Gene Effects on Body Weight, Carcass Yield, and Meat Quality of Thai Indigenous Chicken

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The selection of rapidly growing animals in breeding programs has had inadvertent detrimental effects on meat quality. Thus, the aim of the present study was to investigate the relationship between body weight (BW) and meat quality traits, and the effects of genes encoding insulin-like growth factor I (IGF-I), insulin-like growth factor II (IGF-II), melanocortin-4 receptor (MC4R), and calpain 1 (CAPN1) on BW, carcass yield, and meat quality of the Thai indigenous chicken, Leung Hang Khao. Five hundred and ten chickens were used for genotyping. PCR-restriction fragment length polymorphism and PCR-single strand conformation polymorphism were used to determine the genotypes of IGF-I, IGF-II, MC4R, and CAPN1. BWs were collected from 0–16 weeks of age. The chickens were sacrificed at 16 weeks and individual carcass yields and meat qualities (drip loss, cooking loss, and shear force) were recorded. The correlations between BW and meat qualities were determined. Significant correlation between BW and cooking loss and shear force of breast meat and between BW and drip loss of thigh meat were detected ($P<0.05$); however, the magnitude of the association was low ($-0.1$–$0.1$). IGF-I was eliminated from the association analysis because genotype AA was lost and the frequency of occurrence of the AC genotype was low (0.04). Significant associations between IGF-II, CAPN1, and BW, and CAPN1 and meat quality were detected, while non-significant association between MC4R and BW was observed. The results indicated a low, negative relationship between BW and meat quality, and that the IGF-II and CAPN1 could be used as genetic markers in Leung Hang Khao chickens to improve growth and meat quality through breeding.

Key words: body weight, calpain 1, indigenous chicken, insulin-like growth factor I-II, meat quality, melanocortin-4 receptor

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Introduction

Genetic engineering for improving the performance of indigenous chicken is currently a significant issue for developing countries, particularly in Asia, which is a major source of genetically diverse indigenous chickens. Food security and the accessibility of small holder farmers to good breeding practices are important issues for animal husbandry-based industries.

In 2001, the Thailand Research Fund (TRF) and the Department of Livestock Development (DLD) cooperated to collect four varieties of Thai indigenous chickens from around the country, namely, Leung Hang Khao (LHK), Pradoo Hang Dam, Chee, and Deang. Each variety was maintained at different breeding centers of the DLD; LHK, Pradoo Hang Dam, Chee, and Deang were reared at the Kabinburi Livestock Research and Breeding Center in the eastern region, the Chiang Mai Livestock Research and Breeding Center in the northern region, the Tha Pra Livestock Research and Breeding Center in the northeastern region, and the Surat Thani Livestock Research and Breeding Center in the southern region, respectively.

Desired meat texture and flavor are the main advantages of Thai indigenous breeds (Teltathum and Mekchay, 2010). Moreover, the LHK chicken has yellow skin, which is attractive to consumers. However, their slow growth rate compared to that of commercial breeds is an obvious disadvantage, which increases the cost of production. Therefore, from a commercial point of view, improvement of growth performance via genetic manipulations is necessary while maintaining the existing meat quality.

More than 50 years of genetic selection has lead to the development of commercial broiler chickens with rapid growth rate (attaining 2.5–3.0 kg in 37–40 days) (Zerehdaran et al., 2004) and high feed efficiency (Havenstein, 2006).
However, the flavor and texture of the produced meat has deteriorated because of the rapid growth (Dransfield and Sosnicki, 1999). This problem highlights the need for animal breeders to better understand the relationships among various economically desirable traits when designing a breeding program.

Previous studies have concluded that growth, carcass yield, and meat quality traits are negatively correlated. Dransfield and Sosnicki (1999) reported that an increase in growth rate in chickens might induce morphological abnormalities, larger fiber diameters, higher proportions of glycolytic fibers, and lower proteolytic potential in the muscle, which might lower the meat quality. Their findings were in accordance with the results of Duclos et al. (2007), who reported that lean chickens have lower levels of glycolytic stores than fat chickens, which consequently reduced exudation and post-mortem acidification of meat. This is a direct consequence of the speed of growth. Moreover, an indirect effect of higher growth rate is increase in stress, which results in histological and biochemical modifications of the muscle tissue, impairing meat quality (Petracci and Cavani, 2011). These studies provided evidence regarding the antagonistic relationship between growth and meat quality traits. Determining this relationship in an unselected population of LHK chickens is necessary to develop a breeding scheme.

Numerous studies on genetic markers have been performed, such as those by Li and Li (2006), Zhang et al. (2008), Wang et al. (2009), and Promwatee et al. (2011). However, their use in selection programs is not well understood, particularly the relationship between genes that control different economically desirable traits, which might be negatively correlated. In the current study, the genes encoding insulin-like growth factor I (IGF-I), insulin-like growth factor II (IGF-II), melanocortin-4 receptor (MC4R), and calpain 1 (CAPN1) were used to study the relationship between growth, carcass yield, and meat quality traits. 

IGF-I, IGF-II, MC4R, and CAPN1 (accession numbers: M74176, AY 267181, AY 545056 and NC_006090.1, respectively) are located on chromosome 1 (Kajimoto and Rotwein, 1991; Klein et al., 1996), chromosome 5 (Darling and Brickell, 1996; Yokomine et al., 2001), chromosome 2 (Takeuchi and Takahashi, 1998), and chromosome 3 (Zhang et al., 2008), respectively. IGF-I and IGF-II stimulate proliferation, differentiation and metabolism of myogenic cell lines from different species (Florini et al., 1996). IGFs regulate body and muscle growth in chickens (Duclos et al., 1999), whereas MC4R controls food intake, energy balance, and body weight (Li and Li, 2006). MC4R is significantly associated with carcass and meat quality traits (Wang et al., 2009). Regulation of CAPN1 activity is associated with variation in meat tenderness (Geesink and Koolhaar, 1999), and CAPN1 has been associated with live weight, carcass weight, breast muscle weight, and leg muscle weight (Zhang et al., 2008).

Thus, the objective of this study was to investigate the relationship between body weight and meat quality, as well as between IGF-I, IGF-II, MC4R, and CAPN1 and body weight, carcass yield, and meat quality in LHK chickens. The results of this study will be useful for designing breeding programs for LHK and other indigenous chickens in Thailand and developing countries that harbor different varieties of indigenous chicken.

Materials and Methods

Animal and Data Collection

The indigenous chickens used in this study were LHK. They were collected from around the country in 2001, delivered to the DLD and raised in the Kabinburi Livestock Research and Breeding Center. Random mating was used to produce the replacement flock. In 2009, 60 LHK males and 300 LHK females were drawn from the flock and moved to the Suranaree University of Technology. Random mating of this parent stock was used to produce 600 LHK chicks for this study. Each chicken was tagged with an ID for individual data collection.

The chicks were raised conventionally, with free access to a starter diet (21% crude protein) from hatching to 3 weeks of age. Thereafter, they received a grower diet (19% crude protein) from 3 to 6 weeks of age, and a finisher diet (17% crude protein) from 6 weeks of age to slaughter. At 16 weeks of age, their average body weight reached the market size of 1.4–1.5 kg.

At 16 weeks of age, the chickens were fasted for 10 h before being weighed and slaughtered by manual exsanguination. The dressing-out percentage, abdominal fat, breast meat (pectoralis major) and thigh meat (biceps femoris) were weighed. The dressing-out percentage was calculated as the ratio between the dressing-out weight and live weight after fastening. The percentages of breast meat, leg meat, and abdominal fat were calculated as a percentage of the dressing-out weight.

The percentage drip loss was measured for raw meat samples weighing approximately 4–5 g, cut into pieces with dimensions of approximately 1.0×2.0×0.5 cm (width, length, and height, respectively). The breast and thigh meat samples were trimmed at both ends and weighed before and after storage. The samples were wrapped in absorption pads and placed in polyethylene bags before being hung on hooks in a refrigerator for 24 h and 48 h at 4°C. Drip loss percentages were calculated as:

\[
\frac{\text{Weight before storage} - \text{Weight after storage}}{\text{Weight before storage}} \times 100
\]

Shear force was measured on cooked breast and thigh meat according to the method of Dawson et al. (1991). Both parts of the meat were boiled until the core temperature was 78–80°C in 10 min, before being cut into pieces with dimensions of of approximately 1.0×2.0×0.5 cm (width, length, and height, respectively). A TA-XT2 texture analyzer (Stable Micro System, Godalming, UK) with a Warner-Bratzler shear apparatus was used. The operating parameters consisted of a cross-head speed of 2 mm/s and a 5 kg load cell. The descriptive data for all traits measured in the study are shown in Table 1.

The numbers of samples shown in Table 1 were 510, 500,
and 317 for body weight, carcass yield, and meat qualities, respectively. The reasons behind the variations in sample number were unidentified ID and outlier records for certain samples, which were eliminated from the analysis. Moreover, the number of body weights used for relationship analysis (504) was slightly different from the number of body weights shown in Table 1 (510) because the samples could not be identified with their ID.

In this study, we assumed normality of data; therefore, some data, for example, percentage of abdominal fat, breast meat, thigh meat, total meat, and drip loss of breast and thigh meat at 24 h and 48 h were transformed using the common logarithm (log10). The exception was percentage of abdominal fat, which had some data points equal to zero. Therefore, 1 was added to each value and they were then transformed by log10. After completion of statistical analysis, all transformed data were back-transformed with $10^{X'} - 1$ for percentage of abdominal fat, where $X'$ is the transformed data.

All experimental procedures were approved by the Institutional Animal Care and Use Committee of the Suranaree University of Technology (The certificate ID: 24/2555).

**Genotyping**

Blood samples were collected from 510 LHKS. Genomic DNA was extracted from whole blood using a DNA mini kit for blood per manufacturer’s instructions (Geneaid Biotech Ltd, New Taipei City, Taiwan). DNA was quantified spectrophotometrically and diluted to $10 \mu g/\mu l$.

The genotypes of *IGF-I* and *IGF-II* were analyzed using PCR-restriction fragment length polymorphism (PCR-RFLP), as reported by Zhou *et al.* (2005) and Amills *et al.* (2003), respectively.

The genotypes of *MC4R* and *CAPN1* were analyzed using PCR-single strand conformation polymorphism (PCR-SSCP), as described by Wang *et al.* (2009) and Zhang *et al.* (2008), respectively.

**Statistical Analysis**

Linkage disequilibrium (LD) between *IGF-II* and *MC4R*, *IGF-II* and *CAPN1*, and *MC4R* and *CAPN1* were analyzed using GENEPOP version 3.4 (Raymond and Rousset, 2003).

| Trait          | Number of samples (N) | Mean | SD  | Min | Max |
|----------------|-----------------------|------|-----|-----|-----|
| **Body weight**|                       |      |     |     |     |
| 0 week         | 32.8                  | 3.25 | 23  | 42  |     |
| 2 weeks        | 86.1                  | 16.64| 32  | 143 |     |
| 4 weeks        | 208.8                 | 41.06| 65  | 435 |     |
| 6 weeks        | 385.3                 | 73.13| 170 | 920 |     |
| 8 weeks        | 588.2                 | 116.8| 260 | 1280|     |
| 10 weeks       | 827.2                 | 153.7| 380 | 1750|     |
| 12 weeks       | 1065.8                | 205.94| 460 | 2100|     |
| 14 weeks       | 1211.1                | 215.71| 400 | 1900|     |
| 16 weeks       | 1457.6                | 264.3| 580 | 2260|     |
| **Carcass yield**|                      |      |     |     |     |
| Dressing %     | 66.34                 | 2.66 | 50.85| 82.86|     |
| AbF %          | 0.64                  | 0.67 | 0.00 | 5.48 |     |
| BM %           | 12.35                 | 1.40 | 6.73 | 22.61|     |
| TM %           | 15.39                 | 1.47 | 5.96 | 29.44|     |
| ToM %          | 27.74                 | 2.29 | 18.93| 48.57|     |
| **Meat quality**|                       |      |     |     |     |
| 24 h drip % B  | 2.64                  | 0.64 | 1.09 | 4.97 |     |
| 48 h drip % B  | 2.16                  | 0.58 | 0.82 | 4.28 |     |
| 24 h drip % T  | 2.18                  | 0.39 | 1.31 | 4.09 |     |
| 48 h drip % T  | 1.88                  | 0.35 | 1.07 | 3.36 |     |
| Cooking % B    | 21.11                 | 2.12 | 11.19| 26.23|     |
| Cooking % T    | 26.57                 | 2.53 | 16.50| 35.39|     |
| SFB (g/mm)     | 148.96                | 41.09| 73.73| 280.42|     |
| SFT (g/mm)     | 108.59                | 28.03| 57.53| 214.59|     |

Percentage carcass yield: Dressing % - dressing-out percentage; AbF % - abdominal fat; BM % - breast meat, TM % - thigh meat, ToM % - total meat.

Percentage drip loss: 24 h drip % B - 24 h breast meat; 48 h drip % B - 48 h breast meat; 24 h drip % T - 24 h thigh meat; 48 h drip % T - 48 h thigh meat.

Percentage cooking loss: cooking % B - breast meat; cooking % T - thigh meat.

Shear force: SFB - breast meat; SFT - thigh meat.

Table 1. Characteristics for body weight, carcass yield traits, and meat quality traits of the Leung Hang Khao chickens used in this study
Groups of loci with significant associations were rearranged as composite genotypes. The significant effects of genotype or composite genotype on body weight, carcass yield, and meat quality were analyzed using a general linear model with sex, genotype, and interaction between sex and genotype as fixed effects. Analysis of variance was used to test the significance of differences between measured phenotypic traits in individual genotypes. The level of significance was defined at \( P < 0.05 \). SPSS for Windows (Release 10.0; SPSS Inc., Chicago, IL, USA) was used for the analysis.

Results and Discussion

Allelic and Genotypic Frequency

The allelic and genotypic frequencies of all genes are shown in Table 2. \textit{IGF-II}, \textit{MC4R}, and \textit{CAPN1} showed a potential for use as genetic markers in selection programs because there was more than one genotype at each locus and each genotype showed a suitable frequency. However, \textit{IGF-I} was eliminated from the analysis because the frequency of genotype \( CC \) exceeded 0.96, whereas the \( AC \) and \( AA \) genotypes were rare (0.04) and absent, respectively.

The low frequencies of the \( AA \) and \( AC \) genotypes of \textit{IGF-I} observed in the present study are in agreement with the results of Promwatee \textit{et al.} (2011), and Moe \textit{et al.} (2009), who studied other indigenous Thai chicken lines (Pradu Hang Dam and Chee), and indigenous chickens from Asian countries (Cambodia, Laos, and Myanmar). The results are in contrast with those obtained with commercial broilers (Moe \textit{et al.}, 2009; Kadlec \textit{et al.}, 2011). Based on these results, we speculated that the main role of \textit{IGF-I} in chickens involves growth, development, and adaptability.

Hardy-Weinberg Equilibrium and Linkage Disequilibrium (LD)

Significant deviations from the Hardy-Weinberg equilibrium (HWE) were detected for \textit{MC4R} and \textit{CAPN1}, while \textit{IGF-I} and \textit{II} remained in equilibrium (Table 2). The LHK population used was randomly mated and there was no migration. However, historically, the breed was selected by farmers for cock-fighting purposes, who tended to select the stronger chickens. The allele set involved in determining these traits would thus have been indirectly selected for and passed on to the next generation. This may provide an explanation for the deviation of the genes involved in growth from the HWE. Significant associations of \textit{MC4R} with growth performance were reported by Li and Li (2006) and Qiu \textit{et al.} (2006). \textit{CAPN1} also deviated significantly from the HWE. These could be explained if these genes are involved in growth or another mechanism, which could have been affected by selection; however, this speculation should be investigated in future experiments.

In the case of \textit{IGF-I}, low frequency of the \( A \) allele may be common in native chickens, because natural or long periods of indirect selection almost annihilate the \( A \) allele and fix the \( C \) allele fixed. As a consequence, this locus is still in HWE. Meanwhile, for \textit{IGF-II}, it is possible that the allelic frequencies were not affected by any kind of selection.

LD is non-random association of alleles at different loci. In the present study, significant LD was not observed. Therefore, single loci were used as genetic markers.

Correlation between Final Body Weight and Meat Quality

The final body weight showed significant negative and positive correlations with cooking loss and the shear force of breast meat, respectively. For thigh meat, we observed sig-
significant positive correlations between body weights and drip loss after 24 and 48 h of storage. However, despite the significance of these associations, the correlation coefficients were all relatively low. No significant correlation between body weights, drip loss of breast meat at 24 and 48 h, cooking loss, and shear force of thigh meat were observed. The results are presented in Table 3.

Weak and no correlation between body weight and meat qualities might be explained by the high association of growth rate with the toughness of the meat, fiber size (Dransfield and Sosnicki, 1999; and Zhao et al., 2011), and drip loss (Dransfield and Sosnicki, 1999). However, there was a high degree of genetic variation in the chickens used in the present study, as they were drawn from an unselected population of LHK chickens, while the same genetic background of chickens were used by Zhou et al. (2011). This might explain the discrepancy in the results of our study and those of previous studies. Moreover, the correlations between breast and thigh meat also varied as different fiber types and size cause differences in metabolism (aerobic and anaerobic) and texture of meat (Dransfield and Sosnicki, 1999; and Listat et al., 2016), which might explain our results.

Relationship between IGF-II and Body Weight, Carcass Yield, and Meat Quality Traits in LHK Chickens

Genotype had a significant effect on body weight at 16 weeks of age (P value < 0.05) (Table 4). However, the genotypes did not differ significantly for carcass yield or meat quality (Tables 5 and 6).

The results for body weight are in agreement with those of previous studies (Darling and Brickell, 1996; Dransfield and Sosnicki, 1999), which confirm that IGF-II plays a major role in chicken growth and development by stimulating proliferation, differentiation, and metabolism of myogenic cell lines (Florini et al., 1996). The results are in contrast with those of Amills et al. (2003), who studied the same region of the gene (exon 3). The significant effect may be attributed to a C to T substitution; the current results imply that this substitution may lead to differences in peptide sequence, which may alter the activity of the hormone. Thus, differences in the genetic structure of the populations

Table 3. Correlation coefficient between body weight and meat quality of Leung Hang Khao chickens

| Gene   | Number of chickens | 0 wk | 2 wks | 4 wks | 6 wks | 8 wks | 10 wks | 12 wks | 14 wks | 16 wks |
|--------|--------------------|------|------|------|------|------|------|------|------|------|
| IGF-II |                    |      |      |      |      |      |      |      |      |      |
| AA     | 126                | 33.33| 82.61| 199.57| 382.35| 586.24| 821.84| 1062 | 1152 | 1413B |
|        |                    | (0.27)| (1.33)| (3.60)| (6.42)| (10.24)| (13.03)| (16.04)| (19.14)| (20.91) |
| AB     | 252                | 32.96| 84.19| 209.30| 384.08| 589.14| 827.84| 1076 | 1190 | 1452AB |
|        |                    | (0.20)| (0.96)| (2.59)| (4.55)| (7.20)| (9.29)| (11.40)| (14.05)| (14.43) |
| BB     | 126                | 33.30| 84.17| 204.84| 386.59| 590.56| 832.53| 1081 | 1202 | 1484B |
|        |                    | (0.27)| (1.36)| (3.61)| (6.46)| (10.12)| (13.06)| (16.05)| (17.99)| (20.31) |
| P-value|                    | 0.43| 0.59| 0.08| 0.77| 0.95| 0.81| 0.69| 0.11| 0.05 |

Table 4. Least square means and standard errors of body weight (grams) in Leung Hang Khao chickens

| Gene | Number of chickens | 0 wk | 2 wks | 4 wks | 6 wks | 8 wks | 10 wks | 12 wks | 14 wks | 16 wks |
|------|--------------------|------|------|------|------|------|------|------|------|------|
| A1A1 | 296                | 32.49B | 87.62A | 208.60 | 378.62B | 580.16 | 820.59 | 1048 | 1214 | 1459 |
|      |                    | (0.19)| (0.97)| (2.40)| (4.14)| (6.47)| (8.35)| (10.66)| (10.97)| (12.19) |
| A1A2 | 77                 | 32.77AB | 83.25B | 206.01 | 379.74AB | 575.95 | 811.44 | 1052 | 1219 | 1479 |
|      |                    | (0.37)| (1.91)| (4.63)| (8.08)| (12.76)| (16.38)| (20.95)| (22.55)| (28.62) |
| A2A2 | 131                | 33.43A | 84.31AB | 209.72 | 397.57A | 604.94 | 85.60 | 1087 | 1173 | 1406 |
|      |                    | (0.28)| (1.48)| (3.62)| (6.30)| (9.97)| (12.67)| (16.08)| (18.64)| (22.90) |

A, B, C different letters indicate significant differences at P < 0.05.
wk – week.
used in this study with those used by Amills et al. (2003) and Zhang et al. (2008) might explain the inconsistent results.

Since IGF II is mainly associated with growth and muscle development, we expected significant differences in the quantity of meat produced in terms of carcass yield; however, our results were to the contrary. This could be explained by the differences in the magnitude of the effect of various genotypes on muscle development, which was negligible in our study. Hence, the C to T substitution may have had limited effect on muscle development. Alternatively, the genotype might affect the number of muscle fibers or fiber size. Duclos et al. (1999) showed that the IGFs regulate body and muscle growth. In the current study, however, these traits were not measured.

Toughness and tenderness are indicators of meat texture and quality. This can be measured using parameters such as drip loss and shear force. Dransfield and Sosnicki (1999) and Zhao et al. (2011) reported that growth rate is associated with muscle fiber size and number, and that fiber size is associated with toughness and tenderness. Additionally, Tesseraud et al. (2003) found high concentration of IGF-II in a high-quality chicken meat line. Therefore, growth rate is indirectly related to drip loss and shear force. In the current study, IGF-II showed significant effects on body weight, but non-significant effects on all meat quality traits. This may be because the differences in the growth rates of the chickens were not large enough to affect either fiber size or the number of muscle fibers. Alternatively, the absence of any significant effect might be explained if the traits measured in the current study, such as drip loss and shear force, depended not only on fiber size, but also on the presence of other biochemical compounds in meat, particularly collagen (Nakamura et al., 1975), which was not measured.

### Relationship between MC4R and Body Weight, Carcass Yield, and Meat Quality Traits in LHK Chickens

In contrast to the hypothesized role of MC4R, the genotypes did not differ significantly for any of the traits measured (Tables 4, 5, and 6). This is also in contrast to the results of Li and Li (2006), Qiu et al. (2006), and Wang et al. (2009), who reported that different genotypes were associated with significantly different carcass traits and body weights. For example, Wang et al. (2009) showed that the GT genotype had a superior effect than the GG and TT genotypes. On the contrary, Li and Li (2006) studied different regions of this gene and observed that the effects of homozygous genotypes were superior to those of heterozygous genotypes. Schwartz et al. (1996) investigated the role of the melanocortin 4 receptor and demonstrated that it was associated with the control of food intake, energy balance, and body weight. Moreover, it might be involved in certain aspects of lipid metabolism in chickens (McMurtry et al., 1997). Li and Li (2006) reported that different genotypes of MC4R, namely the AA and BB genotypes, showed differences in protein secondary structure, possibly resulting in
differences in its biological function. Thus, variations in animal genotype might manifest as different phenotypes. However, the chickens used in this study were taken from a relatively unselected population, which might explain the contrast between our results and those of previous studies. Each trait showed large variations, which exceeded the effect of the genotype. Thus, the observed differences were non-significant.

**Relationship between CAPN1 and Body Weight, Carcass Yield, and Meat Quality Traits in LHK Chickens**

Significant association between CAPN1 and body weight was detected at 0, 2, and 6 weeks of age ($P$ value = 0.02, 0.04, and 0.02, respectively) (Table 4), and the locus was also found to be significantly associated with percentage of drip loss at 48 h ($P$ value = 0.03) (Table 6). The A2A2 genotype had a positive effect on body weight at 0, 2, and 6 weeks of age, and it was also associated with improved drip loss.

Our results are consistent with those of Zhang et al. (2008), Felicio et al. (2013), and Shu et al. (2015), who studied different breeds of chickens. The results can be explained by the results of Goll et al. (2003), who reported that calpains are involved in muscle growth and development. Moreover, Koohmaraie (1996) also reported that CAPN1 degrades myofibrillar proteins under postmortem conditions and appears to be the primary enzyme in the postmortem tenderization process. This may explain the effect of this gene on the measured traits; however, the reasons for the variations in the effect of different CAPN1 genotypes remain unclear. Page et al. (2002) observed that mutations altered the amino acid sequence of the enzyme, which correlated with beef tenderness. It is possible that a similar phenomenon exists in chickens, the mechanism of which should be investigated in a future study.

The observations of this study suggest that meat quality may be negatively affected when growth performance is improved. Therefore, it is important that meat quality traits are monitored when selection for growth performance improvement is performed. Single loci could be used as genetic markers as no significant LD was detected. IGF-II and CAPN1 could be used as genetic markers when both growth improvement and meat quality are the main goals of breeding.

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References

Abdullah A and Matarneh S. Broiler performance and the effects of carcass weight, broiler sex, and postchill carcass aging duration on breast fillet quality characteristics. Journal of Applied Poultry Research, 19: 46–58. 2010.

Amills M, Jimenez N, Villalba D, Tor M, Molina E, Cubillo D, Marcos C, Francesch A, Sanchez A and Estany J. Identification of three single nucleotide polymorphisms in the chicken insulin-like growth factor I and 2 genes and their associations with growth and feeding traits. Poultry Science, 82: 1485–1493. 2003.

Darling DC and Brickell PM. Nucleotide sequence and genomic structure of the chicken insulin-like growth factor-II (IGF-II) coding region. General and Comparative Endocrinology, 102: 283–287. 1996.

Dawson P, Sheldon B and Miles J. Effect of aseptic processing on the texture of chicken meat. Poultry Science, 70: 2359–2367. 1991.

Decuyper E, Leenstra F, Buyse J, Huyberechts L, Buonomo F and Berghman L. Plasma levels of growth hormone and insulin-like growth factor-I and-II from 2 to 6 weeks of age in meat-type chickens selected for 6-week body weight or for feed conversion and reared under high or normal environmental temperature conditions. Reproduction Nutrition Development, 33: 361–372. 1993.

Dransfield E and Sosnicki A. Relationship between muscle growth and poultry meat quality. Poultry Science, 78: 743–746. 1999.

Duclos M, Becvacín C and Simon J. Genetic models for the study of insulin-like growth factors (IGF) and muscle development in birds compared to mammals. Domestic Animal Endocrinology, 17: 231–243. 1999.

Duclos M, Berri C and Le Bihan-Duval E. Muscle growth and meat quality. Journal of Applied Poultry Research, 16: 107–112. 2007.

Felicio A, Boschierno C, Balieiro J, Ledur M, Ferraz J, Michelan Filho T, Moura ASAMT and Coutinho L. Identification and association of polymorphisms in CAPN1 and CAPN3 candidate genes related to performance and meat quality traits in chickens. Genetics and Molecular Research, 12: 472–482. 2013.

Florini JR, Ewton DZ and Coolican SA. Growth hormone and the insulin-like growth factor system in myogenesis. Endocrine Reviews, 17: 481–517. 1996.

Geesink GH and Koohmaraie M. Effect of calpastatin on degradation of myofibrillar proteins by mu-calpain under postmortem conditions. Journal of Animal Science, 77: 2685–2692. 1999.

Goll DE, Thompson VF, Li H, Wei W and Cong J. The calpain system. Physiological Reviews, 83: 731–801. 2003.

Havenstein GB. Performance changes in poultry and livestock following 50 years of genetic selection. Lohmann Information, 41: 30–37. 2006.

Kadlec J, Hosnedlová B, Řehout V, Čítek J, Večerek L and Hanusová L. Insulin-like growth factor-I gene polymorphism and its association with growth and slaughter characteristics in broiler chickens. Journal of Agrobiology, 28: 157–163. 2011.

Kajimoto Y and Rotwein P. Structure of the chicken insulin-like growth factor I gene reveals conserved promoter elements. Journal of Biological Chemistry, 266: 9724–9731. 1991.

Klein S, Morrice D, Sang H, Crittenden L and Burt D. Genetic and physical mapping of the chicken IGF1 gene to chromosome 1 and conservation of synteny with other vertebrate genomes. Journal of Heredity, 87: 10–14. 1996.

Koohmaraie M. Biochemical factors regulating the toughening and tenderization processes of meat. Meat Science, 43: 193–201. 1996.

Li C and Li H. Association of MC4R gene polymorphisms with growth and body composition traits in chicken. Asian Australasian Journal of Animal Sciences, 19: 763. 2006.

Listrat A, Lebret B, Louveau I, Astruc T, Bonnet M, Lefaucheur L, Picard B and Bugeon J. How muscle structure and composition influence meat and flesh quality. Scientific World Journal, 2016:3182746. doi: 10.1155/2016/3182746. 2016.

Lu J, McMurtry J and Coon C. Developmental changes of plasma insulin, glucagon, insulin-like growth factors, thyroid hormones, and glucose concentrations in chick embryos and hatched chicks. Poultry Science, 86: 673–683. 2007.

McMurtry J, Francis G and Upton Z. Insulin-like growth factors in poultry. Domestic Animal Endocrinology, 14: 199–229. 1997.

Moe HH, Shimogiri T, Kawabe K, Nishibori M, Okamoto S, Hashiguchi T and Maeda Y. Genotypic frequency in Asian native chicken populations and gene expression using insulin-like growth factor 1 (IGF1) gene promoter polymorphism. Journal of Poultry Science, 46: 1–5. 2009.

Musa H, Chen G, Cheng J, Shuipe E and Bao W. Breed and sex effect on meat quality of chicken. International Journal Poultry Science, 5: 566–568. 2006.

Nakamura R, Sekoguchi S and Sato Y. The contribution of intramuscular collagen to the tenderness of meat from chickens with different ages. Poultry Science, 54: 1604–1612. 1975.

Page BT, Casas E, Heaton MP, Cullen NG, Hyndman DL, Morris CA, Crawford AM, Wheeler TL, Koohmaraie M and K eele JW. Evaluation of single-nucleotide polymorphisms in CAPN1 for association with meat tenderness in cattle12. Journal of Animal Science, 80: 3077–3085. 2002.

Petracci M and Cavani C. Muscle growth and poultry meat quality issues. Nutrients, 4: 1–12. 2011.

Promwatee N, Duangjinda M, Boonkum W and Loapaiboon B. Association of single nucleotide polymorphisms in GHSR, IGF1, cGH and IGFBP2 genes on growth traits in Thai Native Chickens (Chee and Pradu Hang Dam). Khon Kaen Agricultural Journal, 39: 261–270. 2011.

Qiu X, Li N, Deng X, Zhao X, Meng Q and Wang X. The single nucleotide polymorphisms of chicken melanocortin-4 receptor (MC4R) gene and their association analysis with carcass traits. Science in China Series C: Life Sciences, 49: 560–566. 2006.

Raymond M, and Rousett F. GENEPOP (version 3.4): population genetics software for exact tests and ecumenicism. Journal of Heredity, 86: 248–249. 2003.

Schneider B, Renema R, Betti M, Carney V and Zuidhof M. Effect of holding temperature, shackling, sex, and age on broiler
breast meat quality. Poultry Science, 91: 468-477. 2012.
Schwartz MW, Seeley RJ, Campfield LA, Burn P and Baskin DG. Identification of targets of leptin action in rat hypothalamus. Journal of Clinical Investigation, 98: 1101. 1996.
Shu J, Zhang M, Shan Y, Xu W, Chen K and Li H. Analysis of the genetic effects of CAPN1 gene polymorphisms on chicken meat tenderness. Genetics and Molecular Research, 14: 1393-1403. 2015.
Takeuchi S and Takahashi S. Melanocortin receptor genes in the chicken—tissue distributions. General and Comparative Endocrinology, 112: 220-231. 1998.
Teltathum T and Mekchay S. Relationships between Pectoralis muscle proteomes and shear force in Thai indigenous chicken meat. Kasetsart Journal (Natural Science), 44: 53-60. 2010.
Tesseraud S, Pym R, Le Bihan-Duval E and Duclos M. Response of broilers selected on carcass quality to dietary protein supply: live performance, muscle development, and circulating insulin-like growth factors (IGF-I and-II). Poultry Science, 82: 1011-1016. 2003.
Wang Y, Su Y, Jiang X, Liu Y, Li X, Zhang Z, Du H and Zhu Q. Study on association of single nucleotide polymorphism of MC3R and MC4R genes with carcass and meat quality traits in chicken. Journal of Poultry Science, 46: 180-187. 2009.
Yokomine T, Kuroiwa A, Tanaka K, Tsuzuki M, Matsuda Y and Sasaki H. Sequence polymorphisms, allelic expression status and chromosome locations of the chicken IGF2 and MPR1 genes. Cytogenetic and Genome Research, 93: 109-113. 2001.
Zerehdaran S, Vereijken ALJ, Van Arendonk JAM, and Van der Waaij EH. Estimation of genetic parameters for fat deposition and carcass traits in broilers. Poultry Science, 83: 521-525. 2004.
Zhang ZR, Liu YP, Jiang X, Du HR and Zhu Q. Study on association of single nucleotide polymorphism of CAPN1 gene with muscle fibre and carcass traits in quality chicken populations. Journal of Animal Breeding and Genetics, 125: 258-264. 2008.
Zhao G, Cui H, Liu R, Zheng M, Chen J and Wen J. Comparison of breast muscle meat quality in 2 broiler breeds. Poultry Science, 90: 2355-2359. 2011.
Zhou H, Mitchell A, McMurtry J, Ashwell C and Lamont SJ. Insulin-like growth factor-I gene polymorphism associations with growth, body composition, skeleton integrity, and metabolic traits in chickens. Poultry Science, 84: 212-219. 2005.