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ORIGINAL ARTICLE

Selection against abdominal fat percentage may increase intramuscular fat content in broilers

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Keywords

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Summary

Excessive abdominal fat content (AFC) has negative impacts on feed efficiency and carcass quality. Unlike AFC, intramuscular fat content (IMFC) could be a favourable trait, which has a positive impact on meat quality. To meet consumers' needs, a long-term goal of broiler breeders is to decrease AFC and improve the IMFC simultaneously. The current study was designed to investigate the relationship between AFC and IMFC and to compare IMFC, including the pectoral major muscle fat content (PIMFC) and intramuscular fat content of leg muscle (LIMFC), between two broiler lines divergently selected for abdominal fat percentage over 17 generations. The results showed that there was a significant difference in PIMFC and LIMFC between the two lines in all five generation populations used. The birds in the lean line had significantly lower AFC but higher PIMFC and LIMFC than the birds in the fat line. We also detected differences in the liver fat content (LFC) between the two lines and the results showed that birds in the fat line had significant higher LFC than birds in the lean line. Our results indicated that a desirable broiler line with higher IMFC but lower AFC could be obtained by genetic selection.

Introduction

Poultry production is an important component of agriculture. Poultry products including eggs and meat are a healthy part of human diets. Intensive selection for growth in broilers has increased their growth rate at an unprecedentedly level. However, long-term intense selection for fast juvenile growth in broiler chickens has increased their abdominal fat content (AFC) and resulted in metabolic changes (Emmerson 1997; Scheele 1997; Julian 2005). Excessive deposition of abdominal fat has negative impacts on feed efficiency and carcass quality (Demeure *et al.* 2013; Ramiah *et al.* 2014). Therefore, broiler breeders worldwide have focused on the selection of more efficient lean broiler lines (Decuypere *et al.* 2010; Zuidhof *et al.* 2014).

Unlike AFC, the intramuscular fat content (IMFC) could be a favourable trait. In animals, IMFC not only is the meat quality trait with the most economic importance, but also has a positive impact on meat characteristics such as tenderness, flavour and juiciness (Gerbens *et al.* 2001). The results of previous studies showed that increasing IMFC could improve muscle tenderness and flavour (Eikelenboom *et al.* 1996; Costa *et al.* 2012; Bonny *et al.* 2015). Therefore, IMFC was used as an important indicator of meat quality.

Broiler breeders have given attention to abdominal fat to improve both meat quality and efficiency of feed conversion (Li *et al.* 2013). Previous studies showed that there were no significant differences of IMFC in leg muscle (Ricard *et al.* 1983) or breast muscle (Sibut *et al.* 2008) between two lines divergently selected for abdominal fat percentage. This may be because abdominal fat deposition and intramuscular fat are subject to different regulatory mechanisms (Li *et al.*

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2013). The aims of this study were to compare IMFC between two broilers lines divergently selected for abdominal fat percentage for 17 generations and to investigate the relationship between AFC and IMFC.

Materials and methods

Ethics statement

All animal work was conducted according to the guidelines for the Care and Use of Experimental Animals established by the Ministry of Science and Technology of the People's Republic of China (approval number: 2006-398) and approved by the Laboratory Animal Management Committee of Northeast Agricultural University.

Experimental populations

The broilers used in this study were derived from the Northeast Agricultural University (NEAU) broiler lines divergently selected for abdominal fat content (NEAUHLF) which were named as the lean and fat lines. The lean and fat lines have been selected since 1996, using abdominal fat percentage (AFP) and plasma very low-density lipoprotein (VLDL) concentration as selection criteria. AFP was calculated as the ratio of abdominal fat weight (AFW) to body weight at 7 weeks of age (BW7). A previously published study by our group described the breeding scheme in detail (Guo *et al.* 2011). There were significant differences in AFW and AFP between the lean and fat lines from the 4th generation onwards.

Trait measurement

In this study, a total of 2211 male birds randomly selected from the 8th, 13th, 14th, 15th and 17th generation populations of NEAUHLF (Table 1) were slaughtered at 7 weeks of age after 12-h fasting, and BW7, AFW and AFP were measured. Approximately 20–30 g pectoralis major (the upper part of pectoralis muscle, left side of the body), leg muscle (the thigh muscle, left side of the body) and liver (left side of the body) tissues of each individual were dissected. These tissues were immediately stored at −20°C for further use. The pectoralis major, leg muscle and the liver tissue were minced thoroughly after being thawed and dried in two 12-h stages (65°C, then 105°C), followed by cooling in a desiccator for at least 30 min. The intramuscular fat content of pectoral major muscle (PIMFC), intramuscular fat content of leg muscle (LIMFC) and liver fat content (LFC) were determined by extraction with petroleum ether in a Soxhlet apparatus (Zerehdaran *et al.* 2004) and expressed as percentages on the basis of weight of dry muscle samples.

Statistical analysis

Statistical differences of AFW, AFP, PIMFC, LIMFC and LFC between birds from the lean and fat lines of every generation were analysed using JMP version 7.0 (SAS Institute, Cary, NC) with Model 1. We also combined the data from all five generations for the statistical analysis and using Model 2 to carry out the difference analysis, which included generation as the fixed effect.

$$Y_{ijkl} = \mu + L_i + S_j(L) + D_k(S, L) + \mathrm{BW7} + e_{ijkl} \quad \text{(Model 1)}$$

$$y_{ijklm} = \mu + L_i + G_j + L_i * G_j + S_k(L, G) + D_l(S, L, G) + \mathrm{BW7} + e_{ijklm} \quad \text{(Model 2)}$$

where y is the phenotypic value of AFW, AFP, PIMFC, LIMFC and LFC, μ is the population mean, L is the fixed effect of the line, G is the fixed effect of the generation, $L*G$ is the interaction effect of line by generation, S (L) is the random effect of sire within line, S (L, G) is the random effect of sire within line and generation, D (S, L) is the random effect of dam within sire and line, D (S, L, G) is the random effect of dam within sire, line and generation, BW7 is treated as a covariate (BW7 was not used as the covariate when analysing AFP), and e is the random residual effect. The differences between the least squares means of phenotypes of the lean and fat lines were calculated, and $p < 0.05$ was used to indicate significant difference.

The genetic and phenotypic correlations between AFC, IMFC and LFC were estimated using MTDFREML software (http://aipl.arsusda.gov/curtvt/mtdfreml.html), with generation and line treated as two fixed effects. The bivariate model was used to

Table 1 Number of male birds selected from the 8th, 13th, 14th, 15th and 17th generation populations that are used in the current study

Generations	Lean line	Fat line	Total
G8	216	164	380
G13	173	180	353
G14	320	291	611
G15	152	153	305
G17	329	233	562
Total	1190	1021	2211

calculate the genetic and phenotypic correlations. The standard errors (SE) of correlations between IMFC, LFC and AFC were approximated as described in Falconer & Mackay (1996).

The genetic model used for parameter estimations is described as follows:

$$y = X\beta + Zu + e \qquad \text{(Model 3)}$$

in which y is an n-dimensional vector of observed values for the traits, X is an n × p matrix of the fixed effects, β is a p-dimensional vector of the fixed effects, Z is an n × q matrix of the random effects, u is a q-dimensional vector of the random genetic effects, and e is an n-dimensional vector of the random residual effects. The random effects u and e were assumed to follow the normal distributions with mean 0, that is, Expectation [y] = Xβ. The variances of u and e were assumed to be Var(u) = Ag and Var(e) = Ir, respectively, in which A is the numerator relationship matrix of all animals in the pedigree file, g is the additive genetic variance–covariance matrix between traits for the bivariate model analysis, I is the identity matrix of order equal to the number of animals with phenotypes, and r is the variance–covariance matrix between residuals on the same animal when performing the bivariate model analysis, where residual covariance equal to 0 (Dong *et al.* 2015). The statistical significance of the correlation data was estimated using the *t*-test.

Results

Differences in AFC between the birds in lean and fat lines

The lean and fat lines were divergently selected for AFP over 17 generations, and the AFP between the two lines was significantly different from the 4th generation onwards. There were 380, 353, 611, 305 and 562 individual males, respectively, from the 8th, 13th, 14th 15th and 17th generation populations randomly selected to detect the IMFC and LFC (Table 1). We first compared the differences of AFC (AFW and AFP) between the experimental birds from the lean and fat lines in each generation using Model 1. The result showed that the birds in the fat line had significantly ($p < 0.05$) higher AFW and AFP than the birds in the lean line in all five generations (Figure 1a, b). The differences of AFW and AFP between the birds in the lean and fat lines increased with the generations. In other words, the AFW and AFP increased in the fat line, and decreased in the lean line with each generation (Figure 1a, b). We then combined the data from all generations for the statistical analysis and using Model 2 to carry out the difference analysis. The result from the combined data also showed that the birds in the fat line had significantly ($p < 0.05$) higher AFW and AFP than the birds in the lean line (Figure 1c, d).

Differences in IMFC between the birds in lean and fat lines

The differences of PIMFC and LIMFC between the birds of the lean and fat lines were compared (Figure 2). The results showed that selection for AFC was attended by significant differences of PIMFC and LIMFC between the birds in the two lines in all the five generation populations used (Figure 2a, b). In all five generations, the birds in the lean line had significantly higher PIMFC and LIMFC compared with the birds in the fat line. Furthermore, the LIMFC in the lean and fat lines have increased tendency along with generations, while increased tendency of PIMFC was not as obvious. The significant difference for PIMFC and LIMFC was also confirmed using the combined data (Figure 2c).

Differences in LFC between the birds in lean and fat lines

There were significant differences of LFC between the birds in the lean and fat lines in all five generation populations (Figure 2d). Indeed, the difference of LFC between lean and fat lines was small in G8, grew up until G14 and then became smaller and almost disappeared at G17 (although being significant) (Figure 2d). The birds in the lean line had significantly lower LFC compared with the birds in the fat line, which was the opposite of IMFC (Figure 2d). This significant difference of LFC between the birds from the lean and fat lines was also confirmed using the combined data (Figure 2c).

Genetic and phenotypic correlations between AFC, IMFC and LFC

The genetic and phenotypic correlations between IMFC (PIMFC and LIMFC), LFC and AFC (AFW and AFP) were estimated using the combined data from the five generations (Table 2). A very significant ($p < 0.01$) negative genetic correlation coefficients (r_g) were found between PIMFC and abdominal fat traits (AFW and AFP) ($r_g = -0.33$ and $r_g = -0.26$), whereas LIMFC showed lower negative genetic

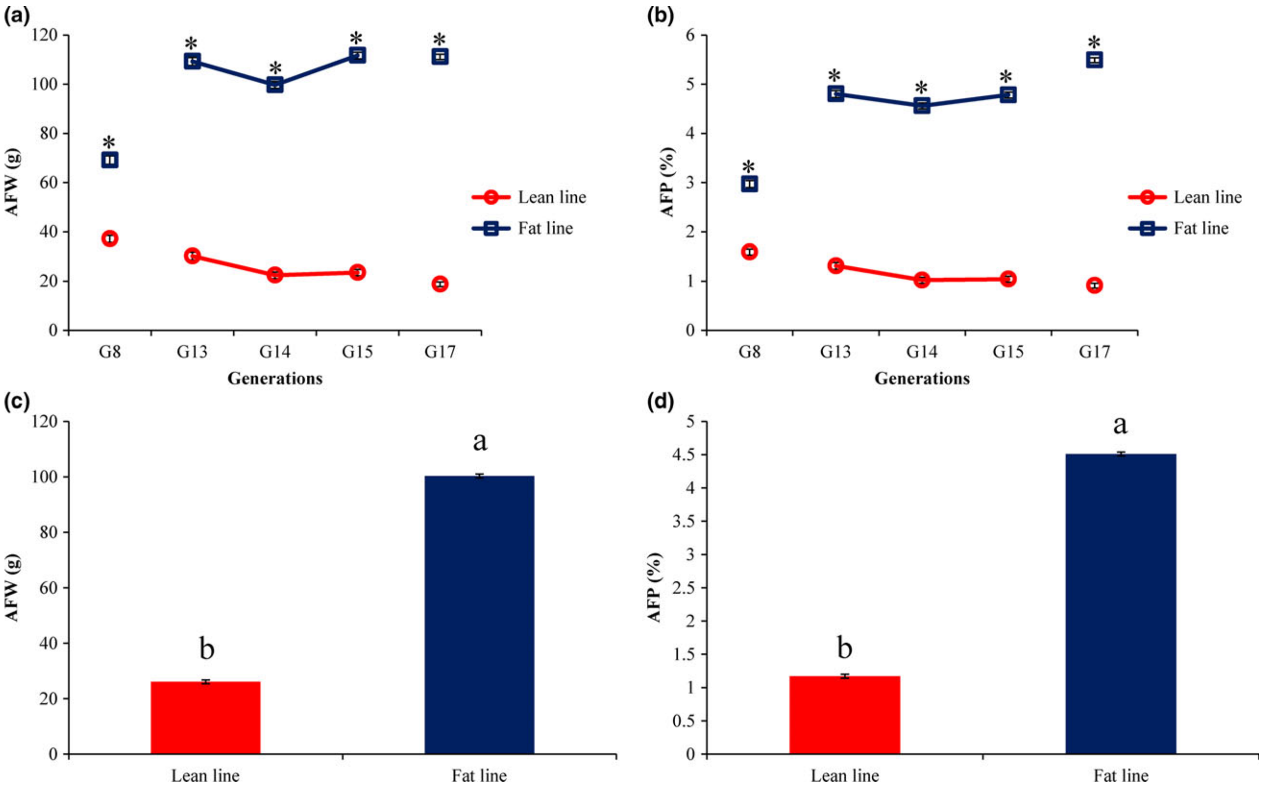

Figure 1 Differences in AFW and AFP between lean and fat lines in all five generations and in the combined data. (a) Difference of AFW between the lean and fat lines in all five generations. (b) Difference of AFP between the lean and fat lines in all five generations. (c) Difference of AFW between the lean and fat lines in the combined data of the five generations. (d) Difference of AFP between the lean and fat lines in the combined data of the five generations. AFW, abdominal fat weight; AFP, abdominal fat percentage. The asterisk (*) above the connecting lines and different lowercase letters above the columns indicate significant differences ($p < 0.05$) between the lean and fat lines.

correlations with abdominal fat traits ($r_g = -0.16$ and $r_g = -0.15$), although the genetic correlation between LIMFC and AFP did not reach the significant level with $p = 0.06$ (Table 2). There were almost no genetic correlations between LFC and abdominal fat traits ($r_g = -0.01$ and $r_g = -0.06$). The phenotypic correlation coefficients (r_p) between IMFC, LFC and abdominal fat traits were found to be relatively low ($0.03 \leq |r_p|\ 0.09$) (Table 2).

Discussion

Selection against abdominal fat resulted in higher IMFC

Due to intensive selection, the growth rate, feed efficiency, breast muscle weight and other attributes of the modern broiler have been greatly improved to meet the consumers' requirements (Wang *et al.* 2012). However, excessive fat deposition, especially abdominal fat, is still one of the major problems in poultry industry (Zhou *et al.* 2006). In general, excessive abdominal fat deposition is an unfavourable trait for both producers and consumers because it is considered to be wasted dietary energy and a waste product with low economic value, which also reduces the carcass yield and affects consumer acceptance (Emmerson 1997). More and more researchers have focused on studies related to the genetic mechanism of abdominal fat deposition and some lean lines have been bred (Decuypere *et al.* 2010). We also produced two broiler lines divergently selected for abdominal fat content. The lean and fat lines have been selected for 17 generations, and the AFP between the two lines was significantly different from the 4th generation onwards. However, unexpectedly, current study showed that the birds in the lean line had significantly higher IMFC compared with the birds in the fat line across all of the selected five generations. The results indicate that the selection against abdominal fat resulted in a higher IMFC. The IMFC is an indicator of meat quality in animals, which is related with sensory

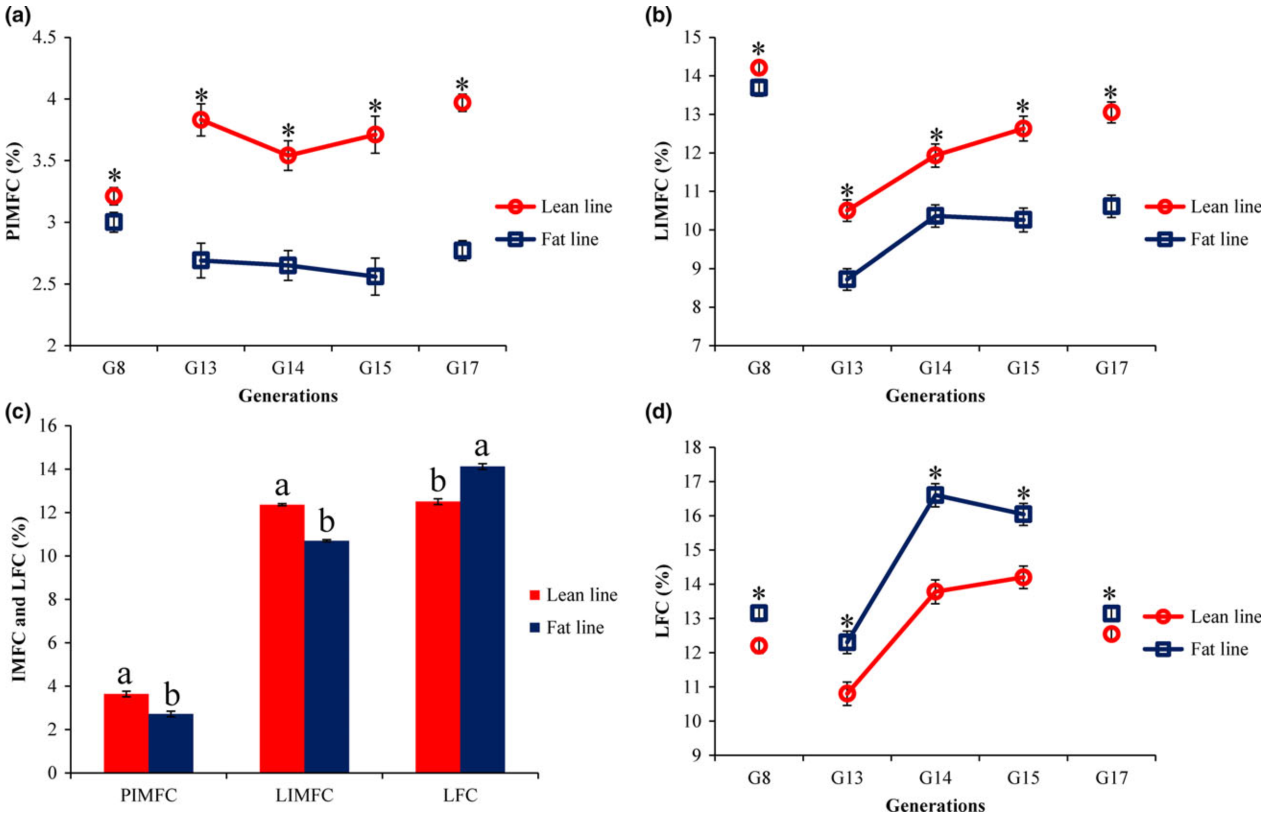

Figure 2 Differences in PIMFC, LIMFC and LFC between lean and fat lines in all five generations and in the combined data. (a) Differences of PIMFC between the lean and fat lines in all five generations. (b) Differences of LIMFC between the lean and fat lines in all five generations. (c): Difference of PIMFC, LIMFC and LFC between the lean and fat lines in the combined data of the five generations. (d) Differences of LFC between the lean and fat lines in all five generations. PIMFC, pectoral major muscle fat content; LIMFC, intramuscular fat content of leg muscle; LFC, liver fat content. The asterisk (*) above the connecting lines and different lowercase letters above the columns indicate significant differences ($p < 0.05$) between the lean and fat lines.

Table 2 The genetic and phenotypic correlations between PIMFC, LIMFC, LFC and AFW, and PIMFC, LIMFC, LFC and AFP

	Genetic correlation		Phenotypic correlation	
Parameter	AFW	AFP	AFW	AFP
PIMFC	−0.33 ± 0.07**	−0.26 ± 0.07**	−0.07 ± 0.08	−0.03 ± 0.08
LIMFC	−0.16 ± 0.08*	−0.15 ± 0.08	−0.04 ± 0.08	−0.03 ± 0.08
LFC	−0.01 ± 0.09	−0.06 ± 0.08	0.09 ± 0.08	0.07 ± 0.08

PIMFC, pectoral major muscle fat content; LIMFC, intramuscular fat content of leg muscle; LFC, liver fat content; AFW, abdominal fat weight; AFP, abdominal fat percentage.
*means $p < 0.05$, and **means $p < 0.01$.

satisfaction, meat flavour, tenderness and juiciness (Eikelenboom *et al.* 1996; Fernandez *et al.* 1999; Gerbens *et al.* 2001; Suzuki *et al.* 2005; Ye *et al.* 2014). Together with the result that there was a significant negative genetic correlation between IMFC and AFC, and the differences in IMFC grew from G8 on, these results indicated that they were attending the selection for lean line.

The compared result of IMFC between the lean and fat lines was similar with a previous study which showed that Baicheng-You chickens (a local breed in China) had much lower AFC, but much higher IMFC of thigh muscle than Arbor Acres broilers (Sarsenbek *et al.* 2013). However, the results of current study were inconsistent with some other studies that showed that no significant difference of IMFC was detected between the low and high abdominal fat lines (Ricard *et al.* 1983; Berri *et al.* 2005). The result of a previous study showed that almost no significant genetic correlation (0.02) was detected between breast muscle IMFC and AFW (Zerehdaran *et al.* 2004). However, another study reported a high positive genetic correlation (0.66) between IMFC and AFW was discovered in the Chinese Beijing-You chickens (a famous Chinese native chicken breed) (Chen *et al.* 2008). In the current study, we found that the genetic correlation between IMFC and AFC was −0.26 to −0.33. These inconsistencies may be because of the different breeds, environmental effects, goals of the genetic selection, and sampling sizes used in the different studies.

Selection against abdominal fat resulted in lower LFC

Excessive hepatic lipid deposition can cause fatty liver haemorrhagic syndrome (FLHS). This disease is often characterized by broilers being significantly obese, with steeply decreased egg-laying rates, and even sudden death (Wolford & Polin 1972; Thomson *et al.* 2003; Yousefi *et al.* 2005; Yeh *et al.* 2009). The diseased birds were paunch, and there were large amounts of fat deposited in their liver and abdomen. Additionally, the enlarged liver was easily damaged and prone to bleeding, and internal haemorrhage occurred in the liver as well (https://en.wikipedia.org/wiki/Fatty_liver_hemorrhagic_syndrome).

Some traits were reported to be more or less related to FLHS, such as the AFC and LFC. Chickens with FLHS were often found to have excessive abdominal and liver fat, while FLHS was absent in chickens with less liver fat content (Wolford & Polin 1972). The correlation between FLSH and liver fat percentage was found to be high (Yeh *et al.* 2009). Therefore, these traits, including abdominal and liver fat content, play very important roles in the occurrence and development of FLHS.

Liver fat content results of the birds in the lean and fat lines in the current study showed that the birds in the fat line not only had a significantly higher AFC but also had significantly higher LFC than the birds in the lean line. The result may suggest that selection against AFC could reduce the occurrence of FLHS.

In summary, we found that apart from different AFC, the lean and fat lines had also different IMFC and LFC. Considering the special population characteristics and breeding purposes, the divergent selection for AFC could also change the IMFC and LFC. Further research is required to help understand the mechanisms underlying the relationship between AFC, IMFC and LFC.

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