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Association of *MyoD1* Gene Polymorphisms with Meat Quality Traits in Domestic Pigeons (*Columba livia*)

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Myogenic differentiation 1 (*MyoD1*) belongs to the *MyoD* family and plays a key role in myogenesis and consequently, in determining muscle fiber characteristics. In this study, single nucleotide polymorphisms (SNPs) in the exons of *MyoD1* were identified in 200 domestic pigeons (*Columba livia*) by direct DNA sequencing, and the association between *MyoD1* polymorphisms and meat quality traits was analyzed. We found four novel variations (A2967G, G3044A, A3164C, and C3311G) in exon 3. The SNP A2967G is a synonymous mutation, while the other 3 SNPs are located in the 3′ untranslated region. The analysis revealed 3 genotypes, in which allele A was the predominant allele in the SNP A2967G, while allele B was the predominant allele in the SNPs G3044A and A3164C. The mutations A2967G and G3044A were significantly associated with meat quality traits in pigeon. Pigeons with AA or AB genotypes had higher breast muscle concentrations of inosinic acid and intramuscular fat than those of BB genotype. Moreover, these 2 SNPs had significant effects on *MyoD1* mRNA expression. The SNPs A2967G and G3044A were organized into 4 haplotypes, which formed 7 diplotypes. Association analysis showed that the diplotypes were not significantly associated with meat quality traits. Our results implied that associations do exist between *MyoD1* gene polymorphisms and meat quality traits in domestic pigeons, and the AA and AB genotypes could be applied as genetic markers in marker-aid pigeon breeding.

Key words: genotype, meat quality, *MyoD1*, pigeon, polymorphism

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Introduction

It is well known that quantitative traits of economic interest in animal production exhibit continuous variation among individuals, but their underlying genetic architecture is very complex. The candidate gene approach may provide a direct understanding of the genetic basis for the expression of quantitative differences between individuals by identifying single nucleotide polymorphisms (SNPs) in genes that seem to cause variation in a phenotypic trait (Shin and Chung, 2007).

Recently, meat quality has become the main objective of animal breeding because it has steadily decreased with the improvement of growth rate (Han *et al*., 2012). Meat quality traits are economically important in meat-producing animals, and they are controlled by multiple genes as complex quantitative traits. Previous studies have suggested that muscle fiber characteristics play a key role in meat quality (Picard *et al*., 2002). The myogenic differentiation (*MyoD*) gene family, including *MyoD1* (*myf3*), *MyoG* (*myf4*), which encodes myogenin, *myf5*, and *MRF4* (*myf6*), plays a key role in myogenesis and consequently, in determining muscle fiber characteristics (Olson, 1990; Weintraub, 1993). These highly conserved genes encode basic helix-loop-helix proteins that regulate embryonic muscular development (Daou *et al*., 2013). Because the phenotypic changes derived from MyoD1 function are involved in both myofiber-type transformation and myofiber hypertrophy in pigs (Olson, 1990; Li *et al*., 1992), polymorphisms within *MyoD1* are thought to influence muscle fibers and may serve as markers for meat quality (te Pas and Visscher, 1994).

Associations between SNPs in *MyoD1* and meat quality traits have been described in livestock, particularly, in pigs (Liu *et al*., 2008; Han *et al*., 2012; Lee *et al*., 2012). To our best knowledge, however, few studies have reported on the relationship between *MyoD1* polymorphisms and poultry meat quality traits. Domestic pigeons are reared as meat poultry in southern China and are known for their delicious, nutritious meat. The objectives of this study were to investigate SNPs in the *MyoD1* gene and to evaluate whether these polymorphisms affect meat quality traits in pigeon. We expected our study to reveal whether *MyoD1* is an important candidate gene for selecting meat quality traits in

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the pigeon industry.

Materials and Methods

Animals

The population we used for SNP identification in the *MyoD1* gene consisted of Taishen King pigeons (*Columba livia*), which were provided by Xingliang commercial pigeon farm (Wenzhou, China). Blood samples and phenotypic data on meat quality traits were collected from 200 randomly selected (male:female＝1:1) pigeons at 25 days of age. The pigeons were hatched on the same day and were fed by the parents until 25 days of age. The parents were housed one pair per cage under the same managerial conditions in a windowed poultry house and were fed a mixed-grain diet of cereals and pulses (16.89% CP and 11.47 MJ/kg ME). The experiment was conducted in accordance with the Chinese guidelines for animal welfare and was approved by the animal welfare committee of the Animal Science College, Zhejiang University.

Phenotypic Measurements

Meat quality was evaluated by using the left side of each breast muscle at 30 min postmortem. Breast muscle pH was measured in duplicate using a pH Star 6.05 (Matthäus, Nobitz, Germany). Drip loss was measured by the press technique, as described by Liu *et al*. (2008), and drip loss rate was calculated by the following equation: drip loss rate (%)＝[sample weight before press (g)－sample weight after press (g)] / sample weight before press (g)×100. Meat color was measured in triplicate using a portable colorimeter (spectrophotometer model 968; X-Rite Inc., Grandville, MI, USA) set on the L*, α*, b* system with white and black tiles as standards (Esperanza *et al*., 2009). Breast muscle shear force was measured according to Tang *et al*. (2009), using a shear tool (digital muscle tenderometer of model C-LM3, Northeast Agricultural University, Harbin, China). The intramuscular fat percentage of the breast muscle was determined by chloroform-methanol extraction, according to Bligh and Dyer (1959). Concentrations of inosinic acid in breast muscle samples were determined by using a high-performance liquid chromatography method (Veciana-Nogues *et al*., 1997).

DNA Extraction, Primer Design, PCR Amplification, and Sequencing

Blood was collected and stored at －20℃. Genomic DNA was isolated by using a Genome DNA Extraction Kit (TIANGEN, Beijing, China) according to the manufacturer's instruction. Primer pairs used for amplifying exon regions of *MyoD1* were designed from reference sequences of the pigeon *MyoD1* gene in GenBank (accession no: 102096590) by using Primer Premier 5.0 software (Premier Biosoft International, Palo Alto, CA). The primers were synthesized by TSINGKE Biotech Co., Ltd. (Hangzhou, China) and are listed in Table 1.

The PCR amplification was performed in reaction mixtures with a total reaction volume of 50 μL, containing 25 μL 2× Taq PCR MasterMix (including Mg^{2+}, dNTP, and Taq DNA polymerase), 2 μL of each primer, 2 μL genomic DNA, and double-distilled water. The cycling protocol was 5 min at 94℃, 30 cycles of 94℃ for 30 s, 40 s at the annealing temperature (Table 1), and extension at 72℃ for 1 min, with a final extension at 72℃ for 10 min. The PCR products were verified by 1.5% agarose gel electrophoresis and sequenced by Hangzhou Qingkezixi Biotech Co., Ltd (Hangzhou, China). To identify SNPs, sequences were analyzed with the DNAMAN software (DNAMAN Application 4.0.1.1, Lynnon BioSoft, San Ramon, CA, USA).

Real-time Reverse-transcription PCR

Total RNA was isolated from the breast muscle of individual pigeons of different genotypes using TRIzol reagent (Invitrogen, Carlsbad, CA, USA) according to the manufacturer's instructions. cDNA was synthesized by using reverse transcriptase (M-MLV; Takara, Dalian, China) at 42℃ for 60 min with oligo dT-adaptor primer, per the manufacturer's protocol. The primer sequences were as follows: forward, 5′-AACTGCTCTGACGGCATGAT-3′ and reverse, 5′-GTGCTTTGGATCGTTCGGTG-3′. The abundance of mRNA was determined on a StepOne Plus Real-Time PCR system (ABI 7500; Applied Biosystems, Foster City, CA, USA) using SYBR Premix PCR kit (Takara). The PCR program was 95℃ for 30 s followed by 40 cycles of 95℃ for 3 s and 60℃ for 30 s. Relative expression of the *MyoD1* gene was analyzed by the $2^{-\Delta\Delta Ct}$ method (Livak and Schmittgen, 2001) using the β-*actin* gene for normalization.

Statistical Analysis

Genotypic frequencies, heterozygosity (*He*), effective allele numbers (*Ne*), polymorphism information content (PIC), and Hardy–Weinberg equilibrium were analyzed using the Genepop software (version 4.0). Haplotypes was analyzed

Table 1. **Primers used for PCR amplification of the pigeon *MyoD1* gene**

Name	Sequence (5′–3′)	Tm (℃)	Product size (bp)	Amplified region
Primer pair 1	CCCTCTCTTGTGATCCCCTC AGCAGAAGATGGAAACAGATGTC	55	1025	Exon 1
Primer pair 2	TTGATGGTGTTTCAGCCAGGAC AACAGCTCGCTGGTTCCTCTTT	55	343	Exon 2
Primer 3	GCCCCAGACAGAGCATAGTTTG CAATGCGAGGAAAGTAGACCC	55	1276	Exon 3

MyoD1＝myogenic differentiation 1, Tm＝annealing temperature.

using HaploView 4.2 version (Broad Institute, Cambridge, MA, USA). To address concerns about population stratification, we conducted principle component analysis as implemented in the R software. All individuals in the pigeon population were clustered together and could not be assigned to any subgroups, indicating that there was no significant stratification within the population (Fig. 1). Association analyses between genotypes or diplotypes and phenotypic traits were performed using the general linear model procedure in SPSS20.0 (SPSS, Chicago, IL). The model used was as follows:

$$Y_{ijm}=u+G_i+s_j+e_{ijm}$$

Where Y_{ijm} is a phenotypic value, u is the population mean, G_i is the effect of genotype, s_j is the effect of sex, and e_{ijm} represents the random error.

Results

Analysis of the sequencing data revealed that 4 SNPs (A2967G, G3044A, A3164C, and C3311G) existed in exon 3 of *MyoD1*, while no base variation was found in exon 1 or exon 2 (Table 2). The SNP A2967G is a synonymous mutation, while the other 3 SNPs are located in the 3′ untranslated region (3′ UTR).

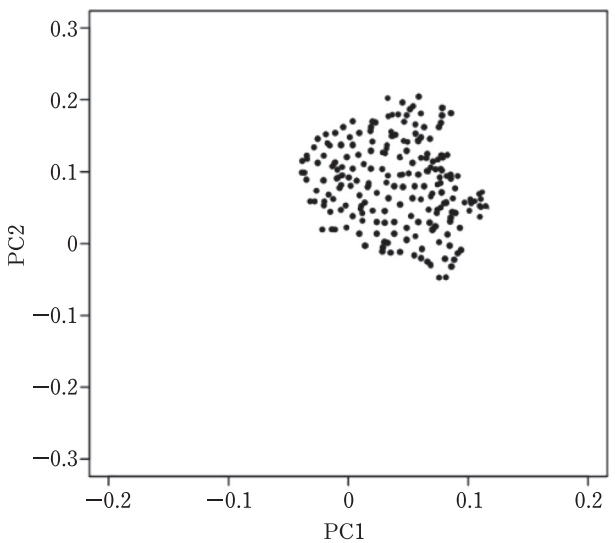

Fig. 1. **Principal component analysis plot of the Taishen King pigeon population.**

The genotypic and allelic frequencies, and estimated values of population genetic indexes (*He*, *Ne,* and PIC) are listed in Table 3. The variant C3311G was excluded from further analysis because it was detected at a low frequency in the investigated samples. Three genotypes (AA, AB, and BB) were detected for the SNPs A2967G, G3044A, and A3164C. The results showed that allele A was the predominant allele for the SNP A2967G, while for other SNPs, allele B was the predominant allele. A chi-square test showed that A2967G, G3044A, and A3164C deviated from Hardy–Weinberg equilibrium ($P>0.05$).

Association studies of all SNP genotypes and meat quality traits revealed that 2 SNP (A2967G and G3044A) genotypes were significantly associated with meat quality traits of pigeon. As for SNP A2967G, breast muscle concentrations of inosinic acid and intramuscular fat were significantly higher ($P<0.05$) in the AA and AB genotypes than in the BB genotype (Table 4). As for G3044A, individuals with the AA or AB genotype had higher ($P<0.01$) breast muscle inosinic acid concentration than those with the BB genotype (Table 5). *MyoD1* mRNA expression was compared between the genotypes of both SNPs (Fig. 2). Individuals with the AA and AB genotypes had significantly higher ($P<0.05$) *MyoD1* mRNA expression levels than individuals with the BB genotype.

Haplo- and diplotypes were constructed from SNPs A2967G and G3044A (Table 6). Four haplotypes and seven diplotypes were detected in *MyoD1*. Among them, haplotypes 1 and 2 were the main haplotypes in pigeon. In the diplotype study, the H1H2 diplotype was the most frequent, while the H1H3 diplotype was the least frequent. No significant association was observed between the diplotypes and meat quality traits (Table 7).

Discussion

The *MyoD1* gene belongs to the *MyoD* gene family and plays key roles in muscle development from cell commitment and proliferation to muscle fiber formation (Olson, 1990; Weintraub, 1993). Muscle fiber characteristics play a key role in meat quality (Picard *et al*., 2002). Thus, *MyoD1* is considered to be a candidate gene for meat quality traits owing to its crucial roles in muscle fiber development (te Pas and Visscher, 1994). Despite the fact that the biological functions of *MyoD1* in mammals and chicken have been identified (Nakamura, 1993), its biological functions as well as genetic mutations in pigeon are still unclear. In this study,

Table 2. **SNPs identified within the pigeon *MyoD1* gene**

SNP	Position	Coded site (bp)	Amino acid mutation
A2967G	Exon 3	2967	Leu
G3044A	Exon 3	3044	/
A3164C	Exon 3	3164	/
C3311G	Exon 3	3311	/

MyoD1=myogenic differentiation 1. "/" indicates the SNP is located in the 3′ UTR.

Table 3. **Genotypic and allelic frequencies, and diversity parameters of SNPs in the *MyoD1* gene**

SNP	Genotypic frequency			Allele frequency		*P*	χ^2	Diversity parameter		
	AA	AB	BB	A	B			PIC	*He*	*Ne*
A2967G	0.6950 (139)	0.2100 (42)	0.0950 (19)	0.8000	0.2000	0.0000	23.6328	0.2688	0.3200	1.4706
G3044A	0.2350 (47)	0.3850 (77)	0.3800 (76)	0.4275	0.5725	0.0025	9.1133	0.3697	0.4895	1.9588
A3164C	0.0050 (1)	0.0300 (6)	0.9650 (193)	0.0200	0.9800	0.0009	11.0162	0.0384	0.0392	1.0408
C3311G	0.0050 (1)	0.0000 (0)	0.9950 (199)	0.0050	0.9950	0.0000	200.0000	0.0099	0.0099	1.0100

n=200; *MyoD1*=myogenic differentiation 1. $P>0.05$ suggested the population conforms to Hardy–Weinberg equilibrium.

Table 4. **Association of the A2967G SNP genotypes of *MyoD1* gene with meat quality traits in pigeon**

SNPS	Meat quality traits	Phenotypic value of different genotypes		
		AA	AB	BB
A2967G	Meat color L*	41.29±0.36	40.94±0.56	40.65±0.74
	Meat color α*	14.29±0.16	14.26±0.28	14.63±0.37
	Meat color b*	16.67±0.26	16.89±0.49	15.79±0.42
	pH	5.82±0.01	5.82±0.03	5.83±0.02
	Shear force (N)	15.03±0.39	17.10±0.70	15.40±1.19
	Drip loss (%)	33.13±0.67	30.56±1.30	31.92±1.47
	Inosinic acid (mg/g)	1.25±0.01^{a}	1.25±0.03^{a}	1.10±0.03^{b}
	Intramuscular fat (%)	2.24±0.03^{a}	2.29±0.07^{a}	2.03±0.10^{b}

MyoD1=myogenic differentiation 1. Different lowercase letters indicate significant differences ($P<0.05$) among the tree genotypes.

Table 5. **Association of the G3044A SNP genotypes of the *MyoD1* gene with meat quality traits in pigeon**

SNP	Meat quality trait	Phenotypic value of the genotype		
		AA	AB	BB
G3044A	Meat color L*	41.46±0.66	41.42±0.46	40.71±0.42
	Meat color α*	14.47±0.27	14.29±0.22	14.26±0.20
	Meat color b*	16.86±0.49	16.75±0.37	16.37±0.26
	pH	5.83±0.02	5.80±0.01	5.83±0.02
	Shear force (N)	16.14±0.72	14.84±0.53	15.78±0.54
	Drip loss (%)	33.79±1.16	32.08±0.83	32.06±0.98
	Inosinic acid (mg/g)	1.28±0.02^{A}	1.28±0.02^{A}	1.17±0.02^{B}
	Intramuscular fat (%)	2.26±0.06	2.23±0.05	2.23±0.04

MyoD1=myogenic differentiation 1. Different capital letters indicate highly significant differences ($P<0.01$) among the tree genotypes.

MyoD1 was selected as a candidate gene to investigate associations of gene polymorphisms with meat quality traits in domestic pigeons.

We found 4 novel variations (A2967G, G3044A, A3164C, and C3311G) in exon 3 by direct DNA sequencing. As the variant C3311G was detected at a low frequency in the investigated samples, it was excluded from further analysis. The SNP A2967G is a synonymous mutation that does not cause amino acid variations. It is worth noting that silent mutations may also affect protein expression, as well as function, by altering or increasing the stability of the mRNA, as described by Ren *et al*. (2014) and Wang *et al*. (2014). The SNPs G3044A, A3164C, and C3311G are 3′ UTR variants in *MyoD1*. The ability of microRNAs to bind to

messenger (mRNA) in the 3′UTR is critical to the regulation of the mRNA level and protein expression (Chen *et al*., 2008). Previous studies indicate that 3′UTR polymorphisms disrupting microRNA binding can be functional and can act as genetic markers (Chin *et al*., 2008; Pongsavee *et al*., 2009).

The analysis revealed 3 genotypes, in which allele A was the predominant allele in the SNP A2967G, while allele B was the predominant allele in the SNPs G3044A and A3164C. The genotypic frequencies of A2967G, G3044A, and A3164C were not in agreement with Hardy–Weinberg equilibrium, which might be attributed to the fact that the studied pigeon breeds underwent intensive selection during long-term commercial breeding, as described by Wu *et al*. (2012). Heterozygosity, *Ne*, and PIC are preferable indexes of gene polymorphism. If those indexes are large, the genetic variation at a given locus will be high (Fang *et al*., 2012). According to the classification of PIC (Chen *et al*., 2015), the SNPs detected in the current study (except A3164C) presented moderate (0.25＜PIC＜0.5) polymorphisms in pigeon, indicating that *MyoD1* is rich in polymorphisms.

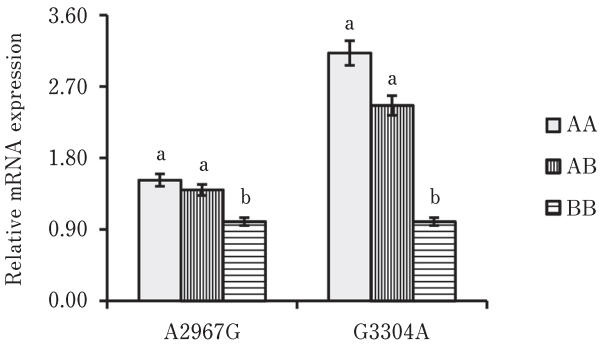

Fig. 2. **mRNA expression levels of the pigeon *MyoD1* gene for each SNP site.** Different letters above the bars indicate significant differences between genotypes for the SNP site ($P<0.05$). *MyoD1*＝myogenic differentiation 1.

Polymorphisms within the *MyoD1* gene have been reported to be significantly associated with meat quality traits in different species. Lee *et al*. (2012) found that the SNPs C489T (exon 1) and C1264A (intron 1) were significantly associated with muscle fiber characteristics, lean meat production, and meat quality traits in Yorkshire and Berkshire pig breeds. Han *et al*. (2012) reported that the SNP A257C in exon 3 was significantly associated with muscle pH value and drip loss in Large White pigs. Du *et al*. (2013) identified that G782A in exon 1 was significantly associated with loin muscle area in beef cattle. However, Liu *et al*. (2008) showed that *MyoD1* intron 1 Ddel polymorphism was not significantly associated with any of the meat quality traits tested in Large White×Meishan F2 pig populations. Based

Table 6. **Frequency of haplotypes and diplotypes in the pigeon *MyoD1* gene**

Haplotype	A2967G	G3044A	Frequency	Diplotype	A2967G	G3044A	Frequency
H1	A	G	0.4175 (167)	H1H1	AA	GG	0.2150 (43)
H2	A	A	0.3825 (153)	H1H2	AA	GA	0.3000 (60)
H3	G	G	0.0100 (4)	H1H3	AG	GG	0.0200 (4)
H4	G	A	0.1900 (76)	H1H4	AG	GA	0.0850 (17)
				H2H2	AA	AA	0.1800 (36)
				H2H4	AG	AA	0.1050 (21)
				H4H4	GG	AA	0.0950 (19)

MyoD1＝myogenic differentiation 1.

Table 7. **Association of diplotypes with meat quality traits in pigeon the *Myod1* gene**

Meat quality trait	Diplotype						
	H1H1	H1H2	H1H3	H1H4	H2H2	H2H4	H4H4
Meat color L*	41.52±0.72	41.36±0.51	40.87±1.29	41.66±1.14	40.94±0.74	40.37±0.60	40.65±0.74
Meat color a*	14.55±0.28	14.27±0.26	13.59±1.27	14.38±0.46	14.03±0.33	14.30±0.37	14.64±0.38
Meat color b*	17.13±0.51	16.57±0.43	14.00±1.80	17.40±0.89	16.29±0.41	17.04±0.54	15.80±0.42
pH	5.84±0.024	5.81±0.014	5.78±0.041	5.79±0.053	5.82±0.023	5.86±0.058	5.83±0.029
Shear force (N)	15.95±0.75	14.33±0.62	18.22±3.06	16.66±0.92	15.13±0.69	17.26±1.11	15.40±1.19
Drip loss (%)	33.42±1.21	32.42±0.87	37.86±4.06	30.92±2.29	33.98±1.64	28.89±1.57	31.93±1.47
Inosinic acid (mg/g)	1.28±0.028	1.27±0.019	1.28±0.042	1.32±0.063	1.18±0.038	1.20±0.031	1.16±0.033
Intramuscular fat (%)	2.27±0.072	2.23±0.064	2.25±0.024	2.26±0.14	2.24±0.059	2.33±0.10	2.14±0.10

MyoD1＝myogenic differentiation 1.

on the results of the above studies, one may conclude that the significance of the effect of genotype at the *MyoD1* locus on meat quality may vary depending on the breed or line.

In the current study, two novel SNPs, A2967G and G3044A in exon 3, were significantly associated with meat quality traits in pigeon. In addition, different genotypes had significantly different effects on the studied phenotypic traits. Pigeons with the AA or AB genotypes had higher breast muscle concentrations of inosinic acid and intramuscular fat than those of the BB genotype. Moreover, real-time PCR results showed that the effects of these SNPs on *MyoD1* expression were similar to the associations of individual SNPs. Intramuscular fat with a high heritability of 0.61 is a key factor for meat quality and is also closely related to a special flavor, juiciness, and tenderness (Pang *et al*., 2006). Inosinic acid is known as a flavor substance (Davidek and Khan, 2006). Therefore, higher intramuscular fat and inosinic acid are major considerations in for meat-producing animal breeding programs. We speculate that the genotypes AA and AB of *MyoD1* are promising candidates for improving meat quality in domestic pigeons. The significant effect of SNPs on inosinic acid in the current study was rather astonishing. More studies are needed to verify whether *MyoD1* polymorphisms affect inosinic acid content in other species. It is worth noting that the *MyoD1* diplotypes were not associated with meat quality traits in pigeon. The high number of diplotypes observed at the *MyoD1* gene resulted in divergent sample sizes between groups of individuals with various diplotypes. Thus, further research involving larger sample sizes will be necessary to confirm the association between interactions of multiple SNPs within *MyoD1* and meat quality traits of pigeon.

In conclusion, we present the first data on *MyoD1* gene polymorphisms in domestic pigeons, and our results indicate that *MyoD1* potentially is a major gene affecting meat quality traits in pigeons. The AA and AB genotypes could be used as molecular markers for superior meat quality traits in pigeons. Further analysis should be performed to validate both the association and the physiological significance of the mutations in exon 3 of the *MyoD1* gene.

Acknowledgments

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