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Polymorphism in Exons of the Myostatin Gene and Its Relationship with Body Weight Traits in the Bian Chicken

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Abstract In our research, single nucleotide polymorphisms (SNPs) of exon regions of the myostatin gene were detected by PCR–SSCP in the Bian chicken and three reference chicken populations (Jinghai, Youxi, and Arbor Acre). Four novel SNPs (G2283A, C7552T, C7638T, and T7661A) were detected. The findings from the least square means showed that Bian chickens with EE and DE genotypes had significantly higher body weight, at 6–18 weeks of age, than those of the DD genotype ($P < 0.05$). The results suggest that the mutation G2283A, detected in exon 1, has potential as a genetic marker for body weight traits in the Bian chicken.

Keywords Bian chicken · Myostatin gene · SSCP · Body weight

Introduction

Myostatin, or growth and differentiation factor 8 (GDF8), is a member of the transforming growth factor-β superfamily; it functions as a negative regulator of skeletal muscle development and growth in mammals (McPherron and Lee 1997). The myostatin gene consists of three exons and two introns in all species studied (Bellinge et al. 2005). Although myostatin is principally found in skeletal muscle, it has also been localized to adipose tissue, where it serves as a negative regulator of preadipocyte differentiation (Feldman et al. 2006). The effects of the myostatin gene were first described in mice, where loss of myostatin expression in knock-out mice was associated with both an increase in the number of muscle fibers (hyperplasia)

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and an increase in fiber size (hypertrophy). The muscles of myostatin knock-out mice weighed about twice as much as those of wild-type mice. Later, an extreme form of muscularity (double muscling) seen in the Belgian Blue and Piedmontese cattle breeds was shown to result from mutations in the coding region of the myostatin gene (Kambadur et al. 1997; McPherron and Lee 1997; Wiener et al. 2009). Other heavily muscled cattle breeds have also been shown to carry polymorphisms in this gene (Dunner et al. 2003; Grobet et al. 1998). In chickens, Gu et al. (2003) found that the myostatin gene not only regulated the skeletal muscle development but also participated in fat metabolism and deposition.

Myostatin as a negative regulator of skeletal muscle development and growth in mammals attracted universal attention. Illuminating the structure and function of the myostatin gene is significantly necessary. Nevertheless, few studies of the association of the myostatin gene with body weight traits have been reported in chickens. The Bian chicken is an eminent Chinese native breed raised for dual purposes (high-weight eggs and high-quality meat). Characterized by its adaptability to poor quality feeds and cold, this breed is now in serious danger of extinction due to its poor commercial performance. In contrast, the Jinghai chicken is a national cultivated meat breed (minitype), and the Youxi chicken is a local breed raised for dual purposes. The Arbor Acre chicken, a commercial broiler selected for meat production, is well known for rapid growth. The objective of this research was to use the method of PCR–SSCP to detect the single nucleotide polymorphisms (SNPs) in exon regions of the myostatin gene in the Bian chicken, with the Jinghai, Youxi, and Arbor Acre breeds as reference populations. The relationship between the gene and body weight traits of the Bian chicken was examined to ascertain whether there were some mutations similar to those detected in cattle breeds (Kambadur et al. 1997; Wiener et al. 2009), thus laying the foundation for marker-assisted selection for chicken body weight traits.

Materials and Methods

Chicken Populations

From the four chicken breeds investigated, including three Chinese indigenous breeds (Bian, Jinghai, and Youxi) and one introduced breed (Arbor Acre), 249 chickens were sampled. Blood samples were taken from 137 female Bian chickens, belonging to generation one, at the age of 18 weeks at the Institute of Animal Husbandry and Veterinary of Shanxi Academy of Agricultural Sciences. The body weight of each female Bian chicken was measured in grams at hatching, 6, 8, 10, 12, 14, 16, and 18 weeks. These birds were hatched on the same day, reared in pens, and transferred to laying pens at the age of 10 weeks. Birds had access to feed (commercial corn–soybean diets meeting the National Research Council's requirements) and water ad libitum. Blood from 50 Jinghai chickens (male–female ratio 1:1) and 32 Arbor Acre chickens (1:1) was sampled at age 16 weeks at the Jiangsu Jinghai Poultry Industry Group Co. Blood from 30 Youxi chickens (1:1) was

sampled at age 16 weeks at the National Gene Bank for Local Chickens in the Poultry Institute, Chinese Academy of Agricultural Sciences.

Blood samples were taken from the wing vein with sodium heparin as an anticoagulant and stored at −20°C. Genomic DNA was extracted from the whole blood using the phenol–chloroform method. DNA concentrations were quantified spectrophotometrically.

Primer Design and PCR Amplification

Eight pairs of primers (Table 1) were designed with Primer Premier 5.0 software to amplify the exon regions of the myostatin gene, based on the chicken DNA sequence of the myostatin gene (GenBank accession no. AF346599; Fig. 1).

Table 1 Primers used to amplify exon regions of the myostatin gene in Bian chickens

Primer	Primer sequence (5′–3′)	Position in AF346599 (location)	Annealing temp. (°C)	Fragment length (bp)
MYOE1-3	F: GCATTAGCAGGGACGTTAT	2261–2446 (exon 1)	56	186
	R: GAAAGCAGCAGGGTTGTTA			
MYOE2-1	F: CTTTTTGTTCCCTGTTCAGTAA	4471–4755 (exon 2)	56	285
	R: CTGCCAGATACCAGTGCC			
MYOE2-2	F: GCTGGCAGAGTATTGATGTG	4747–4988 (exon 2)	56	241
	R: GCTTCATCTGCCATTCTCG			
MYOE3-1	F: GATTACATACGCCTACCTTG	7106–7415 (exon 3)	56	310
	R: GACCTCTGGGATTTGCTT			
MYOE3-2	F:TACACCAAGCAAATCCCAGAG	7392–7619 (exon 3)	56	228 (225)
	R: CAAAGATGGATGAGGGGATA			
MYOE3-3	F: GCTATATCCCCTCATCCATC	7596–7826 (exon 3)	56	231
	R: TTGATTCCCTCACAGTGTAAGA			
MYOE3-4	F: TCTTACACTGTGAGGGAAT	7805–8128 (exon 3)	56	324
	R: ATGGAAACACTGCTAAATAC			
MYOE3-5	F: TTCCTGAAGTTAGGGATGGTA	8084–8344 (exon 3)	56	261
	R: TTCCGTGCTGCCTTTTGT			

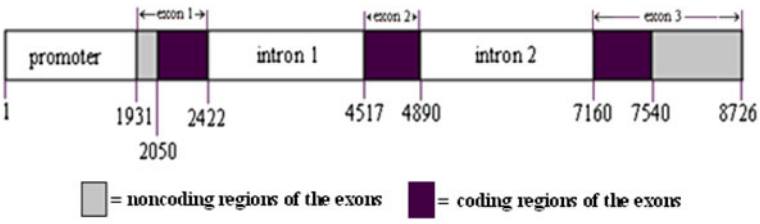

Fig. 1 The structure of the myostatin gene based on AF346599

PCR was carried out in 25 μl reactions consisting of 2 μl template DNA (50 ng/μl), 1 μl each primer (10 μmol/l), 2.5 μl 10 × buffer, 1.5 μl Mg^{2+} (25 mmol/l), 0.2 μl *Taq* DNA polymerase (5 U/μl), 2 μl dNTPs (2 mmol/l), and 14.8 μl sterilized water. The amplification conditions were denaturation at 94°C for 6 min; followed by 30 cycles of denaturation at 94°C for 30 s, annealing at 56°C for 30 s, and extension at 72°C for 30 s; and a final elongation step at 72°C for 10 min. Each amplification product was verified by electrophoresis on a 1.2% agarose gel (5 V/cm) in 0.5 × TBE buffer. Gels were stained with ethidium bromide.

Single-Strand Conformation Polymorphism Analysis

For single-strand conformation polymorphism (SSCP) analysis, 2 μl of each amplification product was added to 7 μl denaturing buffer: 98% formamide, 0.025% bromophenol blue, 0.025% xylene cyanole FF, 10 mmol/l EDTA (pH 8.0), and 10% glycerol. The samples were heat-denatured at 98°C for 10 min and then chilled on ice for 5 min. Electrophoresis was performed at 150 V on 10% nondenaturing polyacrylamide gel (29:1) for 11–13 h at 16°C. SSCP patterns on the gels were visualized by silver staining.

PCR products of homozygous/heterozygous individuals of different genotypes were purified with a DNA Fragment Quick Purification/Recover Kit. The purified PCR products were ligated to pGEM-T Easy vector and transformed into DH5-α *Escherichia coli*. Positive recombinant colonies for each genotype were chosen. The sequencing reactions were completed by Shanghai Invitrogen Biotechnology Co. (The PCR products of heterozygous individuals for MYOE1-3 were directly sequenced.)

Statistical Analysis

The general linear model (GLM) was established to analyze the genotype effects of the myostatin gene on body weight traits. The following linear model was used: $y_{ij} = \mu + G_i + e$, where y_{ij} is the body weight traits, μ is the overall mean, G_i is the genotypic effect of the myostatin gene, and e is the residual error. These statistical analyses were carried out using SPSS 11.0 software.

Results

PCR Amplification and SSCP Analysis

The PCR products amplified by the eight pairs of primers were ideal (not shown). Three pairs of primers (MYOE1-3, MYOE3-2, and MYOE3-3) displayed polymorphisms. For primer MYOE1-3, three genotypes were detected in Bian, Jinghai, and Youxi chickens and named DD, DE, and EE (Fig. 2); the Arbor Acre breed displayed only two genotypes (DE and EE). For primer MYOE3-2, the genotypes FF and FG were detected in Bian, Jinghai, and Youxi chickens (Fig. 3). For primer MYOE3-3, the genotypes HH and HI were detected in Bian, Jinghai, and

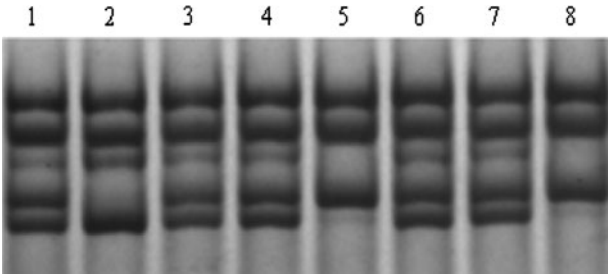

Fig. 2 SSCP analysis of PCR amplification using primer MYOE1-3 in four chicken breeds. *Lanes 5 and 8*: DD genotype; *lanes 1, 3, 4, 6, and 7*: DE genotype; *lane 2*: EE genotype

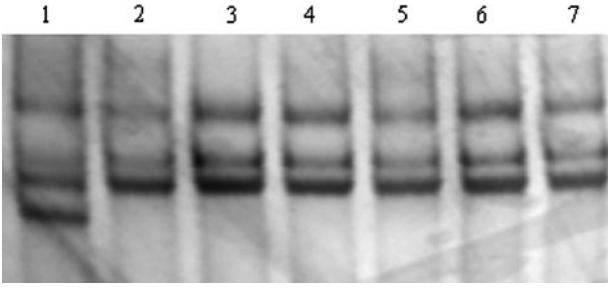

Fig. 3 SSCP analysis of PCR amplification using primer MYOE3-2 in four chicken breeds. *Lanes 2–7*: FF genotype; *lane 1*: FG genotype

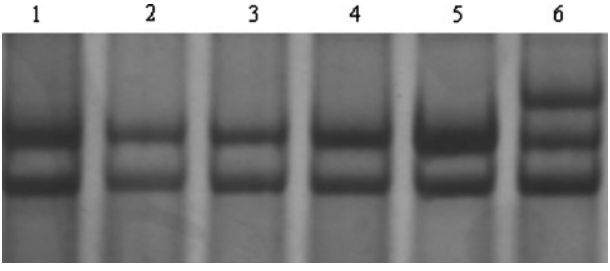

Fig. 4 SSCP analysis of PCR amplification using primer MYOE3-3 in four chicken breeds. *Lanes 1–5*: HH genotype; *lane 6*: HI genotype

Youxi chickens (Fig. 4). The Arbor Acre breed was monomorphic for primers MYOE3-2 and MYOE3-3.

Sequence Analysis

The PCR products of the DD and EE genotypes were cloned and sequenced. Sequencing revealed one nucleotide mutation (G2283A) in exon 1 of the myostatin gene between DD and EE genotypes (Fig. 5); it was a synonymous mutation.

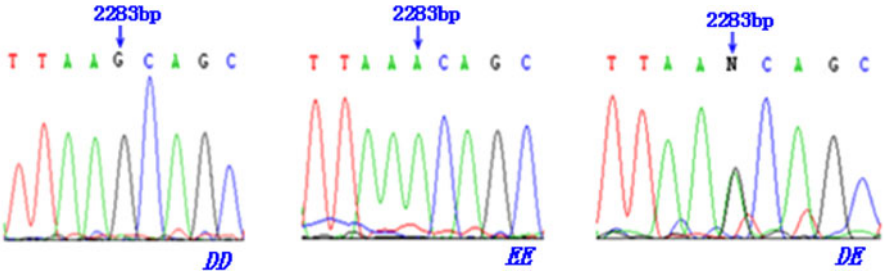

Fig. 5 Sequence alignment of DD, EE, and DE genotypes of primer MYOE1-3 in chickens

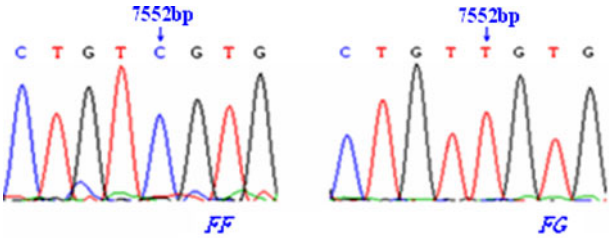

Fig. 6 Sequence alignment of FF and FG genotypes of primer MYOE3-2 in chickens

The PCR products of the FF and FG genotypes were cloned and sequenced. Sequencing revealed one nucleotide mutation (C7552T) in exon 3 of the myostatin gene between FF and FG genotypes (Fig. 6). This mutation was located in the noncoding region of exon 3.

The PCR products of the HH and HI genotypes were cloned and sequenced. Sequencing revealed two nucleotide mutations (C7638T, T7661A) in exon 3 of the myostatin gene between HH and HI genotypes (Fig. 7). They were also located in the noncoding region of exon 3.

Nucleotide Polymorphism Distribution of the Myostatin Gene

Genotype and allele frequencies of the myostatin gene are presented in Table 2. For primer MYOE1-3, allele D was dominant in the Bian breed, with a frequency

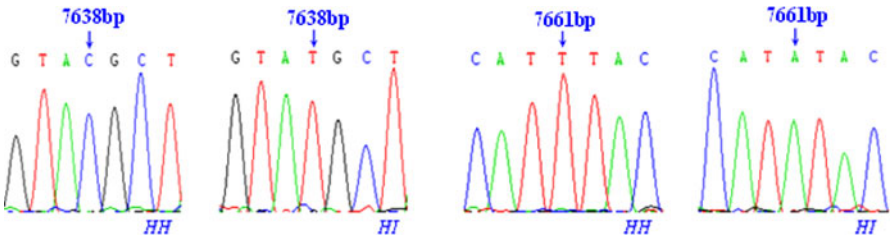

Fig. 7 Sequence alignment of HH and HI genotypes of primer MYOE3-3 in chickens

Table 2 Genotype and allele frequencies of the myostatin gene in four chicken breeds

Primer	Genotype and allele	Breed (number of samples)			
		Bian (137)	Jinghai (50)	Youxi (30)	Arbor Acre (32)
MYOE1-3	DD	0.387 (53)	0.060 (3)	0.033 (1)	0.000 (0)
	DE	0.423 (58)	0.460 (23)	0.433 (13)	0.219 (7)
	EE	0.190 (26)	0.480 (24)	0.533 (16)	0.781 (25)
	Allele D	0.599	0.290	0.250	0.109
	Allele E	0.401	0.710	0.750	0.891
MYOE3-2	FF	0.825 (113)	0.780 (39)	0.767 (23)	1.000 (32)
	FG	0.175 (24)	0.220 (11)	0.233 (7)	0.000 (0)
	Allele F	0.912	0.890	0.883	1.000
	Allele G	0.088	0.110	0.117	0.000
MYOE3-3	HH	0.825 (113)	0.860 (43)	0.767 (23)	1.000 (32)
	HI	0.175 (24)	0.140 (7)	0.233 (7)	0.000 (0)
	Allele H	0.912	0.930	0.883	1.000
	Allele I	0.088	0.070	0.117	0.000

of 0.599. Allele E was dominant in Jinghai, Youxi, and Arbor Acre chickens. For primer MYOE3-2, allele F was dominant in all four breeds. For primer MYOE3-3, allele H was the dominant allele.

A chi-square test of independence of the myostatin gene (Table 3) showed that the genotype distribution was not consistent in the four chicken breeds. For primer MYOE1-3, the genotype distribution of the Bian chicken was significantly different from the three reference breeds ($P < 0.001$). For primers MYOE3-2 and MYOE3-3, the genotype distribution of the Bian chicken was consistent with that of the Jinghai and Youxi chickens. For the Arbor Acre chicken, the genotype distribution was significantly different from the other three breeds for the three primers ($P < 0.05$).

Table 3 Chi-square test of independence of the myostatin gene for four chicken breeds

Primer	Breed	Jinghai	Youxi	Arbor Acre
MYOE1-3	Bian	0.000	0.000	0.000
	Jinghai		0.818	0.000
	Youxi			0.000
MYOE3-2	Bian	0.487	0.458	0.011
	Jinghai		0.890	0.004
	Youxi			0.004
MYOE3-3	Bian	0.567	0.458	0.011
	Jinghai		0.287	0.027
	Youxi			0.004

Association of Genotypes with Body Weight Traits

According to the GLM analysis, the only significant association between the myostatin gene polymorphisms and body weight traits was found in the primer MYOE1-3 results (Table 4). Chickens of the EE and DE genotypes had significantly higher body weight than those of the DD genotype. Chickens of the EE genotype had the highest body weight, and DD had the lowest. The difference in body weight traits between the DE and EE genotypes was not significant ($P > 0.05$). For primer MYOE3-2, no significant difference in body weight traits was detected between genotypes FF and FG, and the body weights of the chickens of the two genotypes were similar (Table 5). For primer MYOE3-3, the differences between genotypes HH and HI were also not significant (Table 6).

Table 4 Association of genotype with body weight traits for MYOE1-3 in female Bian chickens

Age	Least square means of weight in grams ± standard error, by genotype		
	DD ($N = 53$)	DE ($N = 58$)	EE ($N = 26$)
Hatch	35.04 ± 0.54	35.93 ± 0.51	34.92 ± 0.77
6 weeks	411.02 ± 7.77^{Bb}	438.09 ± 7.43^{ABa}	449.77 ± 11.10^{Aa}
8 weeks	559.60 ± 9.51^{B}	606.33 ± 9.09^{A}	615.89 ± 13.57^{A}
10 weeks	723.02 ± 13.09^{b}	769.35 ± 12.52^{a}	777.73 ± 18.69^{a}
12 weeks	875.40 ± 15.39^{B}	943.62 ± 14.71^{A}	959.92 ± 21.97^{A}
14 weeks	1036.81 ± 18.99^{B}	1110.71 ± 18.16^{A}	1137.12 ± 27.12^{A}
16 weeks	1141.74 ± 21.81^{B}	1230.81 ± 20.84^{A}	1263.08 ± 31.13^{A}
18 weeks	1228.87 ± 23.80^{Bb}	1312.02 ± 22.75^{ABa}	1363.04 ± 33.97^{Aa}

Means with different lowercase superscripts differ significantly ($P < 0.05$); means with different capital superscripts differ very significantly ($P < 0.01$)

Table 5 Association of genotype with body weight traits for MYOE3-2 in female Bian chickens

Age	Least square means of weight in grams ± standard error, by genotype	
	FF ($N = 113$)	FG ($N = 24$)
Hatch	35.61 ± 0.37	34.38 ± 0.80
6 weeks	428.59 ± 5.50	435.67 ± 11.93
8 weeks	588.52 ± 6.88	597.33 ± 14.93
10 weeks	753.16 ± 9.22	752.33 ± 20.01
12 weeks	916.65 ± 11.02	937.63 ± 23.91
14 weeks	1082.55 ± 13.50	1108.71 ± 29.29
16 weeks	1196.51 ± 15.56	1230.54 ± 33.75
18 weeks	1281.96 ± 16.89	1325.21 ± 36.64

Table 6 Association of genotype with body weight traits for MYOE3-3 in female Bian chickens

Age	Least square means of weight in grams ± standard error, by genotype	
	HH ($N = 113$)	HI ($N = 24$)
Hatch	35.56 ± 0.37	34.63 ± 0.80
6 weeks	429.35 ± 5.50	432.08 ± 11.94
8 weeks	589.18 ± 6.88	594.25 ± 14.94
10 weeks	754.76 ± 9.21	744.79 ± 19.99
12 weeks	918.54 ± 11.04	928.71 ± 23.96
14 weeks	1086.68 ± 13.53	1089.25 ± 29.36
16 weeks	1200.09 ± 15.60	1213.71 ± 33.84
18 weeks	1285.37 ± 16.94	1309.13 ± 36.75

Discussion

Polymorphsims of the Myostatin Gene

In cattle, the phenotype known as DM (double muscling) is attributed to mutations in the myostatin gene, which exerts a regulatory influence on muscle deposition. Several mutations have been identified that could be responsible for this phenotype in various cattle breeds (Grobet et al. 1997; Kambadur et al. 1997; Gill et al. 2009). In other animals, Li et al. (2002) detected mutations in exons 2 and 3 in the swine myostatin gene; Hickford et al. (2009) reported a g.+6723G-A SNP in the myostatin gene of New Zealand Texel sheep; Zheng et al. (2008) found two SNPs located in the promoter region of the myostatin gene (T769G, C543T) and one in intron 1 (A1632G) in 10 goose breeds. There has been little research on polymorphsims of the gene in chickens. Gu et al. (2002), using PCR–SSCP, scanned the 5′ regulatory region, the 3′ regulatory region, and part of the coding regions of the chicken myostatin gene. They detected five SNPs (G167A, T177C, G304A, A322G, and C334T) in the 5′ regulatory region and two (A6935G and A7263T) in the 3′ regulatory region, in different chicken lines. They detected no polymorphism in the exon 1 region, although the breeds they sampled also included the Arbor Acre chicken, which was used as a reference breed in our research.

We scanned the SNPs in exon regions of the myostatin gene in the Bian chicken. The products amplified by primers MYOE1-3, MYOE3-2, and MYOE3-3 displayed polymorphisms. Genotype DD was not detected in the Arbor Acre chicken for primer MYOE1-3, and the Arbor Acre chicken was monomorphic for primers MYOE3-2 and MYOE3-3. The three Chinese native breeds, therefore, demonstrated richer polymorphism than the Arbor Acre breeds at these loci. Although the four mutations (G2283A, C7552T, C7638T, and T7661A) found in our research were in the exon regions, three were at the noncoding region of the exons. The only variant in the coding region of exon 1 was a synonymous mutation (G2283A), which thus did not cause the amino acid change. Among the four mutations, three were transitions (G2283A, C7552T, and C7638T) and one was a transversion (T7661A).

We did not detect the two mutations found by Gu et al. (2002; A6935G and A7263T), but we found four novel ones.

Relationship of the Myostatin Gene with Some Economic Traits

The myostatin gene has been under strong selection in a number of cattle breeds because of its influence on muscle conformation and association with the double-muscling phenotype (Wiener et al. 2009). Sellick et al. (2007) and Esmailizadeh et al. (2008) found that a leucine–phenylalanine substitution in the myostatin gene was positively associated with meat weight, silverside percentage, eye muscle area, and meat percentage in a crossbred Limousin × Jersey population. Wiener et al. (2009) found that the mh (muscle hypertrophy) allele was associated with increased calving difficulty, carcass weight, muscle conformation, and ratio of polyunsaturated to saturated fatty acids, as well as with reduced growth rate, carcass and meat fatness, and desirable flavor. Hickford et al. (2009) reported an association between a g.+6723G-A SNP in the myostatin gene and carcass traits in New Zealand Texel sheep. In chickens, research focusing on the relationship between the myostatin gene and economic traits is scarce. Ijiri et al. (2009) reported the roles of the myostatin gene in the increase of skeletal muscle and transformation of fiber type in cold-exposed chicks. Gu et al. (2003) studied the effects of SNPs of the regulatory region on slaughter traits of chickens, concluding that the myostatin gene not only regulated the skeletal muscle development but also participated in fat metabolism and deposition.

Our analysis detected no significant difference in body weight traits between genotypes for primers MYOE3-2 and MYOE3-3. The findings from the least square means of genotypes DD, DE, and EE for primer MYOE1-3 were the most interesting. Bian chickens of the EE and DE genotypes had significantly higher body weight than chickens of the DD genotype from 6 to 18 weeks of age ($P < 0.05$). Allele E was the additive gene for body weight traits. A study by Casas et al. (1998) showed that cattle inheriting a single copy of the mutant mh allele from a crossbred Belgian Blue or crossbred Piedmontese sire had increased longissimus muscle area and retail yield, with reduced external and intramuscular fat deposition, compared with animals receiving no copies of the mutant mh allele. Our results show that female Bian chickens with the mutant allele have increased body weight by 27.07 g (at 6 weeks old) to 89.07 g (16 weeks), compared with the wild type. The female homozygotes carrying two copies of the mutant allele have increased body weight by 38.75 g (6 weeks) to 134.17 g (18 weeks). The difference between genotypes DE and EE was not significant ($P > 0.05$). The Arbor Acre chicken is internationally known for its rapid growth and high body weight; the frequency of the favorable genotype (EE, 0.781) and allele (E, 0.891) may be responsible for the high body weight of this breed. This is a synonymous mutation and does not cause amino acid change; we speculate that it functions as a negative regulator by depressing the expression of the myostatin gene in the female Bian chicken.

Our research detected four novel mutations in the exon regions of the myostatin gene in the female Bian chicken, using the Jinghai, Youxi, and Arbor Acre chickens as reference populations. The results suggest that the myostatin gene has certain

effects on body weight traits in the female Bian chicken and that the mutation G2283A has the potential to be a genetic marker for body weight traits in the female Bian chicken.

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