

Association of *FATP1* gene polymorphisms with chicken carcass traits in Chinese meat-type quality chicken populations

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Abstract In this study, we aimed to detect the single nucleotide polymorphisms (SNPs) of the chicken *FATP1* gene and discern the potential association between *FATP1* SNPs and chicken carcass traits. A total of 620 meat-type quality chickens from six commercial pure lines (S01, S02, S03, S05, S06 and D99) and two cross lines (S05 × S01 and S06 × S01) were screened by using the single-strand conformational polymorphism analysis (SSCP) and DNA sequencing. Five SNPs [g.49360G > A, g.48195G > A, g.46847A > G, g.46818A > G, and g.46555A > G] were identified in chicken *FATP1* gene. SNP g.46818 A > G was a rare variant and was not considered in the subsequent analysis. Sixteen haplotypes were reconstructed on the basis of the other four SNPs. The linear regression model analysis indicated that there were significant associations of certain diplotypes with part of carcass traits, such as live weight (LW), carcass weight (CW), and semi-eviscerated weight (SEW) ($P < 0.05$). In particular, diplotype H2H4 had a negative effect on LW, CW, SEW, and abdominal fat weight (AW); diplotype H6H10 had the highest reducing

effect on subcutaneous fat thickness (SFT). Our results suggested that *FATP1* gene polymorphisms were associated with chicken carcass traits or was linked with the major gene. The SNPs in this gene may be utilized as potential markers for marker-assisted selection (MAS) during chicken breeding.

Keywords *FATP1* gene · Association analysis · Carcass traits · Chicken · SNP

Introduction

Because of the balanced amino acid, low cholesterol, good tenderness, and juiciness, poultry meat is very popular and serves as one of the major dishes in China [1–3]. More and more attention has been paid on how to improve chicken meat quality and to provide a quick marker assisted selection during the breeding in recent years. One of the factors that affect meat quality is tissue-specific distribution of fat that is positively correlated with carcass quality [4, 5]. Thus, it is essential to study the characteristics of fat deposition in birds and the related species.

FATP1 (Fatty acid transport protein 1 or SLC27A1) is highly expressed in adipose tissues and skeletal muscles [6–8]. It is considered as one of the important candidate genes that can influence the obesity because of its active role in mediating fatty acid uptake [9]. The *FATP1* gene was first isolated and characterized by Schaffer and Lodish [8]. Subsequently, single nucleotide polymorphisms (SNPs) in the *FATP1* gene were widely studied in human by using various genotyping methods. Intronic polymorphism in *FATP1* gene was found to be associated with increased plasma triglyceride levels in a French population [10], but had no effect on the metabolic syndrome [11].

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The expression of *FATP1* gene presented a gender-related variance in skeletal muscle of lean individuals and might not actively contribute to the alterations of fatty acid uptake in patients with obesity and/or type 2 diabetes [12].

Up to now, there is no study on poultry *FATP1* gene despite that it has been extensively studied in human and mouse. Similar association study with other genes was reported recently [13, 14]. In this study, we aimed to characterize the sequence variation of the chicken *FATP1* gene in 620 individuals from eight different chicken breeds. We identified potential association of the *FATP1* gene SNPs with chicken carcass traits in our experimental animals.

Materials and methods

Resource population

A total of 620 chickens from eight meat-type quality chicken populations, including S01 ($N = 128$), S02 ($N = 60$), S03 ($N = 56$), S05 ($N = 136$), S06 ($N = 82$), D99 ($N = 64$), S05 × S01 ($N = 42$), and S06 × S01 ($N = 52$) (which were development by Dahan Poultry Breeding Company and Sichuan Animal Science Academy), were randomly selected from each of the commercial population. These populations differ considerably in carcass composition and appearance. All chickens were hatched on the same day, housed on the deep-litter bedding and moved to the growing pens at 7 weeks of age. Birds had access to feed (commercial con-soybean diets meeting the National Research Council's [NRC] requirements) and water ad libitum. Before slaughter, blood was collected and the genomic DNA was isolate by the standard phenol/chloroform method.

Phenotypic measurements

Carcass traits were measured at 91 days of age as described in our previous study [15, 16]. In brief, live weight (LW) was measured on live birds after 12 h with no access to feed. After the slaughter of chicken of the same age at the same day, seven carcass traits, including carcass weight (CW), eviscerated weight (EW), semi-eviscerated weight (SEW), breast muscle weight (BMW), leg muscle weight (LMW), abdominal fat weight (AW), and subcutaneous fat thickness (SFT) were measured. The CW was measured on the chilled carcass removed feather; semi-eviscerated weight was measured on the carcass removed trachea, esophagus, gastrointestinal tract, spleen, pancreas, and gonad. Eviscerated weight was measured on the semi-eviscerated weight after removal of head, claws, heart, liver, gizzard, glandular stomach, and abdominal fat.

Subcutaneous fat thickness was measured at the caudal spondyle including the skin and fat width with a vernier caliper after dressing. The ratios of each of the above traits to CW were calculated as breast muscle percentage (BMWP), leg muscle percentage (LMWP), and abdominal fat percentage (AP), respectively.

Genotyping of *FATP1* gene polymorphisms

Ten primer pairs were designed according to the genomic sequence of *Gallus gallus* *FATP1* gene (GenBank Accession number NW_001488613). The amplified products were expected to cover a region from nucleotide position 33 to nucleotide position 7531 that contains all the exons and partial introns of *FATP1* gene. Polymerase chain reaction (PCR) amplification was carried out on Gene Amp PCR System 9700 in a volume of 10 μ l reaction, which contains 40 ng genomic DNA, 3 pmol of each primer, 2 \times Taq PCR Master mix (including Mg²⁺, dNTP, Tag DNA Polymerase; Beijing TIAN WEI Biology Technique Corporation, Beijing, China). A hot start (94°C for 5 min) was used at the beginning of the thermal cycles, followed by 35 cycles of 94°C for 45 s, 55°C (or other apt temperature) for 35 s, 72°C for 45 s, and ended with a final extension at 72°C for 7 min.

PCR products were resolved by SSCP analysis. Several factors were tested for each fragment in order to optimize the amount of PCR products, denaturing solution, gel concentration, glycerol, voltage, running time, and temperature. Each PCR product was diluted in denaturing solution (95% formamide deionized, 0.05% of bromophenol blue, 0.25% xylene cyanole and 10% glycerol) and was denatured at 99°C for 10 min, then quickly chilled on ice for 5 min. Three microliters of mixture was resolved on 12% polyacrylamide gel (polyacrylamide:bisacrylamide = 39:1) using 1 \times TBE buffer and run for 9–14 h at 130–150 V. The gel was washed in 10% ethanol for 10 min, then in deionized water for 1 min, followed by an incubation for 10 min in 0.1% silver nitrate, and ended with an incubation in 1.5% sodium hydroxide, 0.01% sodium borohydride, and 0.4% (v/v) formaldehyde for 10 min. The bands on the gel were visualized by gel imaging system. Samples showing different bands in the gel were further amplified and purified, and were sequenced by a commercial sequencing company (Shanghai Yingjun Biology Technique Corporation, Shanghai, China).

Statistical analyses

We reconstructed the haplotypes of the *FATP1* gene based on the identified SNPs in 620 chicken samples using PHASE 2.0 software [17]. Marker-trait association analyses were performed with SAS GLM procedure (SAS Institute,

1996) and the genetic effects were analyzed using the following mixed model:

$$Y = \mu + B_i + S_j + G_k + A_f + e_{ijkf}$$

where Y = the dependent variable, μ = the population mean, B_i = fixed effects of breed, S_j = fixed effects of sex, G_k = genotype value, A_f = fixed effects of age, and e_{ijkf} = random error. The interaction $G \times S$ and $G \times A$ were not significant for any trait and therefore was not included in the model. Significant differences ($P < 0.05$) were found among different genotypes in the light of least square means using Duncan's multiple-range test.

The data of some fat traits such as AP, BMWP and LMWP were not normally distributed. Therefore, CW, EW, SEW, BMW, LMW and AW were analyzed using the linear model with parameters estimated on the Square Root scale; the BMW, LMWP and AP traits were shifted and rescaled to achieve approximate normality and equality of variance.

Results

Genetic polymorphisms of *FATP1* gene in chicken populations

We used ten pair of primers to amplify and screen SNPs in the entire exons of the chicken *FATP1* gene (Table S1). PCR products from four pairs of primers (P-3, P-5, P-7, and P-8), which cover exons 3, 5, 7, and 8, respectively, presented a profile suggesting for SNPs by the SSCP method (Fig. 1). Three individuals with the same genotype for each primer pair were sequenced to confirm the sequence variations.

We numbered the SNPs relative to the *Gallus gallus* genomic sequence (NW_001471503) in GenBank (Table S2).

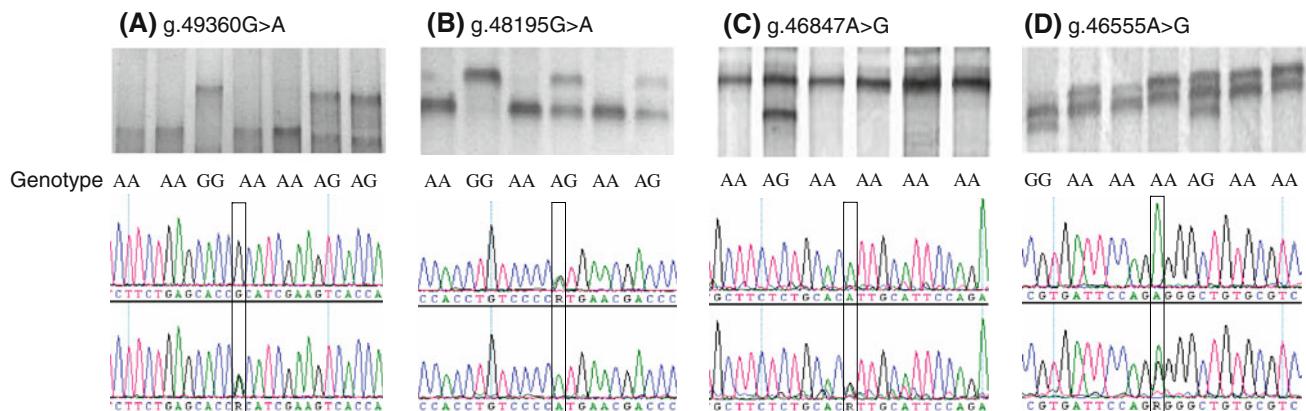


Fig. 1 Identification of single nucleotide polymorphisms in chicken *FATP1* gene by using PCR-SSCP and sequencing. Genotypes of **a** g.49360G > A, **b** g.48195G > A, **c** g.46847A > G, and **d** g.46555A

The substitution of G > A at nt49360 (which is located in exon 3) caused an amino acid change from A to S (Table S2). The other polymorphisms, G > A at nt48195 in intron 5, A > G at nt46847 and A > G at nt 46818 in intron 7, and A > G at nt46555 in exon 8 were either synonymous or were located in the intron regions (Fig. 1).

Frequencies of *FATP1* gene genotypes and alleles

We analyzed the genotypes and alleles of the identified SNPs in the *FATP1* gene in chicken populations. Because variant g.46818A > G was a rare SNP in our samples, we did not include it in the following analyses. The genotype and allele frequencies of the other four SNPs in the eight chicken populations were shown in Table S3. The AA genotype at nt49360 had the highest frequency in populations S01, S03, S05, S06 and D99, but had a lower frequency in S02, S05 × S01 and S06 × S01; the GG genotype at this site was even absent in S03 and D99. The observed genotype frequencies in each population were in agreement with Hardy-Weinberg equilibrium (HWE) ($P > 0.05$), except for S01, S05 and S06 × S01. The allele G at nt48195 was identified as the dominant allele among all populations (average = 79.79%). The frequency of GG genotype at nt48195 had the highest value among all populations with the exception of D99, in which the GA genotype had the lowest frequency. Meanwhile, the genotype AA at nt48195 was not found in S02. Using the χ^2 -test, we found that the genotype frequencies at nt48195 in populations S01, S02, S03, S05, S06 and S05 × S01 were in agreement with HWE, while D99 and S06 × S01 were deviated from HWE ($P < 0.01$). There were no GG genotype at nt46847 in all populations, and the frequency of AA was higher than that of AG. In S06 × S01 chicken samples, we only observed the AA genotype. The frequency of genotype AA at nt46555 was very high and reached a value

> G were well resolved on SSCP gel and confirmed by sequencing. The boxes in the sequencing electropherograms indicated the sites with the nucleotide changes

of 0.953 in D99. The allele A was identified as the dominant allele among all populations due to the highest allele frequency (average = 0.927). Furthermore, variant g.46555A > G was deviated from the HWE in samples S01, S02, S03, S05, S06 and S05 × S01, whereas variant g.46847A > G was not violated the HWE.

Association of SNPs with chicken carcass traits

The GLM analysis of potential association between the *FATP1* SNPs and carcass traits in the chicken populations was summarized in Table 1. Traits LW, CW, SEW, EW and BMWP were significantly associated with *FATP1* genotypes at nt49360 ($P < 0.05$). Chickens with AA genotype at nt49360 had a higher value for LW, CW, SEW and EW than those with genotypes AG and GG. For g.48195G > A, chicken with the AA genotype had significantly higher LW, CW, SEW, EW, LMW, BMWP and LMWP than those with GG or GA ($P < 0.05$), and there

was no difference between chickens with GG and GA ($P > 0.05$). The A allele at nt48195 had a favorably positive effect on LW, CW, SEW, EW, LMW, BMWP, and LMWP. For g.46847A > G, the genotypes of at nt46847 were significantly associated with LW and CW ($P < 0.05$), but not associated with the other carcass traits ($P > 0.05$). The LW and CW of chickens with the AA genotype was significantly higher than those of the chickens with the AG genotype ($P < 0.05$). The genotypes at nt46555 were not associated with all carcass traits except for LMWP, which had a significantly higher value in chicken with the GG genotype than the other genotypes.

Haplotypes of *FATP1* gene in chicken populations

Haplotypes were reconstructed with the four SNPs in all 620 experimental chickens by employing the PHASE program [17]. Table 2 listed all sixteen haplotypes, which were accounted for 100% of all the observations. Among them,

Table 1 Least square means of the carcass traits, by genotype, of chicken *FATP1* gene

Traits	SNP1 (g.49360G > A)			SNP2 (g.48195 G > A)		
	AA	AG	GG	GG	GA	AA
LW (g)	1958.23 ± 24.03 ^A	1954.61 ± 36.33 ^A	1745.35 ± 87.06 ^B	1938.67 ± 23.66 ^B	1919.20 ± 36.59 ^B	2253.85 ± 94.64 ^A
CW (g)	1749.98 ± 22.02 ^A	1746.38 ± 33.51 ^A	1547.26 ± 79.39 ^B	1728.41 ± 21.74 ^B	1721.47 ± 33.47 ^B	2024.40 ± 88.05 ^A
SEW (g)	1654.37 ± 24.82 ^A	1633.97 ± 37.78 ^A	1443.06 ± 89.50 ^B	1636.44 ± 24.57 ^B	1604.05 ± 37.82 ^B	1892.60 ± 99.48 ^A
EW (g)	1367.06 ± 18.02 ^A	1368.62 ± 27.43 ^A	1207.42 ± 64.99 ^B	1351.69 ± 17.78 ^B	1342.72 ± 27.37 ^B	1600.60 ± 72.01 ^A
BMW (g)	110.09 ± 55.06	265.22 ± 83.69	103.70 ± 198.26	176.11 ± 54.67	106.19 ± 84.06	128.73 ± 221.14
LMW (g)	153.66 ± 4.53	160.46 ± 6.89	134.53 ± 16.31	154.87 ± 4.49 ^B	149.24 ± 6.90 ^B	187.98 ± 18.14 ^A
AW (g)	46.82 ± 2.08	51.28 ± 3.16	38.02 ± 7.47	48.40 ± 2.06	45.87 ± 3.21	47.42 ± 8.34
SFT (mm)	0.43 ± 0.01	0.44 ± 0.02	0.39 ± 0.04	0.43 ± 0.01	0.44 ± 0.01	0.38 ± 0.04
BMWP (%)	8.42 ± 0.09 ^B	8.64 ± 0.15 ^{AB}	9.21 ± 0.34 ^A	8.60 ± 0.09 ^{AB}	8.28 ± 0.14 ^B	9.10 ± 0.42 ^A
LMWP (%)	10.98 ± 0.12	10.36 ± 0.20	10.76 ± 0.45	10.79 ± 0.12 ^B	10.71 ± 0.18 ^B	12.21 ± 0.55 ^A
AP (%)	2.21 ± 0.14	2.65 ± 0.23	2.13 ± 0.51	2.43 ± 0.14	2.11 ± 0.21	1.92 ± 0.63
Traits	SNP3 (g.46847A > G)			SNP5 (g.46555A > G)		
	AA	AG	GG	AA	AG	GG
LW (g)	1954.56 ± 19.95 ^A	1755.20 ± 96.99 ^B	—	1945.24 ± 20.67	1935.00 ± 95.49	1974.57 ± 82.30
CW (g)	1746.05 ± 18.30 ^A	1557.50 ± 90.29 ^B	—	1735.80 ± 18.98	1741.35 ± 87.10	1780.43 ± 75.07
SEW (g)	1645.24 ± 20.63	455.63 ± 101.78	—	1636.16 ± 21.39	1629.62 ± 98.13	1668.71 ± 84.58
EW (g)	1365.13 ± 14.98	1219.17 ± 73.92	—	1356.86 ± 15.53	1359.42 ± 71.27	1398.57 ± 61.43
BMW (g)	156.52 ± 45.73	96.12 ± 230.44	—	158.68 ± 47.33	111.21 ± 216.92	116.80 ± 186.96
LMW (g)	155.61 ± 3.76	129.84 ± 18.93	—	154.19 ± 3.89	146.50 ± 17.83	167.52 ± 15.37
AW (g)	48.11 ± 1.73	36.05 ± 8.67	—	48.46 ± 1.79	42.13 ± 8.16	38.83 ± 7.14
SFT (mm)	0.43 ± 0.01	0.41 ± 0.04	—	0.44 ± 0.01	0.39 ± 0.04	0.39 ± 0.03
BMWP (%)	8.54 ± 0.07	8.14 ± 0.37	—	8.48 ± 0.08	9.15 ± 0.35	8.63 ± 0.29
LMWP (%)	10.83 ± 0.10	10.57 ± 0.49	—	10.79 ± 0.11 ^B	9.79 ± 0.45 ^C	11.87 ± 0.38 ^A
AP (%)	2.33 ± 0.12	2.05 ± 0.55	—	2.36 ± 0.12	2.05 ± 0.52	1.92 ± 0.44

LW live weight (g); CW carcass weight (g), SEW Semi-eviscerated weight (g), EW eviscerated weight (g), BMW breast muscle weight (g), LMW leg muscle weight, AW abdominal fat weight (g), SFT subcutaneous fat thickness (mm), Percentage sign (%) indicates the marked traits were relative to CW. Different uppercase letters mean significant difference at the $P < 0.05$ level for chickens with different genotypes of certain SNP

Table 2 Haplotype frequency and main diplotypes in the chicken *FATP1* gene

Haplotype	SNP ^a				Frequency (%)	Diplotype	Frequency (%)
	g.49360G > A	g.48195G > A	g.46847A > G	g.46555A > G			
H1	A	G	A	A	59.65	H1H1	38.87
H2	A	G	A	G	4.43	H1H2	1.61
H3	A	G	G	A	1.09	H1H3	1.45
H4	A	G	G	G	0.24	H1H4	0.16
H5	A	A	A	A	13.08	H1H5	16.45
H6	A	A	A	G	1.26	H1H6	0.65
H7	A	A	G	A	0.22	H1H7	0.32
H8	A	A	G	G	0.11	H1H8	0.16
H9	G	G	A	A	14.67	H1H9	16.77
H10	G	G	A	G	1.30	H2H2	2.10
H11	G	G	G	A	0.21	H2H4	0.16
H12	G	G	G	G	0.10	H2H6	0.97
H13	G	A	A	A	3.30	H2H8	0.32
H14	G	A	A	G	0.22	H2H10	0.81
H15	G	A	G	A	0.04	H3H9	0.48
H16	G	A	G	G	0.08	H5H5	1.45
–	–	–	–	–	–	H5H6	0.16
–	–	–	–	–	–	H5H7	0.16
–	–	–	–	–	–	H5H9	7.58
–	–	–	–	–	–	H5H12	1.94
–	–	–	–	–	–	H6H6	0.32
–	–	–	–	–	–	H6H9	0.32
–	–	–	–	–	–	H6H10	0.32
–	–	–	–	–	–	H7H9	0.32
–	–	–	–	–	–	H9H12	0.65
–	–	–	–	–	–	H9H9	3.39
–	–	–	–	–	–	H10H10	0.32
–	–	–	–	–	–	H13H14	0.16

^a The rare variant g.46818 A > G was not included for the analysis

three haplotypes, H1 (A-G-A-A), H5 (A-A-A-A), and H9 (G-G-A-A) were prevalent and counted for 87.4% of the observations. Twenty-eight diplotypes were obtained based on these sixteen haplotypes. Among them, the frequencies of 18 diplotypes were higher than 6.0%. Three diplotypes, H1H1, H1H5 and H1H9, totally accounted for 72.09% (Table 2).

The mixed model analysis indicated that there were significant associations between the haplotypes and carcass traits (Table 3). Haplotypes were associated with LW, CW, SEW, EW, SFT, BMW and LMWP ($P < 0.05$). Significantly and suggestively dominant effect of the diplotype H5H7 were observed for LW, CW, SEW and EW. Diplotype H1H9 had a higher BMW. Diplotype H2H6 had a higher LMW, and diplotype H10H10 was associated with BMW and LMWP. Remarkably, diplotype H2H4 had a negative effect on LW, CW, SEW, and AW. H6H10 had

the highest reducing effect on SFT, and H1H4 had the highest reducing effect on SFP.

Discussion

Since the first characterization of the *FATP1* genes [8], numerous association studies have been carried out to discern a correlation between the *FATP1* gene polymorphisms and disorders. Meirhaeghe et al. [10] found that the intronic SNP of human *FATP1* gene was associated with the alterations in human lipid homeostasis. Gertow et al. [18] also found the A/G polymorphism in intron 8 of human *FATP1* gene was associated with elevated post-prandial lipaemia and alterations in LDL particle size distribution in Swedish populations. All these studies suggested that *FATP1* gene

Table 3 Association between diplotypes and the chicken carcass traits

Diployte	Traits	LW*	CW*	SEW*	EW*	BMW	LMW	AW	SFT*	BMWP*	LMWP*	AP
H1H1	1945.02 ± 30.58 ^{ABC}	1735.43 ± 28.02 ^{ABC}	1651.94 ± 31.95 ^{AB}	1354.20 ± 22.92 ^{BC}	109.51 ± 72.32	150.41 ± 5.87	47.46 ± 2.70	0.43 ± 0.01 ^{AB}	8.53 ± 0.12 ^B	10.82 ± 0.15 ^{BC}	2.29 ± 0.18	
H1H2	1964.00 ± 151.37 ^{ABC}	1761.50 ± 137.88 ^{ABC}	1651.00 ± 157.17 ^{AB}	1375.00 ± 112.79 ^{BC}	115.41 ± 355.76	151.16 ± 28.92	47.76 ± 13.29	0.47 ± 0.06 ^{AB}	9.35 ± 0.54 ^B	9.88 ± 0.69 ^C	2.30 ± 0.83	
H1H3	1695.56 ± 159.56 ^{BC}	1471.88 ± 154.15 ^{BC}	1380.00 ± 175.73 ^{AB}	1148.12 ± 126.10 ^{BC}	97.09 ± 425.22	131.88 ± 34.56	33.00 ± 15.89	0.40 ± 0.07 ^{AB}	8.19 ± 0.64 ^B	10.77 ± 0.82 ^{BC}	1.86 ± 0.99	
H1H4	1700.00 ± 478.68 ^{BC}	1475.00 ± 435.99 ^{BC}	1375.00 ± 497.04 ^{AB}	1175.00 ± 356.67 ^{BC}	107.70 ± 1125.02	133.50 ± 91.46	13.50 ± 42.03	0.36 ± 0.15 ^{AB}	9.17 ± 1.71 ^B	11.36 ± 2.18 ^{BC}	0.79 ± 2.61	
H1H5	1943.82 ± 47.39 ^{ABC}	1742.16 ± 43.17 ^{ABC}	1628.48 ± 49.21 ^{AB}	1358.87 ± 35.31 ^{BC}	107.56 ± 111.39	153.15 ± 9.05	48.16 ± 4.22	0.44 ± 0.02 ^{AB}	8.18 ± 0.17 ^B	10.98 ± 0.22 ^{BC}	2.15 ± 0.26	
H1H6	2087.50 ± 239.34 ^{ABC}	1862.50 ± 218.00 ^{ABC}	1743.75 ± 248.52 ^{AB}	1456.25 ± 178.34 ^{ABC}	115.00 ± 562.51	167.07 ± 45.73	19.68 ± 21.01	0.31 ± 0.07 ^{AB}	7.89 ± 0.85 ^B	11.45 ± 1.09 ^{BC}	0.96 ± 1.30	
H1H7	1420.00 ± 338.48 ^C	1250.00 ± 308.30 ^C	1162.50 ± 351.46 ^B	937.50 ± 252.20 ^C	74.10 ± 795.51	95.25 ± 64.67	58.00 ± 29.72	0.56 ± 0.11^A	7.95 ± 1.21 ^B	10.16 ± 1.54 ^{BC}	3.86 ± 1.84	
H1H8	1420.00 ± 478.58 ^C	1250.00 ± 435.99 ^C	1175.00 ± 497.04 ^B	1000.00 ± 356.67 ^C	70.10 ± 1125.02	8.170 ± 91.46	23.30 ± 42.03	0.39 ± 0.16 ^{AB}	7.01 ± 1.71 ^B	8.17 ± 2.17 ^C	1.64 ± 2.61	
H1H9	1984.27 ± 47.17 ^{ABC}	1768.41 ± 43.38 ^{ABC}	1663.46 ± 49.45 ^{AB}	1387.37 ± 35.49 ^{ABC}	379.68 ± 111.94	169.41 ± 9.10	55.88 ± 4.18	0.45 ± 0.03 ^{AB}	8.63 ± 0.20 ^B	10.44 ± 0.26 ^{BC}	3.08 ± 0.31	
H2H10	1780.00 ± 214.07 ^{BC}	1592.00 ± 194.98 ^{BC}	1500.00 ± 222.28 ^{AB}	1267.00 ± 159.51 ^{BC}	102.00 ± 503.12	143.56 ± 40.90	37.22 ± 18.79	0.44 ± 0.16 ^{AB}	8.99 ± 0.76 ^B	9.98 ± 0.97 ^C	2.21 ± 1.17	
H2H2	1965.38 ± 132.76 ^{ABC}	1775.00 ± 120.92 ^{ABC}	1666.54 ± 137.86 ^{AB}	1390.38 ± 98.92 ^{ABC}	114.78 ± 312.02	171.23 ± 25.36	39.70 ± 11.65	0.40 ± 0.05 ^{AB}	8.39 ± 0.47 ^B	12.37 ± 0.61 ^{BC}	2.06 ± 0.72	
H2H4	1400.00 ± 478.68 ^C	1200.00 ± 435.99 ^C	1150.00 ± 497.05 ^B	950.00 ± 356.67 ^C	71.10 ± 1125.02	122.20 ± 91.46	12.10 ± 42.03	0.32 ± 0.16 ^{AB}	7.48 ± 1.71 ^B	12.86 ± 2.18 ^{BC}	0.86 ± 2.61	
H2H6	2615.00 ± 195.42 ^{AB}	2362.50 ± 177.99 ^{AB}	2216.67 ± 202.92 ^{AB}	1879.17 ± 145.61 ^{AB}	145.98 ± 459.29	218.40 ± 37.34	54.20 ± 17.15	0.45 ± 0.06 ^{AB}	7.73 ± 0.69 ^B	11.36 ± 0.89 ^{BC}	2.13 ± 1.06	
H2H8	1805.00 ± 338.48 ^{BC}	1612.50 ± 308.30 ^{BC}	1512.50 ± 351.46 ^{AB}	1250.00 ± 252.20 ^{BC}	101.35 ± 795.51	118.35 ± 64.67	52.80 ± 29.72	0.48 ± 0.11 ^{AB}	8.02 ± 1.21 ^B	9.44 ± 1.54 ^C	2.81 ± 1.84	
H3H9	2013.33 ± 276.37 ^{ABC}	1795.00 ± 251.72 ^{ABC}	1695.00 ± 286.96 ^{AB}	1416.67 ± 205.92 ^{ABC}	110.80 ± 649.52	163.80 ± 52.80	42.07 ± 24.27	0.42 ± 0.11 ^{AB}	7.84 ± 0.99 ^B	11.52 ± 1.26 ^{BC}	2.18 ± 1.51	
H5H12	2250.00 ± 138.18 ^{ABC}	2016.82 ± 131.46 ^{ABC}	1883.18 ± 149.86 ^{AB}	1584.54 ± 107.54 ^{ABC}	123.95 ± 339.20	181.96 ± 27.57	50.00 ± 12.67	0.38 ± 0.08 ^{AB}	8.68 ± 0.69 ^B	10.54 ± 0.89 ^{BC}	1.94 ± 1.06	
H5H5	2272.22 ± 159.56 ^{ABC}	2027.78 ± 145.35 ^{ABC}	1916.67 ± 165.68 ^{AB}	1615.00 ± 118.89 ^{ABC}	137.77 ± 375.00	215.91 ± 30.48	43.36 ± 14.01	0.42 ± 0.07 ^{AB}	9.75 ± 0.65 ^{AB}	14.70 ± 0.82 ^{AB}	1.74 ± 0.98	
H5H6	2500.00 ± 478.68 ^{AB}	2275.00 ± 435.99 ^{AB}	2125.00 ± 497.04 ^{AB}	1800.00 ± 356.67 ^{AB}	169.40 ± 1125.01	182.50 ± 91.46	92.10 ± 42.03	0.30 ± 0.16 ^{AB}	9.41 ± 1.71 ^B	10.14 ± 2.18 ^{BC}	3.68 ± 2.61	
H5H7	2920.00 ± 478.68^A	2600.00 ± 435.99^A	2325.00 ± 497.04^A	2125.00 ± 356.67^A	99.60 ± 1125.01	143.80 ± 91.46	54.80 ± 42.03	—	—	—	—	
H5H9	1882.77 ± 69.82 ^{BC}	1688.58 ± 64.28 ^{ABC}	1560.22 ± 73.29 ^{AB}	1320.10 ± 52.58 ^{BC}	105.60 ± 165.87	143.92 ± 13.48	47.37 ± 6.19	0.46 ± 0.03 ^{AB}	8.52 ± 0.28 ^B	10.33 ± 0.36 ^{BC}	2.26 ± 0.43	
H6H10	1730.00 ± 338.47 ^{BC}	1562.50 ± 308.30 ^{BC}	1437.50 ± 351.46 ^{AB}	1177.50 ± 252.20 ^{BC}	88.50 ± 795.51	128.40 ± 64.67	17.20 ± 42.03	0.15 ± 0.15^B	7.46 ± 1.21 ^B	10.94 ± 1.54 ^{BC}	0.93 ± 2.61	
H6H6	1780.00 ± 338.48 ^{BC}	1600.00 ± 308.30 ^{BC}	1487.50 ± 351.46 ^{AB}	1250.00 ± 252.20 ^{BC}	103.35 ± 795.50	133.15 ± 64.67	34.65 ± 29.72	0.33 ± 0.11 ^{AB}	8.25 ± 1.21 ^B	10.68 ± 1.54 ^{BC}	1.92 ± 1.84	
H6H9	1870.00 ± 338.47 ^{BC}	1755.00 ± 308.29 ^{ABC}	1617.50 ± 351.46 ^{AB}	1340.00 ± 252.20 ^{BC}	95.20 ± 795.51	142.75 ± 64.67	23.35 ± 29.72	0.23 ± 0.15 ^{AB}	9.56 ± 1.21 ^{AB}	8.17 ± 1.54^C	1.24 ± 1.84	
H7H9	1610.00 ± 338.47 ^{BC}	1460.00 ± 308.29 ^{BC}	1370.00 ± 351.46 ^{AB}	1137.50 ± 252.20 ^{BC}	87.60 ± 795.51	122.30 ± 64.67	21.90 ± 29.72	—	8.94 ± 1.21 ^B	9.39 ± 1.54 ^C	1.40 ± 1.84	
H9H12	1944.29 ± 180.92 ^{ABC}	1730.00 ± 164.79 ^{ABC}	1620.71 ± 187.86 ^{AB}	1342.85 ± 134.80 ^{BC}	110.32 ± 425.21	153.42 ± 34.57	32.25 ± 15.88	0.45 ± 0.15 ^{AB}	10.69 ± 0.76 ^{AB}	8.80 ± 0.98 ^C	1.91 ± 1.17	
H9H9	1677.80 ± 07.04 ^{BC}	1475.00 ± 97.49 ^{BC}	1373.75 ± 111.14 ^{AB}	1153.50 ± 79.75 ^{BC}	94.49 ± 251.56	118.47 ± 20.45	43.22 ± 9.39	0.40 ± 0.04 ^{AB}	8.19 ± 0.41 ^B	10.25 ± 0.53 ^{BC}	2.38 ± 0.63	
H10H10	1590.00 ± 276.37 ^{BC}	1418.33 ± 251.72 ^{BC}	1330.00 ± 286.96 ^{AB}	1111.67 ± 205.92 ^{BC}	137.83 ± 649.52	188.26 ± 52.80	19.83 ± 24.26	0.31 ± 0.15 ^{AB}	12.70 ± 0.98^A	17.21 ± 1.26^A	1.29 ± 1.51	
H13H14	2170.00 ± 478.68 ^{ABC}	2100.00 ± 436.00 ^{ABC}	1925.00 ± 497.04 ^{AB}	1625.00 ± 356.67 ^{ABC}	139.00 ± 1125.01	162.20 ± 91.46	29.10 ± 42.03	0.33 ± 0.15 ^{AB}	8.55 ± 1.71 ^B	9.98 ± 2.18 ^C	1.34 ± 2.61	

Note: Values were presented as least squares means ± standard error. Values in bold refer to the advantageous effect of certain diplootype, whereas values underlined refer to the negative effect of certain diplootype. * $P \leq 0.05$. The superscripts lacking a common uppercase differ great significantly ($P < 0.05$)

played an active role in cell metabolism and would be a good candidate gene in determining the carcass traits in domestic animals. However, there was no formal report about *FATP1* gene polymorphisms in domestic animals so far. One SNP of chicken *FATP1* (rs14729179), which is located in exon 10 and is synonymous, could be retrieved from GenBank (http://www.ncbi.nlm.nih.gov/SNP/snp_ref.cgi?locus_I=426008) recently. In the present study, we screened the SNPs in chicken *FATP1* gene in well-defined meat-type quality chicken populations, in order to detect the potential association between *FATP1* gene and carcass traits. Despite of the low efficiency of the SSCP method to identify unknown SNPs, we still found five SNPs in our chicken samples. We would expect that more SNPs could be identified if these samples were sequenced directly.

Association analysis showed that the identified SNPs in chicken *FATP1* gene (except for one rare SNP) had an effect on chicken carcass traits (Tables 1 and 3). This result confirmed our speculation that *FATP1* gene be a good candidate gene for marker-assisted selection during chicken breeding. In addition, it suggested a conserved role of this gene during the lipid metabolism and fatty acid transport that controlled the metabolism of triglyceride and energy homeostasis [6].

Previous studies have showed that associations of haplotypes with carcass traits were more accurate than those of single SNPs [19, 20]. This result implied that there was an interaction between different SNPs, and that the haplotypes generally provided more information than SNPs [21]. Thus, it was observed that both haplotype diversity and the method of SNP selection based on maximizing haplotype diversity were preferred to single SNPs [20, 22]. Haplotype analysis has gained increasing attention in the mapping of complex-disease genes in recent years, because of the abundance of SNP and the limited power of conventional single-site analyses [23–25]. We reconstructed haplotypes based on four common *FATP1* gene SNPs and discerned an association between the diplotypes and carcass traits. Particularly, H5H7 diplotype was found to contribute more to LW, CW, SEW and EW than the other diplotypes. Diplotypes H1H9, H2H6, and H10H10 were also associated with certain traits.

In short, we screened the SNPs in entire exons of the *FATP1* gene in a large number of chicken samples from eight populations by using the PCR-SSCP approach. Association analysis of the identified SNPs with chicken carcass traits showed that these SNPs would affect the carcass traits, and we identified several diplotypes that showed advantageous effects. This result suggested that *FATP1* gene played an important role in the regulation of carcass traits in chickens and could be of potential usage in molecular MAS program during chicken breeding. More chicken samples and expression analysis of this gene in different chicken tissues may help to further solidify our results.

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References

- Chen GH, Wu XS, Hou SS (1999) Comparison on relative muscle fatty acids content in Chinese native chickens. Chin J Animal Sci 35:27–28 (in Chinese)
- Huang ZG, Xie Z (2004) The development of animal adipose related genes. Animal Husb Vet Med 4:41–43 (in Chinese)
- Zhou SL, Stump D, Sorrentino D (1992) Adipocyte differentiation of 3T3-L1 cells involves augmented expression of a 43-kDa plasma membrane fatty acid-binding protein. J Biol Chem 268:14456–14461
- Griffin HD, Guo K, Windsor D (1992) Adipose tissue lipoge and fat deposition in leaner broiler chickens. J Nutr 122:363–368
- Stahl A, Gimeno RE, Tartaglia LA, Lodish HF (2001) Fatty acid transport proteins: a current view of a growing family. Trends Endocrinol Metab 12:266–273
- Hirsch D, Stahl A, Lodish HF (1998) A family of fatty acid transporters conserved from mycobacterium to man. Proc Natl Acad Sci USA 95:8625–8629
- Pohl J, Ring A, Hermann T, Stremmel W (2004) Role of FATP in parenchymal cell fatty acid uptake. Biochim Biophys Acta 1686:1–6
- Schaffer JE, Lodish HF (1994) Expression cloning and characterization of a novel adipocyte long chain fatty acid transport protein. Cell 79:427–436
- Doerge H, Stahl A (2006) Protein-mediated fatty acid uptake: novel insights from in vivo models. Physiology (Bethesda) 21:259–268
- Meirhaeghe A, Martin G, Nemoto M, Deeb S, Cottel D, Auwerx J, Amouyel P, Helbecque N (2000) Intronic polymorphism in the fatty acid transport protein 1 gene is associated with increased plasma triglyceride levels in a French population. Arterioscler Thromb Vasc Biol 20:1330–1334 Erratum in: Arterioscler Thromb Vasc Biol 2005; 25(10):e139
- Meirhaeghe A, Cottel D, Amouyel P, Dallongeville J (2005) Lack of association between certain candidate gene polymorphisms and the metabolic syndrome. Mol Genet Metab 86:293–299
- Binnert C, Koistinen HA, Martin G, Andreelli F, Ebeling P, Koivisto VA, Laville M, Auwerx J, Vidal H (2000) Fatty acid transport protein-1 mRNA expression in skeletal muscle and in adipose tissue in humans. Am J Physiol 279:1072–1079
- Zhang JQ, Chen H, Sun ZJ, Liu XL, Qiang-Ba YZ, Gu YL (2010) Flesh color association with polymorphism of the Tyrosinase gene in different Chinese chicken breeds. Mol Biol Rep 37(1):165–169
- Fang M, Nie Q, Luo C, Zhang D, Zhang X (2010) Associations of GHSR gene polymorphisms with chicken growth and carcass traits. Mol Biol Rep 37(1):423–428
- Zhang ZR, Liu YP, Yao YG, Jiang XS, Du HR, Zhu Q (2009) Identification and association of the single nucleotide polymorphisms in calpain 3 (CANP3) gene with carcass traits in chickens. BMC Genet 10:10. doi:[10.1186/1471-2156-10-10](https://doi.org/10.1186/1471-2156-10-10)
- Zhou Y, Liu YP, Jiang XS, Du HR, Li XC, Zhu Q (2010) Polymorphism of chicken Myocyte-specific enhancer-binding factor 2A gene and its association with chicken carcass traits. Mol Biol Rep 37:587–594
- Stephens M, Smith N, Donnelly P (2001) A new statistical method for haplotype reconstruction from population data. Am J Hum Genet 68:978–989

18. Gertow K, Skoglund-Andersson C, Eriksson P, Boquist S, Orth-Gomer K, Schenck-Gustafsson K, Hamsten A, Fisher RM (2003) A common polymorphism in the fatty acid transport protein-1 gene associated with elevated post-prandial lipaemia and alterations in LDL particle size distribution. *Atherosclerosis* 167:265–273
19. Daly MJ, Rioux JD, Schaffner SF, Hudson TJ, Lander ES (2001) High-resolution haplotype structure in the human genome. *Nat Genet* 2:229–232
20. Huang QQ, Fu YX, Boerwinkle E (2003) Comparison of strategies for selecting single nucleotide polymorphisms for case/control association studies. *Hum Genet* 113:253–257
21. Stephens JC, Schneider JA, Tanguay DA, Choi J, Acharya T, Stanley SE, Jiang RH, Messer CJ, Chew A, Han JH, Duan JC, Carr JL, Lee MS, Koshy B, Kumar AM, Zhang G, Newell WR, Windemuth A, Xu CB, Kalbfleisch TS, Shaner SL, Arnold K, Schulz V, Drysdale CM, Nandabalan K, Judson RS, Ruano G, Vovis GF (2001) Haplotype variations and linkage disequilibrium in 313 human genes. *Science* 293:489–493
22. Zhang WH, Collins A, Morton NE (2004) Does haplotype diversity predict power for association mapping of disease susceptibility. *Hum Genet* 115:157–160
23. Cardon LR, Abecasis GR (2003) Using haplotype blocks to map human complex trait loci. *Trends Genet* 19:135–140
24. Croucher PJ, Mascheretti S, Hampe J, Huse K, Frenzel H, Stoll M, Lu T, Nikolaus S, Yang SK, Krawczak M, Kim WH, Schreiber S (2003) Haplotype structure and association to Crohn's disease of CARD15 mutations in two ethnically divergent populations. *Eur J Hum Genet* 11:6–16
25. Lin DY (2004) Haplotype-based association analysis in cohort studies of unrelated individuals. *Genet Epidemiol* 26:255–264