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VLDLR gene polymorphism associated with abdominal fat in Gaoyou domestic duck breed

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ABSTRACT: *VLDLR* gene was chosen as a candidate gene influencing abdominal fat trait and body weight due to previous studies in human and mouse. Herein, the objectives of this study were to identify genetic polymorphisms of duck *VLDLR* gene, and to analyze association between combined haplotypes and abdominal fat trait in Gaoyou domestic duck. A total of 207 individuals, including the elite reservation farm Gaoyou duck (FG, n = 50), the newly formed Gaoyou duck (NG, n = 54), the reserve area Gaoyou duck (AG, n = 50), and Hybrid duck (HY, n = 53) were used for study. In this paper, one genomic fragment was sequenced in all ducks encompassing a region from exon 14 to exon 16. Five single nucleotide polymorphisms (SNPs) and three insertions/deletions (indels) were identified. Based on the above eight SNPs, 11 haplotypes were identified. The *H1* was the most common haplotype in AG, FG, and HY populations, which occurred at a frequency of more than 41%. Statistical analysis indicated that four combined haplotypes were associated with body weight at 10 weeks (BW10) ($P < 0.05$) and abdominal fat percentage (AFP) ($P < 0.01$) in Gaoyou FG and AG joint population. This result suggested that the *VLDLR* gene could be a potential gene influencing abdominal fat trait and body weight and may be used in marker-assisted selection (MAS).

Keywords: AFP; SNP; haplotype; association analysis

INTRODUCTION

Domestic duck is an important agricultural poultry species for the production of meat and eggs. Gaoyou duck, one of elite domesticated ducks used primarily for egg and meat production in eastern China, has been farmed for thousands of years. Abdominal and subcutaneous fat are regarded as the main sources of waste in the slaughterhouse. In poultry, high genetic correlations were observed between abdominal fat weight and subcutaneous fat, while there were almost no genetic correlations between abdominal fat weight and intramuscular fat percentage (Zerehdaran et al. 2004; Lotfi et al. 2011). Selection for reduced abdominal fatness and/or increased breast muscle yield should be effective as both traits were found to be highly heritable and favourably correlated (Ikeobi et al. 2002; Jennen et al. 2004; Chabault et al. 2012).

The very-low-density-lipoprotein receptor (VLDLR) is a transmembrane lipoprotein receptor of the low-density-lipoprotein (LDL) receptor family. VLDLR is widely distributed throughout the tissues of the body, including the heart, skeletal muscle, adipose tissue, and the brain, but is absent in the liver (Nimpf and Schneider 2000). Duck *VLDLR* gene is composed of 20 exons and 19 introns and is known to exist as two different protein isoforms. These different isoforms result from variations in alternative splicing. One transcript (variant-a) contains an O-linked sugar domain. The other (variant-b), on the other hand, lacks this sugar domain (Wang et al. 2011).

VLDLR has an important role in cholesterol uptake, the delivery of VLDL-derived fatty acids into adipose tissue, metabolism of apoprotein-E-containing triacylglycerol-rich lipoproteins, and neuronal migration in the developing brain (Go-

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udriaan et al. 2001). Studies using VLDLR-deficient and transgenic mice have provided compelling evidence that VLDLR does indeed play a role in VLDL-triglyceride metabolism, and that it is important for triglyceride storage in the adipocyte (Tacken et al. 2001). In human and mouse, VLDLR were confirmed to be correlated to body weight and adiposity (Brockmann et al. 1998; Rankinen et al. 2006; Clemente-Postigo et al. 2011; Kunej et al. 2012). Significant upregulations of ARG1 (Arginase 1) and VLDLR were observed in the overweight condition and their expression levels are likely to be closely linked to the phenotypic biomarkers for adipose deposition and obesity (disturbed lipid profiles and endothelial dysfunction) (Kim et al. 2012).

VLDLR gene mutations are associated with body weight and adiposity in human and mouse. Unfortunately, to date, no such study on the duck *VLDLR* gene has been performed, despite it has been extensively studied. Although association studies cannot determine whether the gene markers are responsible for the variation in adipose deposition or whether the variation is due to a closely linked locus that influences adipose deposition, there is evidence to suggest that the gene would affect adipose deposition. Therefore, the objectives of the present study were to identify polymorphism in *VLDLR* gene, and to analyze associations between the diplotypes and performance traits in Gaoyou ducks.

MATERIAL AND METHODS

Population and traits. Hatching duck eggs were from the elite reservation farm Gaoyou duck (FG), the newly formed Gaoyou duck (NG), reserve area Gaoyou duck (AG), and one hybrid duck (HY) (Shaoxing duck♀ × Jingding♂). The hatching eggs were obtained from the elite reservation farm of Jiangsu Gaoyou duck group and the conservation area in Jiangsu province. The four duck populations are mainly distributed in the eastern provinces of China. All four duck populations were hatched in Gaoyou duck group elite reservation farm. The investigated duck population consisted of 207 animals (FG: n = 50, NG: n = 54, AG: n = 50, HY: n = 53) raised in floor pens under the same standardized conditions of feeding and management for 10 weeks. Birth weight, body weights in weeks 3–9 were determined on live ducks. Starting from week 10, body weights were measured after 6 h with no access to feed and prior to transporting the ducks for slaughter processing. After slaughter on the same day of age, carcass weights (CW), abdominal fat weight (AFW), and abdominal fat percentage (AFP) were measured. The CW was measured on the chilled carcass after removal of feathers, heart, lungs, liver, kidneys, gastrointestinal tract, and abdominal fat. The ratio of these traits to body weights at 10 weeks of age was calculated as follows:

AFP: (AFW/BW) × 100%

where:
CP = carcass percentage
AFP = abdominal fat percentage
BW = body weight

Because of experimental limitations, subcutaneous and intramuscular fat were not measured.

Genomic DNA samples. Genomic DNA was extracted from the 207 blood samples and was stored at –80°C following standard procedures (Sambrook et al. 2001). The quantification of genomic DNA concentration was assayed by ND-1000 spectrophotometer (NanoDrop, Wilmington, USA), and then DNA was diluted to 50 ng/µl.

Polymorphism detection and genotyping. The *VLDLR* duck genomic sequence (GenBank accession No. HQ446852.1) was used to design one pair of primers (5'-CCA GGA TCG TAG ACT TGT-3' and 5'CAT TTA TCT GAG GAG CAG-3') to amplify a 709 bp fragment using Primer Premier software (Version 5.0, 2000).

Polymerase chain reaction (PCR) was performed in 25 µl reactions using 50 ng DNA templates, 10pM of each primer, 0.20 mM dNTP, 2.5mM $MgCl_2$, and 0.5 U *Taq* DNA polymerase. Thermal cycling began with an initial denaturation step of 94°C for 5 min, followed by 35 cycles of 94°C for 30 s, 53.5°C annealing for 30 s, 72°C for 45 s, and concluded with a final extension at 72°C for 10 min. DNA sequencing of the fragments from all animals was performed using an ABI 3130 Genetic Analyzer (Applied Biosystems, Foster City, USA). Sequencing variants were detected by visual examination of the sequencing map followed by alignment using DNAMAN software (Version 8.0, 2013) (www.lynnon.com).

Statistical analysis. The following items were calculated including allelic frequencies, Hardy-

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Table 1. Main carcass traits in the studied duck populations (LSM ± SEM)

Traits	Population			
	FG	NG	AG	HY
BW10 (g)	2462 ± 294^{A}	2432 ± 236^{A}	2178 ± 250^{A}	1594 ± 161^{B}
CP (%)	90.22 ± 3.99	90.67 ± 2.11	90.19 ± 4.08	89.50 ± 2.82
AFP (%)	2.18 ± 0.67^{A}	2.09 ± 0.56^{A}	1.89 ± 0.58^{A}	1.09 ± 0.76^{B}

FG = elite reservation farm Gaoyou duck, NG = newly formed Gaoyou duck, AG = reserve area Gaoyou duck, HY = hybrid duck, BW10 = body weight at 10 weeks of age, CP = carcass percentage, AFP = abdominal fat percentage
^{A,B}means with different superscripts significantly differ ($P < 0.01$)

Weinberg equilibrium (HWE), polymorphism information content (PIC), effective allele numbers, and gene heterozygosity using Genepop software (Version 1.2, 1995). SHEsis online version (http://analysis2.bio-x.cn/myAnalysis.php) was used to calculate the linkage disequilibrium. Haplotypes were obtained for each animal using the PHASE computer program (Version 2.1, 2003). The SPSS software (Version 15.0, 2006) was used to analyze the relationship between the combined haplotypes (diplotypes) and the performance traits in FG and AG joint population. The association analysis was carried out by ANOVA using the model as follows:

$$Y_{ij} = \mu + S_i + G_j + (S \times G)_{ij} + \varepsilon_{ij}$$

where

Y_{ij} = observed value of each trait
μ = analyzed population mean
S_i = fixed effects of diplotype
G_j = fixed effects of population
$(S \times G)_{ij}$ = interaction between haplotypes (diplotypes) and population
ε_{ij} = random error

Values are considered significant at $P < 0.05$ and are presented as Least Squares Means (LSM) ± standard error of the mean (SEM).

RESULTS

The population mean for carcass traits. The BW10, CP, and AFP in the four studied populations are shown in Table 1. BW10 and AFP in HY were significantly lower than those of the remaining Gaoyou duck populations.

Shaoxing and Jingding duck, which contributed to HY, were two domestic egg-type breeds famous for their egg production, while Gaoyou duck was an excellent dual-purpose (meat and egg) domestic duck breed in China. So the genetic background of HY was apparently different from that of Gaoyou duck.

Polymophism and sequencing of the VLDLR gene. By direct DNA sequencing and comparing all the sequencing results, 8 SNPs were found in 709 bp fragment of the *VLDLR* gene (Table 2) and were deposited in the GenBank database (accession Nos. KJ176655–KJ176658). The HQ446852.1:g.231C>T and g.243G>A mutations, which occurred in the sequence coding for amino acid sequence of functional domain of the VLDLR (exon 15), were synonymous.

Genetic variation in different populations. Minor allelic frequencies, Hardy-Weinberg equilibrium, heterozygosity, effective allele numbers, and PIC for each of the eight SNPs in *VLDLR* gene are shown in Table 3.

The χ^2-test showed that the genotype distributions in NG were different from those of the other 3 populations and were not in agreement with Hardy-Weinberg equilibrium ($P < 0.05$).

Linkage disequilibrium and haplotype analysis. Based on the eight SNPs in this study, we performed linkage disequilibrium analysis in FG, AG, and HY populations, whose genotypic distributions were in Hardy-Weinberg equilibrium. The

Table 2. Identified SNPs in duck *VLDLR* gene and their positions in the reference sequence

Reference sequence	SNP	Location in the *VLDLR* gene
HQ446852.1	*g.167G>A*	intron 14
	g.231C>T	exon 15
	g.243G>A	exon 15
	g.356_357insCT	intron 15
	g.358delT	intron 15
	g.498T>C	intron 15
	g.563_564insGA	intron 15
	g.631G>A	intron 15

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Table 3. Population genetic indexes of eight polymorphisms in duck *VLDLR* gene

SNP	Breeds	Genotypes			Total	MAF	He	*P* (HWE)	Ne	PIC
	FG	*AA* (10)	*AG* (17)	*GG* (23)	50	0.3700	0.4662	0.0556	1.8734	0.3575
	NG	*AA* (11)	*AG* (11)	*GG* (32)	54	0.3056	0.4244	0.0001	1.7373	0.3344
g.167G>A	AG	*AA* (5)	*AG* (13)	*GG* (32)	50	0.2300	0.3542	0.0600	1.5485	0.2915
	HY	*AA* (3)	*AG* (15)	*GG* (35)	53	0.1981	0.3177	0.3819	1.4657	0.2672
	total	*AA* (29)	*AG* (56)	*GG* (122)	207	0.2754	0.3991	0.0001	1.6641	0.3195
	FG	*CC* (49)	*TC* (1)	*TT* (0)	50	0.0100	0.0198	1.0000	1.0202	0.0196
	NG	*CC* (54)	*TC* (0)	*TT* (0)	54	0.0000	0.0000	–	1.0000	0.0000
g.231C>T	AG	*CC* (50)	*TC* (0)	*TT* (0)	50	0.0000	0.0000	–	1.0000	0.0000
	HY	*CC* (22)	*TC* (14)	*TT* (7)	53	0.2642	0.3888	0.0157	1.6360	0.3132
	total	*CC* (185)	*TC* (15)	*TT* (7)	207	0.0700	0.1303	0.0000	1.1498	0.1217
	FG	*AA* (10)	*AG* (17)	*GG* (23)	50	0.3700	0.4662	0.0556	1.8734	0.3575
	NG	*AA* (11)	*AG* (11)	*GG* (32)	54	0.3056	0.4244	0.0001	1.7373	0.3344
g.243G>A	AG	*AA* (5)	*AG* (13)	*GG* (32)	50	0.2300	0.3542	0.0600	1.5485	0.2915
	HY	*AA* (3)	*AG* (15)	*GG* (35)	53	0.1981	0.3177	0.3819	1.4657	0.2672
	total	*AA* (29)	*AG* (56)	*GG* (122)	207	0.2754	0.3991	0.0001	1.6641	0.3195
	FG	++ (0)	+- (0)	-- (50)	50	0.0000	1.0000	0.0000	1.0000	0.0000
	NG	++ (0)	+- (0)	-- (54)	54	0.0000	0.0000	–	1.0000	0.0000
g.356_357insCT	AG	++ (0)	+- (0)	--(50)	50	0.0000	0.0000	–	1.0000	0.0000
	HY	++ (6)	+- (20)	--(27)	53	0.3019	0.4215	0.4038	1.7286	0.3327
	total	++ (6)	+- (20)	--(181)	207	0.0773	0.1426	0.0000	1.1664	0.1325
	FG	++ (10)	+- (17)	--(23)	50	0.3700	0.4662	0.0556	1.8734	0.3575
	NG	++ (11)	+- (11)	--(32)	54	0.3056	0.4244	0.0001	1.7373	0.3344
g.358delT	AG	++ (5)	+- (14)	--(31)	50	0.2400	0.3648	0.0839	1.5743	0.2983
	HY	++ (2)	+- (20)	--(31)	53	0.2264	0.3503	0.6191	1.5392	0.2889
	total	++ (28)	+- (62)	--(117)	207	0.2850	0.4076	0.0001	1.6880	0.3245
	FG	*CC* (23)	*CT* (17)	*TT* (10)	50	0.3700	0.4662	0.0556	1.8734	0.3575
	NG	*CC* (32)	*CT* (11)	*TT* (11)	54	0.3056	0.4244	0.0001	1.7373	0.3344
g.498T>C	AG	*CC* (31)	*CT* (14)	*TT* (5)	50	0.2400	0.3648	0.0839	1.5743	0.2983
	HY	*CC* (22)	*CT* (0)	*TT* (31)	53	0.4151	0.4856	0.0000	1.9439	0.3677
	total	*CC* (108)	*CT* (42)	*TT* (57)	207	0.3768	0.4696	0.0000	1.8855	0.3594
	FG	++ (10)	+- (17)	--(23)	50	0.3700	0.4662	0.0556	1.8734	0.3575
	NG	++ (11)	+- (11)	--(32)	54	0.3056	0.4244	0.0001	1.7373	0.3344
g.563_564insGA	AG	++ (5)	+- (14)	--(31)	50	0.2400	0.3648	0.0839	1.5743	0.2983
	HY	++ (2)	+- (20)	--(31)	53	0.2264	0.3503	0.6191	1.5392	0.2889
	total	++ (28)	+- (62)	--(117)	207	0.2850	0.4076	0.0001	1.6880	0.3245
	FG	*GG* (33)	*AG* (17)	*AA* (0)	50	0.17	0.2822	0.1617	1.3931	0.2424
	NG	*GG* (43)	*AG* (11)	*AA* (0)	54	0.1019	0.1830	0.4288	1.2239	0.1663
g.631G>A	AG	*GG* (36)	*AG* (14)	*AA* (0)	50	0.1400	0.2408	0.2694	1.3172	0.2118
	HY	*GG* (26)	*AG* (20)	*AA* (7)	53	0.3208	0.4357	0.2947	1.7722	0.3408
	total	*GG* (138)	*AG* (62)	*AA* (7)	207	0.1836	0.2998	0.9632	1.4281	0.2548

FG = elite reservation farm Gaoyou duck, NG = newly formed Gaoyou duck, AG = reserve area Gaoyou duck, HY = hybrid duck, MAF = minor allele frequency, He = heterozygosity, Ne = effective allele numbers, PIC = polymorphism information content, + = insertion, – = deletion

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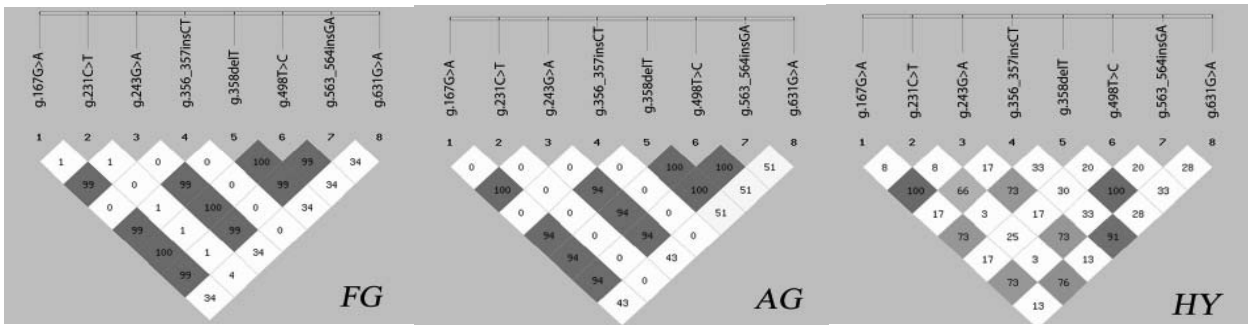

Figure 1. Linkage Disequilibrium (LD) plot of *VLDLR* gene in FG, AG, and HY breeds

FG = elite reservation farm Gaoyou duck, AG = reserve area Gaoyou duck, HY = Hybrid duck

The scheme is according to SHEsis r^2 scheme. Numbers in each cell stand for pairwise r^2-value (%) between the corresponding SNPs

standardized measure of linkage disequilibrium (LD) denoted as r^2 was calculated for all pairs of the eight SNPs (Figure 1).

Haplotypes generally have more information content than individual SNPs. Therefore, we performed haplotype analysis in FG, AG, and HY populations. Theoretically, there are 2^8 (256) haplotypes for 8 SNPs in duck *VLDLR* gene, but none of the populations presented all haplotypes. Detailed haplotype frequency distributions in the three duck populations are presented in Table 4. *H1* was found in FG, AG, and HY populations with the highest frequency out of the total of 11 observed haplotypes (*H1–H11*). The highest number of haplotypes was found in the HY population (8). The haplotypes in HY are much different than those in the other populations. Considering hybrid genetic background of HY, there is a considerable population stratification.

Association analyses. Eight diplotypes were found in FG and AG joint population; of these, four had frequencies higher than 5% (Table 5). Association analysis between the diplotypes and the traits (BW10 and AFP) is presented in Table 5. Diplotype *H1H2* was associated with higher BW10 ($P < 0.05$), but not with CP and AFP. Diplotype *H2H2* had the lowest value for AFP ($P < 0.01$).

Table 4. Haplotypes and their frequencies in FG, AG, and HY populations

Haplotype	SNP								Frequency		
	g.167G>A	*g.231C>T*	*g.243G>A*	*g.356_357insCT*	*g.358delT*	*g.498T>C*	*g.563_564insGA*	*g.631G>A*	FG	AG	HY
H1	*G*	*C*	*G*	–	–	*C*	–	*G*	0.630	0.760	0.415
H2	*A*	*C*	*A*	–	+	*T*	+	*G*	0.200	0.100	0
H3	*A*	*C*	*A*	–	+	*T*	+	*A*	0.160	0.130	0.186
H4	*A*	*T*	*A*	–	+	*T*	+	*A*	0.010	0	0
H5	*G*	*C*	*G*	–	+	*T*	+	*A*	0	0.010	0
H6	*G*	*T*	*G*	+	–	*T*	–	*A*	0	0	0.245
H7	*G*	*C*	*G*	+	–	*T*	–	*A*	0	0	0.045
H8	*G*	*C*	*G*	–	+	*T*	+	*G*	0	0	0.040
H9	*G*	*C*	*G*	–	–	*T*	–	*G*	0	0	0.038
H10	*G*	*T*	*G*	–	–	*T*	–	*A*	0	0	0.019
H11	*A*	*C*	*A*	+	–	*T*	–	*A*	0	0	0.012

FG = elite reservation farm Gaoyou duck, AG = reserve area Gaoyou duck, HY = hybrid duck

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Table 5. Association analysis between diplotypes and performance traits in elite reservation farm Gaoyou duck and reserve area Gaoyou duck joint population (LSM ± SEM)

Diplotype	*n*	Traits		
		BW10 (g)	CP (%)	AFP (%)
H1H1	51	2245.95 ± 57.88^{ab}	90.41 ± 1.34	2.23 ± 0.16^{B}
H1H2	25	2409.68 ± 53.95^{a}	89.05 ± 0.97	1.95 ± 0.16^{ABab}
H1H3	12	2284.19 ± 33.32^{b}	90.27 ± 0.33	2.06 ± 0.08^{b}
H2H2	5	2419.00 ± 118.11^{ab}	89.70 ± 0.68	1.51 ± 0.23^{Aa}

BW10 = body weights at 10 weeks of age, CP = carcass percentage, AFP = abdominal fat percentage
diplotypes *H2H3*, *H3H3*, *H1H4,* and *H1H5* had frequencies in the range of 1–3%
means with different superscripts significantly differ ^{a,b}($P < 0.05$), ^{A,B}($P < 0.01$)

DISCUSSION

Gene heterozygosity and effective allele numbers were low for the eight SNPs. These results clearly indicated that the heredity of these populations and the sites controlling carcass traits were not stable. Furthermore, the genotype distributions in NG were not in Hardy-Weinberg equilibrium ($P < 0.05$). This suggested that the NG population may be affected by selection, mutation or migration and other factors. Generally, PIC was classified into 3 types: low polymorphism (PIC value < 0.25), medium polymorphism (0.25 < PIC value < 0.5), and high polymorphism (PIC value > 0.5) (Mateescu et al. 2005). According to this classification of PIC, most sites belonged to the medium polymorphism level. In loci *g.231C>T* and *g.356_357insCT* of *VLDLR* gene, however, quite low PIC existed in all three Gaoyou populations (even no polymorphism). If $r^2 > 0.33$, the linkage disequilibrium was considered strong (Ardlie et al. 2002). Thus, the eight SNPs of Gaoyou duck were divided into 3 inherited units (*g.167-g.243-g.358-g.498-g.563-564-g.631, g.231,* and *g.356-357*) (Figure 1). For *g.231C>T*, there were only two genotypes in FG population, *CC* and *TC*.

The traditional approach of single-SNP and traits analysis has created many problems, such as noisy, unsatisfactory, and obscured localization information. Haplotypes provided a practical solution to resolve these problems (Daly et al. 2001; Zhang et al. 2008). In this study, haplotypes were constructed with the eight SNPs and were used to analyze the association of combined haplotypes with carcass traits. The results showed that the diplotype *H1H2* had a significantly positive effect on BW10. Moreover, a significantly positive effect of the diplotype *H2H2* on AFP was observed.

The limitation of this study is its relatively small size. Larger studies are needed to confirm these findings about the association of the polymorphisms with abdominal adipose deposition in ducks.

In summary, we identified eight SNPs in *VLDLR* gene, which were divided into 3 inherited units. This is the first study to report an association between the *VLDLR* gene and body weight at 10 weeks of age (BW10) and abdominal fat percentage (AFP) in Gaoyou duck. The result suggests that the *VLDLR* gene could be a potential gene influencing abdominal fat trait and body weight and it can be considered for the use in marker-assisted selection (MAS).

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