
L5	F: GACCGCCTGATGTTTCCAC R: TGGGACATGGTGTTATGTCG	1157-1350/194	60
L6	F: GTGTCCCAGCCTTTGCTAAC R: ATCCCCAGGACATGCTTAGA	1343-1626/284	60

SNP screening and genotyping

All of DNA samples from White Muscovy ducks were used to perform PCR-SSCP. The PCR reactions were carried out in a total volume of 20 μl with 100 ng of genomic DNA, 5 pmol each of the forward and reverse primers, 2.5 μl 10×buffer, 1.5 mM of $MgCl_2$, 0.16 mM dNTP and 1 U Taq DNA polymerase (Sangon Shanghai, China). PCR program: initial denaturation for 10 min at 95°, 30 cycles each 45 s at 94°, 45 s at specific annealing temperatures (Tab. 1), 45 s at 72° and 10 min final extension at 72°.

Aliquots of 5 μl PCR products were mixed with 10 μl denaturing solution (98% formamide, 25 mM EDTA, 0.025% xylene cyanol and 0.025% bromophenol blue), heated for 10-15 min at 98° and cooled on ice. Denatured PCR products were subjected to 10% acrylamide: bisacrylamide (39:1) gels in 1× TBE buffer and constant voltage (130 V) for 12-14 h. The gel was stained with 0.1% silver nitrate and visualized with 2% NaOH solution. The PCR fragments from different SSCP patterns in different individuals were sequenced in both directions (Sangon Shanghai, China). Polymorphism sites were analyzed by sequence comparisons using the DNAStar software.

Association analysis

The genotype and allele frequencies, the effective number of alleles (Ne), heterozygosity (h) and polymorphism information content (PIC) were estimated. The general linear model (GLM) procedures of SPSS 17.0 were used to determine associations between the studied genotypes and meat quality traits according to the following model:

$$y_{ij} = \mu + G1_i + G2_j + G1G2_{ij} + e_{ij}$$

where:

y_{ij} – the observed value of different meat quality traits;

μ – the population mean;

$G1_i$ – the fixed effect of i^{th} genotype at the 53 G>A *locus*;

$G2_j$ – the fixed effect of j^{th} genotype at the 1483 T>- *locus*;

$G1G2_{ij}$ – the fixed effect of the interaction between the *loci*;

e_{ij} – the random error.

Multiple comparisons were performed for the least-squares means; differences are considered significant at $P<0.05$.

Results and discussion

Polymorphism identification and detection

Genomic DNA of White Muscovy ducks was successfully amplified using six pairs of primers (L1 to L6) for the *LXRα* gene. The results showed that amplification fragment sizes were consistent with the target ones and had good specificity, which could directly be analysed by sequencing and SSCP. No base variation was found in primers L2 to L5. However, for primers L1 and L6 three genotypes (AA, AB and BB for L1; TT, T- and -- for L6) and two alleles (A and B for L1; T and - for L6) were observed in different individuals (Fig. 1). The 53 G>A (*LXRα* ss778302970) and

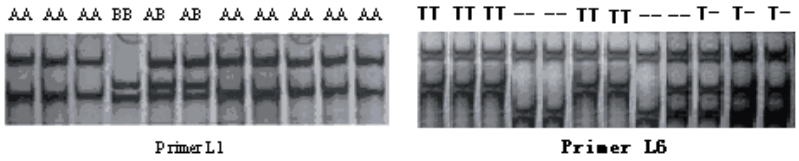

Fig. 1 PCR-SSCP band pattern of primers L1 and L6 on a 10% non-denaturing polyacrylamide gel.

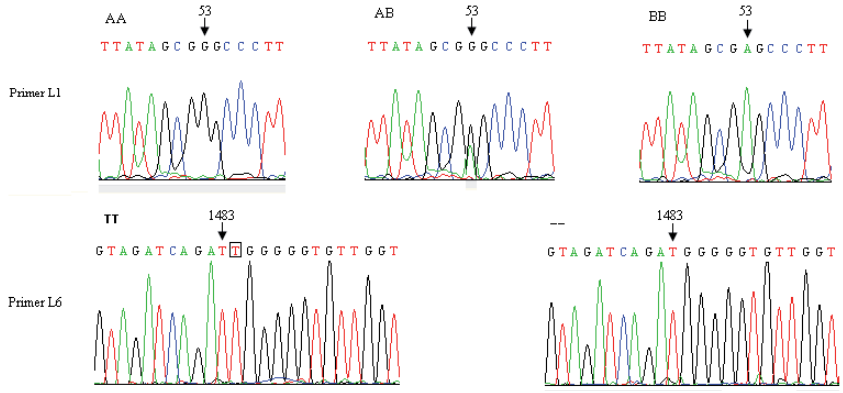

Fig. 2. Sequencing map from different genotypes in primers L1 and L6.

1483 T>-(LXRa ss778302971) mutations were first found in 5'-UTR and 3'-UTR, respectively, of the White Muscovy *LXRα* gene (Fig. 2) by sequence alignment.

Allele and genotype distribution

Allele and genotype frequencies, polymorphism information content (PIC) for White Muscovy breeds were presented in Table 2. For the 53 G>A *locus*, the AA genotype and the A allele were dominant; the A allele frequency and PIC value were 0.776 and 0.287, respectively. For the 1483 T>- locus, the T- genotype and the T allele were dominant; the T allele frequencies and PIC value were 0.533 and 0.372, respectively. The PIC of a marker is the probability that the marker genotype of the offspring of a heterozygous parent affected with a dominant disease allows one to deduce which marker allele the offspring inherited from the parent. Markers with greater numbers of alleles tend to have higher PIC values and thus are more informative. A gene or marker with two alleles has a maximum PIC of 0.375. Botstein *et al*. [1980] reported that PIC value greater than 0.5 is considered to be highly informative, PIC values from 0.25 to 0.5 are considered to be moderately informative, while those of PIC – 0.25 are considered to be slightly informative. Under such a distinction, both SNPs are of medium polymorphism, and are at the Hardy-Weinberg equilibrium (P>0.05), in which genotype frequencies had not been distorted by mutation, migration, selection or other reasons.

Table 2. Allele and genotype frequencies of the *LXRα* gene in the White Muscovy ducks

Locus	Genotype frequencies			Alleles frequencies		PIC	χ^2
53 G>A	AA	AB	BB	A	B	0.287	0.00
	0.604	0.344	0.052	0.776	0.224		
1483 T>-	TT	T-	--	T	-	0.373	1.69
	0.344	0.378	0.278	0.532	0.4675		

PIC – polymorphism information content; χ^2 for Hardy-Weinberg equilibrium ($\chi^2_{0.01(2)}$=9.21, $\chi^2_{0.05(2)}$=5.99).

Association of the 53 G>A and 1483 T>- *loci* of *LXRα* with meat quality traits

In many countries fat, considered unhealthy, is an unpopular constituent of meat for consumers. Yet fat and fatty acids, whether in the adipose tissue or muscle, contribute importantly to various aspects of meat quality and are central to the nutritional value of meat. The candidate gene approach may speed up meat quality improvement in the future. In poultry species, many genes have been confirmed to be associated with meat quality traits, such as the very low density apolipoprotein-II (apoVLDL-II) gene [Zhang *et al*. 2010], the 3-hydroxy-3-methylglutaryl coenzyme A reductase gene (HMGCR) [Wei *et al*. 2012] or the myogenin gene (MyoG) [Wang *et al*. 2007].

Recent studies indicated that the *LXRα* gene has an important effect on mammalian carcass weight, meat quality and growth traits. In mice, the *LXRα* mRNA expression

begins at 11.5 dpc in hepatoblasts of the liver and remains exclusively expressed in this tissue until 13.5 dpc. Between 14.5 and 16.5 dpc, the *LXRα* mRNA also becomes evident in the brown adipose tissue, lung and small intestine tissues, the submandibular gland and the thyroid gland. The general expression pattern is consistent with the role of *LXRα* in lipid metabolism, since the liver, small intestine and brown adipose tissue are all involved in lipid metabolism [Annicotte *et al*. 2004]. In the goose the *LXRα* expression level is the highest in the liver; overfeeding significantly increases the mRNA level of *LXRα* in the liver, abdominal adipose and subcutaneous adipose tissues, suggesting the association of *LXRα* with fat deposition [Han *et al*. 2009]. Yu *et al*. [2006] demonstrated that the *LXRα* intron 8 *HpyCH4* III polymorphism was significantly associated with loin eye area and total lipids in individuals from the Berkshire and Yorkshire resource family, while significant associations were also confirmed between *Bsl* I polymorphism in the *LXRα* exon 2 and the boneless loin proportion, as well as with marbling score in a commercial line. Hoashi *et al*. [2008] reported that the synonymous substitution G>A found in exon 4 caused an amino acid change from valine to isoleucine at the 133 amino acid position, which is located on a Zinc finger DNA binding domain and is believed to affect the structure and thereby subsequently regulate the function of the protein. Hoashi *et al*. [2008] detected a significant association between the SNP with linoleic acid (C18:2n-6) of intramuscular fat in the Japanese black cattle with the VV homozygote exhibiting a significantly lower percentage of C18:2n-6 than the VI genotype. Huang *et al*. [2010] reported that the T1530C (NC_007313) mutation in the *LXRα* exon 2 had a significant effect on backfat thickness, carcass length and marbling score in Qinchuan cattle. Han *et al*. [2013] reported that the G>A single nucleotide polymorphism (SNP) in exon 4 of the *LXRα* gene was associated with the concentration of 9c, 11t C18:2 ($P = 0.04$), total conjugated linoleic acids (CLA) ($P = 0.025$) and 11c C20:1($P = 0.042$). However, the *LXRα* gene polymorphisms have not been reported for associations with duck meat quality.

In the present study, the association of the 53 G>A and 1483 T>- *loci* of the White Muscovy *LXRα* gene with meat quality traits is described in Table 3. For the 53 G>A locus, the birds of the genotype AA had significantly higher values than those of BB for intramuscular fat (IMF), contents of polyunsaturated fatty acids (PUFA) and unsaturated fatty acids (UFA) ($P<0.05$). Moreover, the AB genotype had significantly lower values than AA for the content of unsaturated fatty acids (UFA) ($P<0.05$), and significantly higher than genotype BB for the content of the polyunsaturated fatty acids (PUFA) ($P<0.05$). For the insertion/deletion at the 1483 T>- locus, the birds with genotype -- had significant higher water holding capacity (WHC) than the genotype TT ($P<0.05$). No significant associations of either locus genotypes with the remaining traits were detected ($P>0.05$).

Interaction effects between the 53 G>A and 1483 T>- *loci* of the *LXRα* gene on meat quality traits in the White Muscovy duck are shown in Table 4. Nine polymn genotypes AA--, AAT-, AATT, AB--, ABT-, ABTT, BB--, BBT- and BBTT were found. The birds with polymn genotypes AATT and ABT- had significantly higher

Table 3. Least square means and their standard errors for association of the 53 G>A and 1483 T>- loci of *LXRα* with meat quality traits in the White Muscovy duck

Locus	53 G>A						1483 T>-					
Trait	AA(139)		AB(79)		BB(12)		TT(79)		T-(87)		--(64)	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
pH-value	5.80	0.02	5.81	0.02	5.77	0.06	5.78	0.02	5.81	0.02	5.80	0.03
WHC(%)	19.42	0.73	19.13	0.96	18.18	1.03	17.83^{b}	0.68	19.80^{ab}	0.63	20.05^{a}	0.74
Shear force ($kg.cm^{-1}$)	2.26	0.11	2.45	0.13	2.34	0.33	2.44	0.14	2.26	0.13	2.31	0.15
IMF(%)	6.36^{a}	0.24	5.72^{ab}	0.32	4.47^{b}	0.52	6.141	0.32	6.32	0.31	5.52	0.36
UFA (%)	59.36^{a}	0.85	56.03^{b}	0.61	55.01^{b}	0.77	56.56	0.75	56.49	0.78	55.66	0.93
PUFA (%)	23.09^{a}	0.26	22.80	0.38	21.34^{b}	0.46	23.35	0.60	22.46	0.57	22.87	0.66
EFA (%)	22.34	0.49	22.16	0.62	21.07	0.56	22.91	0.62	21.95	0.60	21.94	0.72

WHC – water holding capacity; IMF – intramuscular fat; UFA – unsaturated fatty acids; PUFA – polyunsaturated fatty acids; EFA – essential fatty acids.
[ab]Within *locus* means bearing different superscripts differ significantly at P<0.05.

Table 4. Least square means and their standard errors for interactions of 53 G>A and 1483 T>- loci of the *LXRα* gene and its genetic effects on meat quality traits in the White Muscovy ducks

Polymn genotype	pH-value		WHC(%)		Shear force ($kg.cm^{-1}$)		IMF(%)		UFA (%)		PUFA (%)		EFA (%)	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
AA--(54)	5.79	0.02	21.56	1.28	2.22^{ab}	0.15	5.65^{ab}	0.19	57.36^{abd}	0.75	23.09^{ab}	0.58	21.94^{a}	0.61
AAT-(39)	5.88	0.03	21.51	1.42	1.88^{a}	0.19	5.95^{ab}	0.25	57.10^{abd}	0.96	23.59^{ab}	0.66	23.24^{ab}	0.62
AATT(46)	5.79	0.03	18.18	1.27	2.44^{b}	0.15	6.46^{a}	0.35	58.05^{b}	0.76	24.11^{a}	0.60	24.60^{b}	0.63
AB--(7)	5.88	0.05	20.51	1.88	2.36^{ab}	0.23	5.61^{ab}	0.68	56.36^{abd}	1.55	23.33^{ab}	1.31	23.50^{ab}	1.02
ABT-(44)	5.80	0.03	19.80	1.33	2.50^{b}	0.16	5.72^{ab}	0.75	55.49^{acd}	0.78	22.48^{ab}	0.63	21.38^{a}	0.76
ABTT(28)	5.90	0.03	18.72	1.53	2.20^{ab}	0.21	6.32^{a}	0.44	54.71^{cd}	2.18	22.70^{ab}	0.94	21.23^{a}	0.93
BB--(3)	5.77	0.06	18.18	2.94	2.34^{ab}	0.33	4.47^{b}	0.79	53.26^{c}	1.82	22.46^{ab}	1.77	22.81^{ab}	1.52
BBT-(4)	5.84	0.05	19.77	2.83	2.00^{ab}	0.29	4.47^{b}	0.72	54.85^{c}	1.81	21.88^{b}	1.57	21.16^{a}	1.32
BBTT(5)	5.83	0.05	17.84	1.92	2.26^{ab}	0.25	5.46^{ab}	0.65	55.02^{ac}	1.76	21.34^{b}	1.54	21.07^{a}	1.08

WHC – water holding capacity; IMF – intramuscular fat; UFA – unsaturated fatty acids; PUFA – polyunsaturated fatty acids; EFA – essential fatty acids.
[ab]In nine polymn genotypes bearing different superscripts differ significantly at P<0.05.

shear force values than those with polymn genotype AAT- (P<0.05). The birds with polymn genotypes AATT and ABTT had significantly higher (P<0.05) IMF content than birds of the BB-- and BBT- genotypes. For contents of UFA, the birds with polymn genotype AATT were superior (P<0.05) to the other five polymn genotypes ABT-, ABTT, BB--, BBT- and BBTT while polymn genotypes AA--, AAT- and AB--

were associated with significantly (P<0.05) higher UFA level than polymn genotypes BB-- and BBT-. The mean content of PUFA for individuals with genotype AATT was significantly (P<0.05) higher compared with birds of polymn genotypes BBT- and BBTT. For the EFA, polymn genotype AATT has an advantage (P<0.05) over the genotypes AA--, ABT-, ABTT, BBT- and BBTT. No significant associations of the other polymn genotypes with other traits were detected (P>0.05).

3'-UTR and 5'-UTR are known to play crucial roles in the post-transcriptional regulation of gene expression, including modulation of the transport of mRNAs out of the nucleus and of translation efficiency, subcellular localization and stability [Velden and Thomas 1999, Silanes *et al*. 2007, Sangeeta and Jayanta 2009]. Under this assumption, the 5'- or 3'-UTR mutations may affect the *LXRα* gene function and thereby result in the variations of the Muscovy meat quality traits. Therefore, further research should be performed in order to validate the causative functions of the Muscovy duck *LXRα* gene on meat quality.

In conclusion, the present study showed that two novel SNPs of the *LXRα* gene have a significant effect on some meat quality traits, especially fatty acid composition. These results suggested that the 53 G>A and 1483 T>- mutations of the *LXRα* gene are potential gene markers for improving meat quality in White Muscovy ducks. Therefore, they may be used in the marker-assisted selection in Muscovy duck breeding. Because of a lack of functional tests and verification of data, the conclusion is not firm and further studies are necessary to validate the function of polymorphisms in question. Meanwhile, studies with larger population sizes are recommended.

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