Estimation of the genetic parameters of traits relevant to feed efficiency: result from broiler lines divergent for high or low abdominal fat content

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ABSTRACT Feed consumption represents a major cost in poultry production and improving feed efficiency is one of the important goals in breeding strategies. The present study aimed to analyze the relationship between feed efficiency and relevant traits and find the proper selection method for improving feed efficiency by using the Northeast Agricultural University High and Low Fat broiler lines that were divergently selected for abdominal fat content. A total of 899 birds were used to measure the feed intake (**FI**), abdominal fat weight (**AFW**), and body weight traits. The abdominal fat percentage (**AFP**), feed conversion ratio (**FCR**), and the residual feed intake (**RFI**) were calculated for each individual broiler. The differences in the AFW, AFP, and in traits relevant to feed efficiency, such as FCR and RFI, between the fat line and the lean line were analyzed, and the genetic parameters were estimated for AFW, AFP, and feed efficiency relevant traits. The results showed that AFW, AFP, body weight gain (**BWG**), FI, FCR, and RFI were significantly higher in the fat line compared with the lean line. The heritability of FI, BWG, FCR, RFI, AFW, and AFP were 0.45, 0.28, 0.36, 0.38, 0.33, and 0.30, respectively. Both FCR and RFI showed high positive genetic correlations with FI, AFW, and AFP and relatively low, negative genetic correlations with BWG. The RFI showed much higher positive genetic correlation with the abdominal fat traits than FCR. In addition, the FCR showed negative genetic correlation with body weight of 4 wk (BW4) and 7 wk (BW7), whereas RFI showed positive genetic correlation with BW4 and BW7. The results showed that both RFI and FCR could be used for improving feed efficiency. When selecting against RFI, the AFP could be significantly reduced, and by selecting against FCR, the body weight could be improved simultaneously.

Key words: feed efficiency, abdominal fat, body weight, genetic parameter, broiler

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INTRODUCTION

Feed accounts for more than 60% of the total cost in the poultry production and the improvement of feed efficiency has always been a primary goal in breeding strategies. Two kinds of methods can be used to improve feed efficiency in broilers. One method involves direct selection for feed efficiency and the other method involves indirect selection, which means selection for traits associated with feed efficiency, including abdominal fat percentage (**AFP**) and body weight gain (**BWG**). In the past decades, it has proven difficult to accurately measure the feed intake of broilers individually and therefore indirect selection methods were used to improve the feed efficiency. For example, excessive fat deposition decreases the feed efficiency and selection against fat deposition therefore contribute to improving feed efficiency (Leenstra, 1988; Leenstra and Pit, 1988). Selection for BWG can result in an indirect improvement of feed conversion (Emmerson, 1997).

With the development of automatic feeding systems and the widespread use of individual cages, feed intake (**FI**) measurements have become much easier and direct

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selection methods for improving feed efficiency have become more practical. Two kinds of indexes are widely used to evaluate feed efficiency in poultry production, including the feed conversion ratio (**FCR**) and the residual feed intake (**RFI**). Feed conversion ratio is the ratio of FI to body weight gain during the trial period. Residual feed intake is the difference between the actual feed intake and the expected feed intake given metabolic body weight and weight gain. The selection of FCR or RFI for improving feed efficiency should be based on both the estimation of the heritability and their genetic correlations with other performance traits. Previous studies have shown that the heritability of FCR and of RFI are moderate in chicken (Aggrey et al., 2010; Yuan et al., 2015; Sell-Kubiak et al., 2017). Therefore, genetic selection for either FCR or RFI could potentially improve feed efficiency in chickens. It has been reported that the FCR is negatively correlated with BWG but positively correlated with feed intake and abdominal fat content in broiler (Gaya et al., 2006; Sell-Kubiak et al., 2017). The RFI is positively correlated with abdominal fat content and feed intake (N'dri et al., 2006; Aggrey et al., 2014; Sell-Kubiak et al., 2017). So far, whether FCR or RFI is more appropriate for improving feed efficiency remains unclear. In this study, a special population, the Northeast Agricultural University High and Low Fat (**NEAUHLF**) lines were used as the material. The NEAUHLF lines originated from the same founder population and were divergently selected with the AFP as a selection index. So far, the NEAUHLF lines have been selected for 23 generations, and the AFP of the birds from the fat line is 9.87 times greater than that of the birds from the lean line, but the body weight traits do not differ significantly between the 2 lines. Therefore, the NEAUHLF lines are highly suitable for analyzing the relationship between the abdominal fat traits and feed efficiency traits. Analyzing the genetic parameters of feed efficiency indexes (FCR and RFI) with other traits is useful for evaluating the indirect effect of selection for feed efficiency indexes (FCR and RFI) and providing information for efficient broiler breeding.

The objectives of the present study were to analyze the relationship between feed efficiency and other important economic traits using a unique population, the NEAUHLF lines, and to estimate the genetic parameters for feed efficiency relevant traits and other traits. The results will provide a reference for the establishment of an appropriate selection strategy directed at improving the feed efficiency in future breeding programs in broiler.

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 Population

In this study, the broilers from the Northeast Agricultural University broiler lines divergently selected for abdominal fat content, which were named as the lean and fat lines (NEAUHLF), were used. In our previously published studies, we have described the population in detail (Guo et al., 2011; Leng et al., 2016). So far, the NEAUHLF lines have been selected for 23 generations. In this study, 459 and 440 birds from the 22nd and 23rd generation of the NEAUHLF population were used, respectively (Table 1). From the time of hatching up to 7 wk, all birds in this study had access to feed and water ad libitum. At 29 d of age, each bird was placed into an individual cage. The feeding experiment was conducted when the broilers were between 29 and 49 d old.

Trait Measurements

Body weights at 4 wk (**BW4**) and at 7 wk (**BW7**) of age were recorded, and BWG during the trial period was calculated by subtracting the BW4 from BW7. The metabolic mid-test body weight (**MMBW**) was calculated by taking the 0.75th power of the average body weight during the trial [(BW at day 29 + BW at day 49)/2]. Total FI of each individual bird was recorded from day 29 to day 49. On day 49, the birds were fasted for 12 h and then weighed and slaughtered. The abdominal fat was dissected and weighed, and the AFP was calculated according the body weight at 49 d. Then, the FCR was calculated, and the RFI was estimated based on linear regression (Koch et al., 1963; Yi et al., 2015; Wen et al., 2018), using the following equations:

$$\mathrm{FCR} = \mathrm{FI}/\mathrm{BWG}$$

$$\mathrm{RFI} = \mathrm{FI} - (\mathrm{b}_0 + \mathrm{b}_1\mathrm{MMBW} + \mathrm{b}_2\mathrm{BWG})$$

Where b_0 is the intercept and b_1, b_2 are partial regression coefficients of FI for MMBW and BWG, respectively.

Statistical Analysis

Statistical differences in various traits (BW4, BW7, BWG, MMBW, FI, FIT, FCR, RFI, AFW, and AFP) between the birds of the lean line and fat line of each

Table 1. Number of samples used in this study from the 22nd (G22) and 23d (G23) generation of the NEAUHLF population.

Generation	Lean line	Fat line	Total
G22	247	212	459
G23	288	152	440
Combined	535	364	899

Abbreviations: NEAUHLF, Northeast Agricultural University High and Low Fat.

generation (G22 or G23) were analyzed according to the Model 1, and the combined data of the 2 generations were analyzed using Model 2 by JMP, version 11.0 (SAS Inc., Cary, NC).

$$y_{ijk} = \mu + L_i + S_j + BW + e_{ijk} \quad \text{(Model 1)}$$

$$y_{ijkl} = \mu + L_i + S_j + G_k + BW + e_{ijkl} \quad \text{(Model 2)}$$

Where: y is the phenotypic value (BW4, BW7, BWG, MMBW, FI, FIT, FCR, RFI, AFW, AFP) of each bird; μ is the value of the population mean; L_i, S_j, and G_k are the fixed effects of the line, sex, and generation, respectively; BW4 is taken as a covariate in the analysis of BWG, and BW7 is taken as a covariate in the analysis of AFW; e_{ijk} and e_{ijkl} are the random residual effect for model 1 and model 2, respectively. The differences between the means of the phenotypic traits of the 2 lines were analyzed, and significant differences were defined as $P < 0.05$.

The genetic parameters for traits relevant to feed efficiency were estimated by the Average Information Restricted Maximum Likelihood method using the WOMBAT software (Meyer, 2010). The animal model (Model 3) used for the genetic parameter estimation is described as follows:

$$Y_{ijkl} = \mu + L_i + S_j + G_k + BW + a_l + e_{ijkl} \quad \text{Model 3}$$

where Y_{ijkl} is the record of the lth chicken from the i^{th} Line, j^{th} sex and k^{th} generation; L_i is the fixed effect of line (i = 1, 2-lean line/fat line); S_j is the fixed effect of sex (j = 1, 2-male/female); G_k is the fixed effect of generation (k = 1, 2-the 22^{th} generation/the 23^{th} generation); BW4 is taken as a covariate in the heritability estimation of BWG, and BW7 is taken as a covariate in the heritability estimation of AFW; a_l is the random direct additive genetic effect of individual l, and e_{ijkl} is the random residual effect. A single trait model was used to estimate the heritability of traits. Bivariate analyses were performed to compute genetic correlations between combinations of traits.

RESULTS

Descriptive Statistics of the Phenotypic Traits and the Differences Between the Fat and the Lean Line

Descriptive statistics of all phenotypic traits in this study are summarized in Table 2. The differences between the 2 lines in the traits relevant to feed efficiency and abdominal fat traits are also shown in Table 2. In each generation and in the combined generation, the birds from the fat line had significantly higher AFW and AFP than the birds from the lean line, but there were no significant differences in BW7 between the 2 lines. For the traits relevant to feed efficiency, the birds from the fat line had significantly higher BWG, MMBW, FI, FIT, FCR, and RFI compared with the birds from the lean line in each generation and in the combined generations. The birds from the fat line had significantly lower BW4 compared with the birds from the lean line in both generations and in the combined generation.

Genetic Parameter Analysis

The genetic parameters of traits relevant to feed efficiency and of abdominal fat traits were estimated with total data of the 22nd and 23rd generation population of NEAUHLF lines, and the results are shown in Table 3. The FI and the BW4 showed the highest heritability among all traits (0.45 and 0.42, respectively), followed by RFI, MMBW, FIT, FCR, BW7, AFW, and

Table 2. Descriptive statistics of phenotypic traits and differences between the fat and lean broiler lines at different generations and at the combined generation.

	G22				G23				G22+G23			
Traits	Line	LSM	SE	*P*-value	Line	LSM	SE	*P*-value	Line	LSM	SE	*P*-value
BW4(g)	Lean	891.73	5.47	<0.0001	Lean	791.23	5.00	0.0002	Lean	840.35	3.80	<0.0001
	Fat	776.30	5.93		Fat	759.53	6.93		Fat	763.61	4.65	
BW7(g)	Lean	1,895.85	12.11	0.066	Lean	1,855.04	10.09	0.6922	Lean	1,875.12	7.85	0.161
	Fat	1,870.61	13.13		Fat	1,848.12	14.00		Fat	1,847.35	9.62	
BWG(g)	Lean	971.13	8.87	<0.0001	Lean	1,058.17	6.46	0.0002	Lean	1,019.10	5.41	<0.0001
	Fat	1,115.63	9.38		Fat	1,100.61	9.03		Fat	1,109.55	6.78	
MMBW(g)	lean	227.89	1.03	<0.0001	Lean	219.21	0.89	0.1022	Lean	223.46	0.68	<0.0001
	fat	217.91	1.11		Fat	216.71	1.24		Fat	216.92	0.84	
FI(g)	lean	2,488.52	20.68	<0.0001	Lean	2,567.27	17.04	<0.0001	Lean	2,530.94	13.47	<0.0001
	fat	3,159.15	22.47		Fat	2,049.92	23.64		Fat	3,113.86	16.51	
FIT(g)	lean	2,658.70	19.66	<0.0001	Lean	2,722.25	14.47	0.1742	Lean	2,694.83	12.43	<0.0001
	fat	2,957.00	21.32		Fat	2,756.16	20.22		Fat	2,870.38	15.27	
FCR	lean	2.49	0.01	<0.0001	Lean	2.41	0.01	<0.0001	Lean	2.45	0.01	<0.0001
	fat	2.94	0.01		Fat	2.81	0.01		Fat	2.88	0.01	
RFI(g)	lean	−162.04	13.75	<0.0001	Lean	−160.08	7.96	<0.0001	Lean	−167.22	7.83	<0.0001
	fat	193.11	14.93		Fat	296.30	11.05		Fat	239.92	9.57	
AFW(g)	lean	9.21	0.08	<0.0001	Lean	9.69	0.59	<0.0001	Lean	9.40	0.48	<0.0001
	fat	102.84	0.85		Fat	104.88	0.82		Fat	104.06	0.59	
AFP(%)	lean	0.52	0.04	<0.0001	Lean	0.51	0.03	<0.0001	Lean	0.51	0.02	<0.0001
	fat	5.48	0.04		Fat	5.62	0.04		Fat	5.56	0.03	

Abbreviations: AFW, abdominal fat weight at week 7; AFP, abdominal fat percentage at week 7; BW4, body weight at week 4; BW7, body weight at week 7; BWG, body weight gain; FCR, feed conversion ratio; FI, feed intake; FIT, feed intake in theory; LSM, least square means; MMBW, mid-test metabolic body weight; RFI, residual feed intake from week 4 to week 7.

Table 3. Heritability (bold, on diagonal), phenotypic (above diagonal), and genetic (below diagonal) correlations, with standard errors (in brackets) for phenotypic traits in the combined population of the 22nd and 23rd generation of NEAUHLF lines.

Traits	BW4	BW7	BWG	MMBW	FI	FIT	RFI	FCR	AFW	AFP
BW4	**0.42 (0.08)**	0.75 (0.02)	0.25 (0.05)	0.88 (0.01)	0.51 (0.03)	0.23 (0.03)	0.49 (0.03)	0.18 (0.04)	0.15 (0.04)	0.19 (0.03)
BW7	0.81 (0.06)	**0.35 (0.08)**	0.89 (0.01)	0.97 (0.01)	0.82 (0.01)	0.80 (0.01)	0.18 (0.03)	−0.21 (0.04)	0.01 (0.05)	0.16 (0.03)
BWG	0.29 (0.17)	0.88 (0.04)	**0.28 (0.07)**	0.77 (0.02)	0.83 (0.01)	0.97 (0.00)	−0.39 (0.03)	−0.61 (0.02)	−0.16 (0.04)	0.03 (0.04)
MMBW	0.91 (0.03)	0.98 (0.01)	0.76 (0.07)	**0.38 (0.09)**	0.77 (0.02)	0.65 (0.02)	0.30 (0.33)	−0.08 (0.04)	0.41 (0.04)	0.18 (0.03)
FI	0.33 (0.13)	0.67 (0.08)	0.825 (0.06)	0.58 (0.09)	**0.45 (0.08)**	0.79 (0.01)	0.40 (0.00)	0.09 (0.04)	0.35 (0.04)	0.23 (0.03)
FIT	0.16 (0.15)	0.68 (0.08)	0.97 (0.01)	0.52 (0.11)	0.85 (0.05)	**0.37 (0.08)**	−0.21 (0.04)	−0.45 (0.03)	−0.16 (0.04)	0.06 (0.04)
RFI	0.32 (0.14)	0.22 (0.16)	−0.19 (0.17)	0.27 (0.15)	0.48 (0.12)	−0.08 (0.16)	**0.38 (0.08)**	0.79 (0.01)	0.30 (0.03)	0.29 (0.03)
FCR	−0.17 (0.17)	−0.11 (0.17)	−0.16 (0.19)	−0.12 (0.17)	0.49 (0.14)	0.01 (0.18)	0.77 (0.07)	**0.36 (0.09)**	0.17 (0.04)	0.20 (0.04)
AFW	0.34 (0.18)	0.14 (0.21)	−0.21 (0.21)	0.58 (0.12)	0.41 (0.15)	−0.15 (0.20)	0.56 (0.17)	0.49 (0.19)	**0.33 (0.09)**	0.87 (0.01)
AFP	0.31 (0.17)	0.18 (0.19)	−0.10 (0.20)	0.24 (0.18)	0.25 (0.16)	−0.04 (0.18)	0.58 (0.159)	0.51 (0.17)	0.92 (0.01)	**0.30 (0.083)**

Abbreviations: AFW, abdominal fat weight at week 7; AFP, abdominal fat percentage at week; BW4, body weight at week 4; BW7, body weight at week 7; BWG, body weight gain; FCR, feed conversion ratio; FI, feed intake; FIT, feed intake in theory; MMBW, mid-test metabolic body weight; NEAUHLF, Northeast Agricultural University High and Low Fat; RFI, residual feed intake from week 4 to week 7.

AFP, which varied from 0.30 to 0.38. On the other hand, BWG showed a relatively low heritability of 0.28.

For the body weight traits, a strong positive genetic correlation was found between BW4 and BW7, BW4 and MMBW, BW7 and BWG, BW7 and MMBW, and MMBW and BWG (0.81, 0.91, 0.88, 0.98, and 0.76, respectively), and similar phenotypic correlations were found for the above pairs of traits (0.75, 0.88, 0.89, 0.97, and 0.77, respectively). For the feed efficiency traits, a high positive genetic correlation and a high phenotype correlation was found between FCR and RFI (0.77 and 0.79, respectively). Furthermore, a positive genetic correlation was found between FCR and FI, and a negative genetic correlation was found between FCR and BWG. Again, the phenotypic correlation trend here was consistent with the genetic correlation. For the RFI and its components, positive genetic correlations were found between RFI and MMBW and between RFI and FI, whereas negative correlations were found between RFI and BWG. Moreover, the phenotype correlation trend was consistent with the genetic correlation. The correlation of FCR and RFI with the abdominal fat traits were also analyzed. Both FCR and RFI showed high positive genetic correlations with AFW and AFP (from 0.49–0.58) and slight to moderate positive phenotypic correlations with AFW and AFP (from 0.17–0.30).

DISCUSSION

Feed represents a major cost in the production of broilers. Consequently, selection for feed efficient birds is becoming more and more important in poultry breeding (Yuan et al., 2015). Feed efficiency varies from species to species but also depends on environmental conditions and management practices. In this study, we used a selected population, divergent in abdominal fat, to evaluate the association of fat deposition with feed efficiency and found strong genetic correlation between feed efficiency traits (FCR, RFI) and abdominal fat traits (AFW, AFP), which means when selection against feed efficiency traits (FCR, RFI), the indirect effect on decreasing abdominal fat could be achieved, and vice versa. The question is whether the direct selection against feed efficiency traits (FCR, RFI) or whether indirect selection against abdominal fat is more appropriate for improving feed efficiency in broiler. The current study will provide a reference for the feed efficiency selection method in broiler.

First, to explore the effect of fat deposition on feed efficiency, we compared the differences of abdominal fat traits and feed efficiency traits between the fat line and the lean line. Our results showed that the abdominal fat traits (AFW, AFP) and the feed efficiency traits indexes (FCR, RFI) of birds from the fat line were significantly higher than those of birds from the lean line, which indicates that selection against or for abdominal fat alters the feed efficiency traits in broilers. Previously, Zhu et al. (2015) also found a negative correlation between fatness and feed efficiency traits in broilers, compared with chickens with high feed efficiency, chickens with low feed efficiency had an increased feed intake and a higher abdominal fat deposition, which is in agreement with our results.

To provide a reference for the broiler breeding program, we assessed the genetic parameters of body weight traits, abdominal fat traits, and feed efficiency-relevant traits. Our findings that the heritability of BW4 and of BW7 were 0.42 and 0.35, respectively, were in line with previous studies by Gaya et al. (2006) and Kuhlers (1996) but differed from the results of Le Bihan-Duval et al. (1998) and Rance et al. (2002). In our study, the heritability of AFW and of AFP were 0.33 and 0.30, respectively, which was close to the values reported by Chen et al. (2008), but lower than the results of Zerehdaran et al. (2004), N'dri et al. (2006), and Chabault et al. (2012). The heritability was 0.36 and 0.38 for the FCR and RFI, respectively, which was in accordance with many reported estimations (Pakdel et al., 2005; Aggrey et al., 2010, 2013; Xu et al., 2016; Sell-Kubiak et al., 2017). Results by us and others confirmed that body weight, abdominal fat, and feed efficiency are selectable in broilers.

Feed efficiency traits showed relatively high heritability, suggesting that the direct selection method could be used in future breeding programs to improve feed efficiency in broiler. The heritability of RFI and FCR were very similar (0.38 and 0.36, respectively), indicating that selection for either FCR or RFI may have similar effects on improving the feed efficiency. It remained to be seen how to judge, based on our results, whether FCR or RFI is more appropriate to be used for selecting feed efficiency. For this, we further compared the phenotypic and genetic correlations between feed efficiency indexes (FCR, RFI) and other important economic traits.

The results showed that both FCR and RFI have a similar negative genetic correlation with BWG and a positive genetic correlation with FI. But the genetic correlation coefficients between RFI and abdominal fat traits (AFW, AFP) was much higher than the genetic correlation coefficients between FCR and abdominal fat traits (AFW, AFP). Moreover, both RFI and FCR showed much higher positive genetic correlation with abdominal fat traits (AFW, AFP) than previously reported (Gaya et al., 2006; N'dri et al., 2006). This highly positive genetic correlation between feed efficiency indexes and abdominal fatness traits is very desirable, which means selection against feed efficiency indexes (FCR and RFI) can achieve a good indirect effect on decreasing abdominal fat. The RFI showed higher genetic correlation level with abdominal fat than FCR, which means selection for lower RFI has much better indirect effect on decreasing the abdominal fat than FCR. For the body weight traits, the FCR showed a negative genetic correlation with BW4 and BW7, whereas the RFI showed a moderate positive genetic correlation with BW4 and BW7. The negative genetic correlation of FCR with BW4 and BW7 meant that selection for decreasing FCR resulted in an increase in body weight, which was in consistent with a previous report (Wen et al., 2018)

Numerous reports have indicated that as a criterion for improving feed efficiency in chicken breeding, RFI is superior over FCR (Gunsett, 1984; Zhang and Aggrey, 2003; Case et al., 2012; Yuan et al., 2015; Xu et al., 2016; Wen et al., 2018). Therefore, it could be concluded that compared with FCR, RFI is superior for improving feed efficiency. However, our results showed that FCR and RFI each have their own advantage when used as a selection index for improving feed efficiency in broilers.

In summary, based on our results of the analysis of the NEAUHLF population, both RFI and FCR can be used as selection index for improving feed efficiency, thereby simultaneously reducing the FI and increasing the BWG in broilers. Selection against RFI significantly reduced abdominal fat content, whereas selection against FCR tends to increase the BW4 and BW7. Therefore, choice of FCR or RFI as the selection index for improving the broiler's feed efficiency should be based on consideration of the indirect selection effect on abdominal fat and body weight. Our results therefore provide a reference for improving the broiler feed efficiency breeding strategy.

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DISCLOSURES

The authors declare that they have no conflict of interest.

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