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

Xinyang Dong, Haiyue Cao, Haiguang Mao, Qihua Hong and Zhaozheng Yin

Animal Science College, Zhejiang University, Zijingang Campus, Hangzhou, 310058, China

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

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 pigeons.
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*, a*, 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°C. 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 Mg2+, 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°C, 30 cycles of 94°C for 30 s, 40 s at the annealing temperature (Table 1), and extension at 72°C for 1 min, with a final extension at 72°C 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°C for 60 min with oligo dT-adaptor primer, per the manufacturer’s protocol. The primer sequences were as follows: forward, 5′-AACCTGCTCTGACGGCATGAT-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°C for 30 s followed by 40 cycles of 95°C for 3 s and 60°C for 30 s. Relative expression of the MyoD1 gene was analyzed by the 2−ΔΔCt 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

| Primer number | Name | Sequence (5′–3′) | Tm (°C) | Product size (bp) | Amplified region |
|---------------|------|-----------------|--------|------------------|-----------------|
| Primer pair 1 | CCCCCTCTCTTGTGATCCCCTC | 55 | 1025 | Exon 1 |
| Primer pair 2 | AGCCAGAAGATGGAACAGATGTC | 55 | 343 | Exon 2 |
| Primer 3 | GCCCCAGACAGACAGCATGTGGCAATCGCAGGAAAGTAGACCC | 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).

The genotypic and allelic frequencies, and estimated values of population genetic indexes (\( H_e \), \( N_e \), 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 diplotype 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,

![Fig. 1. Principal component analysis plot of the Taishen King pigeon population.](image)

| 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.
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

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

| SNP    | Genotypic frequency | Allele frequency | P  | χ²  | 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          |
|      | 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^a |
|      | Intramuscular fat (%) | 2.24±0.03^a | 2.29±0.07^a | 2.03±0.10^a |

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^a |
|        | 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.
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.

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 on the classification of PIC, 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.](image)

Different letters above the bars indicate significant differences between genotypes for the SNP site (P<0.05). MyoD1=myogenic differentiation 1.

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      | A      | 0.0100 (4)   | H1H3      | AG     | GA     | 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 | 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 α*      | 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 β*      | 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±0.244 | 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 (%)      | 32.42±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 Dyer, 2001). 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 diplootypes were not associated with meat quality traits in pigeon. The high number of diplootypes observed at the MyoD1 gene resulted in divergent sample sizes between groups of individuals with various diplootypes. 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.

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