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Estimating the genetic parameters for liver fat traits in broiler lines divergently selected for abdominal fat

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ABSTRACT. Intensive selection of broilers for improved growth rate is known to exert a negative effect on broiler health, such as an increase in body fat (and its related diseases). Excessive fat deposition in the liver can cause fatty liver hemorrhagic syndrome (FLHS); in addition, traits associated with liver fat have also been associated with FLHS. This study explored the genetic relationships among liver fat-related traits. Data was collected from 462 birds derived from 16th generation Northeast Agricultural University broiler lines divergently selected for abdominal fat content. The body weight at 7 weeks of age (BW7), abdominal fat weight (AFW), abdominal fat percentage, liver fat percentage (LFP), liver weight, and liver percentage were measured. The heritability of these traits and the phenotypic and genetic correlations were estimated, using the restricted maximum likelihood (REML) and Gibbs sampling

(GS) methods. The REML and GS methods yielded similar heritability estimates for LFP (0.36 and 0.37, respectively). BW7 showed a high positive genetic correlation with AFW ($r_{A(REML)}$ = 0.74 and $r_{A(GS)}$ = 0.80), and a moderate positive genetic correlation with LFP ($r_{A(REML)}$ = 0.27 and $r_{A(GS)}$ = 0.39). Positive genetic correlations were also observed between AFW and LFP ($r_{A(REML)}$ = 0.35 and $r_{A(GS)}$ = 0.36). These results suggested that selection for growth may increase the AFW and LFP in broilers. LFP is directly related to FLHS; therefore, selection for broiler growth rate may increase the incidence of FLHS.

Key words: Broiler; Liver fat trait; Heritability; Genetic correlation; Restricted maximum likelihood; Gibbs sampling

INTRODUCTION

Chicken are raised as farm animals throughout the world. Intensive selection based on the body weight (BW) and growth rate characteristics of chicken for over 50 years has led to the development of efficient broiler breeds with rapid growth rates, high feed efficiencies, and a reduced market age. However, this has also resulted in negative consequences, such as increased body fat and disease incidence (Griffin, 1996; Deeb and Lamont, 2002; Olawumi and Fagbuaro, 2011).

Excessive hepatic lipid deposition in chicken can cause steatosis and fatty liver hemorrhagic syndrome (FLHS), which is characterized by obesity, an acute drop in egg production, and sudden death from hepatic rupture and hemorrhage (Wolford and Polin, 1972; Thomson et al., 2003; Yeh et al., 2009). Certain traits have been associated with FLHS; a greater prevalence of FLHS was observed in heavier birds, taking the age and phase of production into consideration (Meijering, 1979). In addition, FLHS was associated with the presence of abdominal and liver fat in chicken (Wolford and Polin, 1972), while those with lower liver fat content remained unaffected (Wolford and Polin, 1972; Crespo and Shivaprasad, 2003). Yeh et al. (2009) reported a positive correlation between FLHS and liver percentage (LP). These traits, particularly the BW and abdominal and liver fat content, play important roles in the occurrence and development of FLHS. However, few studies have genetically analyzed these traits and the relationships between them.

The aim of this study was to estimate the genetic parameters of the BW at 7 weeks of age (BW7), abdominal fat weight (AFW), abdominal fat percentage (AFP), liver fat percentage (LFP), liver weight (LW), and the LP. In addition, we investigated the effect of increased abdominal fat content in broilers, which increases with intensive selection for rapid growth, on liver fat content, and further possible influences on FLHS.

MATERIAL AND METHODS

Experimental population

Northeast Agricultural University (NEAU) broiler lines divergently selected for abdominal fat content (NEAUHLF) have been selectively bred based on AFP and plasma very low-density lipoprotein (VLDL) concentrations since 1996 (Guo et al., 2011). In this study, data was collected from 462 male birds from 16th generation (G16) NEAUHLF populations. All selected birds were from one of two hatches: 246 birds in the first hatch (94 birds in the lean line, 152 birds

in the fat line), and 216 in the section hatch (130 birds in the lean line, 86 birds in the fat line).

Traits

At 7 weeks of age, the birds were fasted for 12 h, weighed (BW7), and slaughtered. The abdominal fat pad and adipose tissue was collected from the walls of the gizzard, and weighed (AFW) (Guo et al., 2011). The liver was weighed (LW) and stored at -20°C until use. The AFW and LW values were also expressed as percentages of the BW7 (AFP and LP, respectively). Liver dry matter was measured using a 20-g sample of the right lobe, which was thawed, cleaned of obvious fat, minced, and dried in two 10-12 h stages (the first at 65°C and the second at 105°C). The dried samples were cooled in a desiccator for at least 30 min. The liver fat content was measured by Soxhlet extraction using anhydrous ether, and expressed as a percentage of the liver dry matter (LFP) (Cui et al., 2012).

Statistical analyses

Descriptive statistical analyses were performed using the univariate and GLM procedures, in SAS 9.1 (SAS Institute, Cary, NC, USA). Genetic parameters were estimated using the following model:

$$y = X_1 b + X_2 c + Za + e$$

where, y is the vector of the observations; b is the vector of the fixed line and hatch effects; c is the vector of covariate BW7; a is the additive genetic effect; e is the vector of residual effects; and X_1, X_2, and Z are the incidence matrices of corresponding effects. There were no covariates in the model for BW7, AFP, LP, and LFP.

Restricted maximum likelihood (REML) method

The genetic parameters were estimated by the REML method for animal models, using the multiple trait derivative-free REML software (Boldman et al., 1995). Convergence was defined as the point where the variances of two consecutive iterations were less than 1.0E-09. The estimation was repeated twice for all parameters.

Gibbs sampling (GS) method

The genetic parameters were estimated by GS, using the threshold version of the Multiple Trait Gibbs Sampler for Animal Models (Van Tassell and Van Vleck, 1996). The total length of the Gibbs chain was set to 1,000,000 cycles. The burn-in period and the thinning interval were set to 100,000 and 300 rounds, respectively. Serial correlation and convergence for GS were obtained using the GIBANAL software (Van Kaam, 1998).

RESULTS

Descriptive analysis of phenotypic traits

The descriptive statistics for all traits are summarized in Table 1. The genetic line dif-

ferences between all traits except BW7 were observed to be statistically significant. The mean AFW, AFP, LFP, LW, and LP were significantly higher in the fat line compared to the lean line ($P < 0.01$). The average AFW of 7-week-old male birds was calculated to be 100.06 g in the fat line and 19.58 g in the lean line. The AFP of 7-week-old-fat birds was approximately five times higher than that of lean birds of the same age. The fat line showed a higher LFP (15.67%) compared to the lean line (11.98%). The fat chicken also showed heavier livers; the LW of the lean line was 45.05 g, while the LW of the fat line was 52.43 g. The mean LP of the fat line was 2.68%, which was significantly higher than the mean LP of the lean line (2.37%).

Table 1. Number of animals (N), mean (M), standard deviation (SD), coefficient of variation (CV), and significance of line effect (line effect P value) for all traits.

Trait	N		M		SD		CV (%)		Line effect P value
	LL	FL	LL	FL	LL	FL	LL	FL	
BW7 (g)	224	237	1930.92	1962.08	321.82	304.19	16.67	15.50	0.95
AFW (g)	218	225	19.58	100.06	7.73	24.35	39.50	24.34	<0.01
AFP (%)	218	225	1.00	5.00	0.35	0.91	34.95	18.21	<0.01
LFP (%)	224	238	11.98	15.67	3.00	6.40	25.04	40.82	<0.01
LW (g)	220	225	45.05	52.43	7.85	10.80	17.43	20.59	<0.01
L P (%)	220	225	2.37	2.68	0.54	0.71	22.60	26.42	<0.01

LL = lean line; FL = fat line; BW7 = body weight at 7 weeks of age; AFW = abdominal fat weight; AFP = abdominal fat percentage; LFP = liver fat percentage; LW = liver weight; LP = liver percentage.

Heritability

Heritability estimates for the liver fat-related traits are presented in Table 2 (diagonal values). The heritability estimates of these traits calculated by the REML and GS methods were similar. The heritability of BW7 calculated by both REML and GS methods was 0.20. The heritability estimate for AFW was calculated to be 0.58 by the REML method, and 0.61 by the GS method. The heritability of AFP was 0.53 and 0.56, as determined by the REML and GS methods, respectively. The heritability estimates for LFP were 0.36 and 0.37, as calculated by the REML and GS methods, respectively. The heritability of LW was low; the values estimated by the REML and GS methods were 0.19 and 0.17, respectively. The heritability of LP was similarly low, with estimated values of 0.16 and 0.18 by the REML and GS methods, respectively.

Phenotypic and genetic correlations

The phenotypic and genetic correlations among these traits (calculated by the REML and GS methods) are shown in the lower and upper triangular sections of Table 2, respectively. The results calculated by both methods were similar; therefore, in the text below, only the results obtained using the GS method are described.

A thorough analysis of the relationships between BW and the other traits revealed a higher positive phenotypic and genetic correlation between BW7 and AFW ($r_P = 0.55$ and $r_A = 0.80$, respectively), and a moderate positive correlation between BW7 and AFP ($r_P = 0.21$ and $r_A = 0.20$) and LFP ($r_P = 0.25$ and $r_A = 0.29$). The phenotypic and genetic correlations between BW7 and LW were 0.52 and 0.76, respectively. Moderate positive phenotypic and genetic correlations were also observed between BW7 and LP ($r_P = 0.35$ and $r_A = 0.32$, respectively).

Table 2. Estimates of the heritability of, and genetic correlations and phenotypic correlations between, different traits.

Traits	BW7	AFW	AFP	LFP	LW	LP
BW7	**0.20**	0.74	0.38	0.27	0.75	0.30
	0.20	0.80	0.20	0.29	0.76	0.32
AFW	0.83	**0.58**	0.77	0.35	0.48	0.01
	0.55	**0.61**	0.72	0.36	0.53	0.01
AFP	0.20	0.91	**0.53**	0.24	0.18	0.07
	0.21	0.80	**0.56**	0.26	0.18	0.08
LFP	0.24	0.30	0.23	**0.36**	0.10	0.74
	0.25	0.30	0.22	**0.37**	0.24	0.80
LW	0.05	0.05	0.06	0.20	**0.19**	0.71
	0.09	0.09	0.06	0.18	**0.17**	0.74
LP	0.02	0.02	0.04	0.32	0.74	**0.16**
	0.01	0.01	0.03	0.32	0.74	**0.18**

Heritability estimates are presented diagonally, and are typed in bold. Genetic correlations are located above the diagonal, while the phenotypic correlations are located below the diagonal. For each trait, the results of the REML method are shown above the results of the Gibbs Sampling method. BW7 = body weight at 7 weeks of age; AFW = abdominal fat weight; AFP = abdominal fat percentage; LFP = liver fat percentage; LW = liver weight; LP = liver percentage.

This study also analyzed the relationships between AFW, AFP, and the other traits. High phenotypic and genetic correlations were observed between AFW and AFP ($r_P = 0.80$ and $r_A = 0.72$), while moderate phenotypic and genetic correlations were observed between AFW and LFP ($r_P = 0.30$ and $r_A = 0.36$). AFW showed a very low phenotypic correlation (0.09), but a high genetic correlation (0.53), with LW. The phenotypic and genetic correlations between AFW and LP were discovered to be 0.01. AFP showed moderate positive phenotypic and genetic correlations with LFP ($r_P = 0.22$ and $r_A = 0.26$). The phenotypic and genetic correlations between the AFP and both the LW and LP were low.

A low phenotypic correlation was observed between the LFP and LW (0.18). The phenotypic correlation between LFP and LP was calculated to be 0.32. LFP showed a moderate positive genetic correlation with LW (0.24) and a high positive genetic correlation with LP (0.80). High positive phenotypic and genetic correlations were observed between LW and LP (both 0.74).

DISCUSSION

The lean and fat chicken lines used in this study came from a common genetic background, and had been divergently selected for 16 generations based on the AFP and plasma VLDL concentration. Statistical analyses revealed significantly higher AFW, AFP, LFP, LW, and LP values in the fat birds compared to the lean birds ($P < 0.01$); this indicated the applicability of the NEAUHLF population for exploring the genetic relationships among liver fat-related traits.

The estimation of genetic parameters has long been considered to be an important part of understanding quantitative traits. Efficient selective breeding programs require accurate estimates of genetic parameters (Lynch and Walsh, 1998). Two methods, REML and GS, have been used in this study to estimate the genetic parameters of liver fat-related traits. REML is the standard method for variance component estimation in animal breeding because of its desirable theoretical properties (Thompson et al., 2005; Oliveira et al., 2013). Meanwhile, the Bayesian approach combines the known aspects about the parameter (represented as a prior distribution) with information from the obtained data to determine the posterior distribution

(Lindsten and Schön, 2013). The standard computational approach uses the Markov chain Monte Carlo (MCMC) method to draw samples from posterior distributions. The GS is one of the commonly used MCMC methods, which allows for the estimation of variance using Bayesian techniques with a much lower degree of complexity than REML (Geman and Geman, 1984; de los Campos et al., 2013). In many cases, GS has been reported to be more suitable than REML analyses for the analysis of complicated models, as it can obtain and update all information from the posterior probability distribution without solving the mixed model equations (Gianola and Fernando, 1986; Van Tassell et al., 1995). Therefore, the GS method is increasingly used to estimate the genetic parameters of quantitative traits (Waldmann and Ericsson, 2006; Pardo et al., 2013), such as BW in cattle (Lundgren et al., 2014), feed intake and litter weight in sows (Lopes et al., 2013), and egg production in chicken (Luo et al., 2007).

In this study, a comparison of the estimates obtained using the REML and GS methods were determined to be similar; this was consistent with the results obtained in other studies (Van Tassell and Van Vleck, 1996; Andersen-Ranberg et al., 2005; Stock et al., 2007). Therefore, only the values obtained using the GS method are discussed herein (the results obtained using both methods are presented in Table 2).

A high positive genetic correlation was observed between BW7 and AFW (0.80). This estimate was in agreement with the previously reported estimates, which ranged from 0.46 to 0.82 (Zhao, 1990; Gaya et al., 2006; Chabault et al., 2012). On the other hand, a moderate genetic correlation was observed between BW7 and LFP (0.29), which was similar to the estimate (0.33) reported by Zhao (1990) in 72-week-old Harbin White chicken. The genetic correlation between BW7 and LFP estimated in this study was much lower than that observed by Wang et al. (2011), who reported a high genetic correlation (0.79) between BW7 and LFP in 20-week-old Rugao yellow chicken. These results suggested that selection for BW7 could possibly increase AFW and LFP.

AFW was highly correlated with AFP, with a genetic correlation of 0.72. In 2004, Zerehdaran et al. reported a genetic correlation of 0.96 between AFW and AFP. In this study, the genetic correlation between AFW and LFP was observed to be 0.36. In 1990, Zhao reported a genetic correlation of 0.43 between LFP and AFW. These estimates were similar to the ones observed in our study, and suggest a tendency for higher LFP in chicken with a greater AFW.

The moderate or higher positive genetic correlations between BW7, AFW, and LFP suggest that the selection for BW7 may increase the LFP (Zhao, 1990; Wang et al., 2011), in addition to AFW (Zerehdaran et al., 2004). An increase in AFW will simultaneously increase the liver fat content. In addition, a high genetic correlation was observed between AFW and LW (0.53) in our study. These results are similar to those reported by Abplanalp et al. (1984), and suggest a higher LW in chicken with higher AFW. In this study, chicken from the fat line had higher LFP and LW values compared to those from the lean line ($P < 0.01$). Therefore, an increase in liver fat content may be responsible for the higher LW of chicken in the fat line.

Previously reported heritability estimates for LFP range from 0.12 to 0.91 (Zhao, 1990; Marie-Etancelin et al., 2011; Wang et al., 2011); in this study, the heritability estimate for LFP was determined to be 0.37, which was within the (standard range). Zhao (1990) reported a LFP heritability of 0.91 in 72-week-old Harbin white chicken. The study conducted by Wang et al. (2011), on the other hand, calculated a LFP heritability of 0.12 in 20-week-old Rugao yellow chicken. Marie-Etancelin et al. (2011) estimated the genetic parameters for liver fat traits in 13-week-old ducks, discovering a LFP heritability of 0.16. The variability of the

heritability estimates for LFP may be attributed to the use of different experimental populations, genetic backgrounds, and environmental conditions. Based on the data obtained in this study, and that from previous reports, LFP has been identified as a genetically influenced trait.

So far, several studies have reported heritability estimates for BW7, AFW, and AFP. The obtained estimates for these traits (in this study) were similar to the previously published values for broiler chickens (Zerehdaran et al., 2004; Chabault et al., 2012; Closter et al., 2012). In contrast, few reports have analyzed the genetic correlation between LW and LP. The heritability estimate for LW obtained from our population was 0.17. This was lower than the estimate of Venturini et al. (2014), who reported a heritability of 0.33 for LW in broiler chickens. The heritability estimate for LP in this study was 0.18; this value is similar to that obtained by Wang et al. (2011), who reported a heritability of 0.21 for LP in 20-week-old Rugao yellow chicken. Our results, combined with those of previous investigations, show that the heritability of BW7, AFW, and AFP are moderate or high, while the heritability of LW and LP are moderate or low.

In conclusion, moderate to high genetic correlations were observed between BW7, AFW, and LFP. Intensive selection of broilers for higher growth rate leads to an increase in the AFW value, which results in a higher LFP value. These genetic relationships were confirmed in the NEAUHLF population in our study. The AFW and LFP values in the fat line were significantly higher than those in the lean line. The moderate heritability of LFP indicated that genetic variations accounted for a large proportion of the phenotypic variance in our study population. Furthermore, since LFP has a direct genetic relationship with FLHS, the selection of broilers for rapid growth may potentially result in an increase in FLHS.

Conflict sof interest

The authors declare no conflict of interest.

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