

GENETICS AND GENOMICS

Genetic parameters of feed efficiency traits in laying period of chickens

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ABSTRACT Laying records on 1,534 F₂ hens, derived from a reciprocal cross between White Leghorns and Dongxiang blue-shelled chickens, were used to estimate genetic parameters for residual feed intake (RFI), feed conversion ratio (FCR), daily feed intake (FI), metabolic BW (MBW), BW gain (BWG), and daily egg mass (EM) at 37 to 40 (T1) and 57 to 60 wk age (T2), respectively. Genetic analysis was subsequently conducted with the AI-REML method using an animal model. Estimates for heritability of RFI, FCR, and FI were 0.21, 0.19, and 0.20 in T1, and 0.29, 0.13, and 0.26 in T2, respectively. In T1 and T2, RFI showed high and positive genetic correlations with FCR (0.51, 0.43) and

FI (0.72, 0.84), whereas the genetic correlation between FI and FCR was very low (−0.09, 0.11). Genetically, negative correlations were found between RFI and its component traits (−0.01 to −0.47). In addition, high genetic correlations, from 0.76 to 0.94, were observed between T1 and T2 for RFI, FCR, and FI, suggesting that feed efficiency traits in the 2 stages had a similar genetic background. The results indicate that selection for low RFI could reduce FI without significant changes in EM, while selection on FCR will increase EM. The present study lays the foundation for genetic improvement of feed efficiency during the laying period of chickens.

Key words: feed efficiency, laying period, genetic parameter, REML, chicken

2015 Poultry Science 94:1470–1475
<http://dx.doi.org/10.3382/ps/pev122>

INTRODUCTION

In poultry production, feed represents over 60% of production costs (Arango 2009), especially in developing countries (Ravindran 2012). For breeders, traits related to feed efficiency have been under selection for several decades, resulting in a correlated improvement for feed efficiency in commercial layers (Flock 1998). However, it seems that the previous endeavors have been outpaced by the strong increase of feed demands and the rapid growth of feed prices. Thus, direct selection for more efficient birds is becoming one of the primary goals in poultry breeding.

A commonly used measure of efficiency is feed conversion ratio (FCR), which is defined as the ratio of feed intake (**FI**) per unit of egg mass in egg-type chickens. However, this ratio is not a suitable criterion to be directly used by breeders, because selection for FCR may lead to similar ratios but different FI and outputs (Gunsett 1984; Luiting et al. 1994; Carstens et al. 2003). As an alternative measure of feed efficiency, residual FI (**RFI**) has been first proposed by Koch, et al. (1963), which is defined as the difference between actual FI and expected FI based on requirements for production and maintenance over a specific period. RFI is a more desirable trait for characterizing feed efficiency in animal breeding due to its independence of growth, production and maturity patterns (Sainz and Paulino 2004). In particular, selection for low RFI animals might be helpful to reduce feed cost and nitrogenous waste (Zhang and Aggrey 2003), and minimize the environmental footprint (Moore et al. 2009).

In egg-type chickens, reports for heritability estimates for FCR are quite few, while more estimates for RFI can be found in the literature. The first estimate of heritability for RFI was very small (Nordskog et al. 1972). However, the subsequent studies showed that heritabilities for RFI was moderate to high ranging

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Received December 8, 2014.

Accepted March 18, 2015.

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from 0.30 to 0.60 (Wing and Nordskog 1982; Hagger and Abplanalp 1978; Bentsen 1983; Luiting and Urff 1991b). Later studies on genetic parameters for RFI mainly focused on its correlations with economic traits including egg production and breeder performance (Hagger 1994; Schulman et al. 1994; Tixier-Boichard et al. 1995). Recently, Wolc et al. (2013) reported moderate to high heritability estimates for RFI using pedigree (0.47) and marker (0.14) information in a brown-egg pure line layers population. Nevertheless, genetic parameters for feed efficiency traits involving RFI, FCR, and FI in laying chickens of different genetic background are still lacking. It is known that accurate and reliable genetic parameter estimates are necessary for selection for target traits in a specific population.

The objective of the present study was to characterize measures of feed efficiency traits and to estimate genetic parameters for feed efficiency and relevant traits in 2 separate laying periods of chickens. The findings would help better understanding the genetic background of feed efficiency and production traits and contribute to chicken breeding and further genomic studies.

MATERIALS AND METHODS

Experimental Population

An F₂ population has been constructed for further genetic analysis since 2011. The resource population was established by reciprocal crossing White Leghorn (WL) with Dongxiang blue-shelled chicken (DBS). White leghorn is a dominant commercial layer breed around the world and DBS is a Chinese indigenous breed with blue eggs. Initially, 3 males and 6 non-related females from WL, and 6 males and 6 non-related females from DBS were selected for mating on the basis of their consistency in laying and semen quality to produce a parent generation. Then, reciprocal mating of the 6 WL (♂) × 133 DBS (♀) and 6 DBS (♂) × 80 WL (♀) was used to produce the F₁ generation based on the same criteria, yielding 1,029 WL (♂) × DBS (♀) pair (WB) and 552 DBS (♂) × WL (♀) pair (BW) offspring. At 40 wk age, F₁ chickens, involving 25 males and 406 females from WB and 24 males and 233 females from BW, were randomly selected to produce the F₂ generation. A total of 3,749 chicks including 1,856 males and 1,893 females from 590 full-sib families were created in the same hatch. All F₂ birds were raised at the research station of Jiangsu Institute of Poultry Science. Chickens were housed in individual cages in 2 identical houses under the standard management conditions at the same feedlot. Each bird was provided ad libitum access to water and a commercial corn–soybean diet that met National Research Council requirements during the study period.

A 3-generation pedigree including a total of 2,447 individuals was collected for estimating genetic parameters. The pedigree structure contained 12 sires and 213 dams from the parent generation, 49 males and 639 fe-

Table 1. Descriptive statistics of feed efficiency and relevant traits¹.

Traits ²	Mean	SD	CV (%)	Minimum ³	Maximum ⁴
RFI1, g/d	0.03	6.58	21933.33	-24.44	23.73
RFI2, g/d	0.27	7.11	2633.33	-32.00	23.16
FCR1, g:g	2.61	0.72	27.58	1.72	10.31
FCR2, g:g	3.61	3.08	85.31	1.83	61.96
FI1, g/d	91.6	7.94	8.67	56.1	106.4
FI2, g/d	105.1	7.99	7.60	53.9	125.1
MBW1, g	213.6	18.17	8.51	167.7	313.0
MBW2, g	228.4	20.90	9.15	176.8	309.8
BWG1, g/d	1.24	1.89	152.42	-11.39	14.36
BWG2, g/d	0.02	2.77	13850.00	-25.14	21.21
EM1, g/d	36.5	6.55	17.94	6.9	50.9
EM2, g/d	33.8	8.74	25.83	1.7	51.7

¹n = 1,534.

²RFI1, FCR1, FI1, MBW1, BWG1, and EM1 represent RFI, FCR, daily FI, MBW, daily BWG, and daily EM from 37 to 40 wk, respectively; RFI2, FCR2, FI2, MBW2, BWG2, and EM2 represent corresponding traits from 57 to 60 wk.

³Minimum = Minimum value.

⁴Maximum = Maximum value.

males from the F₁ generation, and 1,534 hens from the F₂ generation. Among these animals, only F₂ birds were measured for phenotypic data of interest.

Data Collection

Individually measured and derived traits are listed in Table 1. These traits were collected in 2 laying periods from 37 to 40 wk age (T1) and from 57 to 60 wk age (T2), respectively. All traits were measured in the same way for both T1 and T2.

In the feeding trial, an individual metal feed trough was used to provide mash feed for each hen. Feed was added by hand and the total weight for each trough was measured. Two to 3 d later the remaining weight was recorded and the individual FI in this interval was calculated. This process was consecutively repeated for a total of 28 days in each feeding period (T1 and T2). The total FI for each hen in each feeding period was calculated by summing the FI data in each interval, and then transformed into the daily FI for each hen in the testing period. Metabolic BW was calculated based on average BW between the start and end of the test. Average daily gain was calculated for each bird. For each bird, we calculated the average egg weight at wk 36 and 40. Average EW for the feeding period was calculated as the average EW of wk 36 and 40. Average daily egg mass (EM) was calculated as the product of average EW and total egg number over the test days. FCR was calculated as a ratio of daily FI and daily egg mass. The following formula proposed by Luiting and Urff (1991a) was used to calculate RFI in terms of FI, metabolic BW (MBW), EM, and BW gain (BWG):

$$\text{RFI} = \text{FI} - (b_0 + b_1\text{MBW} + b_2\text{EM} + b_3\text{BWG})$$

Where b₀, b₁, b₂, and b₃ are partial regression coefficients. In addition, poor hens (no egg mass) were excluded after calculating RFI for the 2 testing periods,

resulting 1,534 shared hens. Thus, the presented descriptive statistics of the measured and derived traits in the 2 stages were calculated with the 1,534 individuals.

Statistical Analysis and Calculation

Box–Cox or Johnson transformation was performed for all non-normal phenotypic data using RStudio (Racine 2012) prior to genetic analysis. RFI in the 2 laying periods (RFI1, $\lambda = 1.40$; RFI2, $\lambda = 1.50$) and MBW in the 2 laying periods (MBW1, $\lambda = -0.60$; MBW2, $\lambda = -0.25$) followed a normal distribution after Box–Cox transformation, while distributions of BWG (BWG1, $\lambda = 0.75$; BWG2, $\lambda = 1.60$) approximated normality. Similar to BWG, after Johnson transformation, FCR, FI, and EM were in an approximately normal distribution. Pedigree information involving 3 generations was included in the relationship matrix. The variance and covariance components were estimated using DMU software package (Madsen and Jensen 2008) with the average information restricted maximum likelihood (AI-REML) (Jensen et al. 1997), which did well in a faster computing time with lower dependence on starting values. In the present study, birds were hatched from the same batch and raised in the same feedlot. Therefore, no fixed effect was included for further analyses.

A univariate animal model was fitted to calculate heritability for each trait as follows:

$$y = XB + Za + e$$

Where y is the phenotypic value of the animal; X and Z are the incidence matrix of fixed effects and random additive effects, respectively; B and a are the vectors of fixed effects and random additive effects, respectively; and e is the random residual effect. Bivariate animal model analysis was applied to calculate genetic and phenotypic correlations.

RESULTS

Descriptive Statistics of Traits

Table 1 shows means, SD, CV, minimum and maximum values for feed efficiency, and its relevant traits in 2 laying periods. Residual feed intake values were close to zero (0.03 and 0.27, respectively). Daily FI and MBW increased with the decrease of EM, resulting in the deterioration of FCR. Daily BWG was very small, and eventually close to zero in T2. The coefficients of variation (CV) of measured traits had a wide range (from 0.08 to 219.33) in both laying periods. Among those, CVs of FI and MBW were less than 10%, while FCR and EM showed higher CV values, greater than 15% in 2 testing periods, indicating a large phenotypic variation of the 2 traits in the resource population.

Genetic Parameters

Estimated genetic parameters for feed efficiency and its relevant traits are presented in Tables 2 and 3. The heritability estimates for RFI, FCR, FI, MBW, and

Table 2. Estimates of heritability (h^2) for feed efficiency and relevant traits along with estimates of genetic (r_a) and phenotypic (r_p) correlations among traits from 37 to 40 wk¹.

Traits ²	RFI1	FCR1	FI1	MBW1	BWG1	EM1
RFI1	0.21 (0.05)	0.51 (0.15)	0.72 (0.08)	−0.13 (0.17)	−0.47 (0.32)	−0.07 (0.19)
FCR1	0.47	0.19 (0.05)	−0.09 (0.20)	−0.40 (0.17)	−0.20 (0.42)	−0.88 (0.05)
FI1	0.83	0.07	0.20 (0.05)	0.49 (0.13)	−0.16 (0.36)	0.56 (0.14)
MBW1	0.06	−0.03	0.42	0.43 (0.07)	0.62 (0.32)	0.53 (0.14)
BWG1	−0.03	0.09	0.17	0.16	0.02 (0.02)	0.01 (0.38)
EM1	−0.02	−0.86	0.43	0.26	0.03	0.25 (0.06)

¹Heritability is given on diagonal, genetic correlations above diagonal and phenotypic correlations below diagonal. SE of estimates are in parentheses.

²RFI1, FCR1, FI1, MBW1, BWG1, and EM1 represent RFI, FCR, daily FI, MBW, daily BWG, and daily EM from 37 to 40 wk, respectively.

Table 3. Estimates of heritability (h^2) for feed efficiency and relevant traits along with estimates of genetic (r_a) and phenotypic (r_p) correlations among traits from 57 to 60 wk¹.

Traits ²	RFI2	FCR2	FI2	MBW2	BWG2	EM2
RFI2	0.29 (0.06)	0.43 (0.16)	0.84 (0.05)	−0.28 (0.14)	−0.05 (0.26)	−0.01 (0.19)
FCR2	0.37	0.13 (0.04)	0.11 (0.20)	−0.19 (0.19)	0.44 (0.27)	−0.87 (0.05)
FI2	0.85	0.004	0.26 (0.06)	0.23 (0.14)	0.12 (0.25)	0.40 (0.17)
MBW2	0.01	−0.01	0.36	0.48 (0.08)	0.54 (0.19)	0.30 (0.18)
BWG2	−0.05	0.21	0.10	0.13	0.06 (0.03)	−0.34 (0.28)
EM2	−0.08	−0.92	0.32	0.14	−0.17	0.15 (0.04)

¹Heritability is given on diagonal, genetic correlations above diagonal and phenotypic correlations below diagonal. SE of estimates are in parentheses.

²RFI2, FCR2, FI2, MBW2, BWG2, and EM2 represent RFI, FCR, daily FI, MBW, daily BWG, and daily EM from 57 to 60 wk, respectively.

Table 4. Genetic (r_a) and phenotypic (r_p) correlations for feed efficiency traits between 2 laying periods¹.

Traits ²	r_a	r_p
RFI	0.76 (0.09)	0.56
FCR	0.94 (0.07)	0.42
FI	0.78 (0.09)	0.62

¹The first test period from 37 to 40 wk, and the second test period from 57 to 60 wk.

²RFI = Residual feed intake; FCR = Feed conversion ratio; FI = Daily feed intake.

BWG in both stages were similar to each other. Estimates of heritability for RFI1 and RFI2 were 0.21 and 0.29, respectively. The heritability estimates for FCR and FI ranged from 0.13 to 0.26 in the moderate level. The largest difference was observed for EM between T1 (0.25) and T2 (0.15). The highest and lowest heritability estimates were for MBW (0.43 and 0.48) and BWG (0.02 and 0.06), respectively.

The estimated genetic and phenotypic correlations between RFI and FCR in T1 (0.51 and 0.47) were slightly higher than those estimated in T2 (0.43 and 0.37). The genetic correlation (0.72) between RFI and FI in T1 was lower than that estimated in T2 (0.84), while the phenotypic correlations exhibited similar results between the 2 stages (0.83 and 0.85). High negative correlations (greater than 0.85) were found between FCR and EM in both stages, whereas the correlations between RFI and EM were close to 0 at both phenotypic and genetic levels. The estimated genetic correlations between FI and EM were positive (0.56 and 0.40) at a moderate to high level in the 2 stages. Both RFI and FCR showed negative genetic correlations with MBW, but these were different in magnitude. In contrast, there is a positive correlation between FI and MBW. The relationships between BWG and feed efficiency traits were irregular, as shown in Tables 2 and 3. As expected, RFI was phenotypically uncorrelated with MBW, BWG and EM, the 3 traits used for calculating the expected FI. Moreover, high estimated genetic and phenotypic correlations between the 2 testing periods were observed for feed efficiency traits, as shown in Table 4, indicating that selection for feed efficiency traits in the early laying period would favor these traits with a similar selection response in the late laying period.

DISCUSSION

In the current study, we characterized feed efficiency and relevant traits using 1,534 F₂ birds in 2 laying periods. The variability in FI and RFI reported from a 2-wk test using a brown pure line strain by Wolc et al. (2013) was higher than that for the same traits in the current study. This is not surprising because the pure-bred brown-egg layer belonged to middle-sized egg-type chicken which lay larger eggs and consume more feed

than the population used in our study. Generally, in the second laying period, hens produced less egg mass due to the older age, and more feed was consumed for a heavier BW. Thus, an increased FCR value was founded.

We estimated heritability for feed efficiency and relevant traits using a single-trait animal model. We also conducted bivariate and multivariate analysis, and the results obtained from the 2-trait and multi-trait model were almost the same as the results obtained from the single-trait model (data not shown). The heritability for RFI was consistent with some previous studies (Wing and Nordskog 1982; Bordas et al. 1992; Mielenz et al. 1994), and moderate estimated heritability (0.29) for RFI2 indicated the presence of sufficient genetic variability for the trait in the resource population. However, our findings diverged from those reported by Hagger (1991) and Katle and Kolstad (1991). The difference implied that longer test periods would result in more stable and higher heritability estimates (Luiting and Urff 1991b). Sabri, et al. (1991) also concluded that the heritability estimates were lowest when calculated for 4-wk periods, compared with other time-intervals larger than 4 wk. The heritability estimates for FCR (0.19 and 0.13) in the current study were slightly lower than those estimated by Mielenz et al. (1994) and Tixier-Boichard, et al. (1995). This implied that different genetic backgrounds could affect the estimates of heritability, as these 2 studies used populations divergently selected for RFI. Fewer heritability estimates are available in the literature for FCR in egg-type chickens. Our estimates were unexpectedly in accordance with those in turkey (Case et al. 2012), but much lower than those in meat-type chickens (Aggrey et al. 2010). Nevertheless, the similar heritability estimates found in the previous and present studies suggested a similar genetic basis for RFI and FCR in different layer populations. The heritability estimates for FI (0.20 and 0.26) in our study agreed well with the previous results in a male broiler line (Gaya et al. 2006), but diverged from several previous heritability estimates ranging from 0.30 to 0.48 in chickens (Luiting and Urff 1991b; Tixier-Boichard et al. 1995; Aggrey et al. 2010; Wolc et al. 2013). In contrast to RFI and FCR, FI was recorded by direct measurement. We inferred that non-additive effects (dominance effect, epistatic effect, and so on) for FI increased in the reciprocal crosses hence a smaller narrow-sense heritability estimate (Falconer and Mackay 1996). Metabolic BW possessed a comparable heritability with BW reported in the literature (Cahaner and Nitsan 1985; Luiting and Urff 1991b; Tixier-Boichard et al. 1995; Aggrey et al. 2010), while heritability estimates of BWG in adult hens were very small. In addition, the heritability estimates of EM (0.25 and 0.15) in the 2 laying periods demonstrated that heritability for traits related to egg production decreased with age (Engström et al. 1992).

Notably, correlation between RFI and FI in our study was much higher than those estimated in previous work

(Schulman et al. 1994; Tixier-Boichard et al. 1995). Similarly, we found that the correlation between RFI and FCR was higher in magnitude than those estimated by Hagger (1994) and Tixier-Boichard et al. (1995). The discrepancy may be due to the different population and slight differences in ages tested (traits at 40 and 60 wk in the present and 37 wk in the previous study). In addition, Savegnago et al. (2011) reported that the genetic parameter estimates may be increased when using divergent strains in reciprocal crosses. Therefore, an F₂ resource population created with the aim to generate recombination would consequently increase the “cross-variance” among these traits and hence an increase in the genetic correlation estimates (Falconer and Mackay 1996). RFI was weakly correlated with EM, which was in agreement with the previous studies by Schulman et al. (1994) and Tixier-Boichard et al. (1995), who reported low genetic correlations between RFI and egg production traits. The low phenotypic and genetic correlation between RFI and EM indicated that the major contributor to variation in RFI was not egg production but the variation in maintenance energy expenditure (Luiting 1990; Herd and Arthur 2009). Thus selection for reducing RFI does not automatically result in a change in EM in the current F₂ population. Interestingly, FCR was negatively correlated with EM but weakly correlated with FI, suggesting that FCR was mainly affected by EM in the resource population. Selection for increased egg production could result in a decreased FCR. Correspondingly, improvement in FCR mainly came from the genetic progress of egg mass in egg-type chicken breeding (Flock 1998). The negative correlations between RFI and MBW for both periods were similar to results published by Luiting (1991). In contrast to Luiting (1991) who did not observe any clear relationship between RFI and BWG, significant correlation between RFI and BWG was observed in the current study, but there was a big difference between the 2 testing periods. It is suggested that changes in the body composition and feeding behavior in the 2 periods may lead to the difference in genetic correlations.

In the current study, the correlation of RFI between the 2 testing periods was positive and high (0.76), which confirmed the findings of Luiting and Urff (1991b). Similarly, the correlations for FCR and FI in 2 different stages were also as high as 0.94 and 0.78, respectively. The high genetic correlation suggests that the feed efficiency traits in T1 and T2 share a similar genetic background. Similar heritability estimates for these traits in 2 stages also supported this suggestion. Based on the high correlations of feed efficiency traits between the 2 stages, early selection for these traits at 40 wk age may be effective and feasible.

In conclusion, our study described several properties of feed efficiency and its relevant traits in 2 laying periods of chickens. The moderate heritability estimates for both RFI and FCR suggest that feed efficiency can be directly improved by proper selection programs. Using

the population studied in the current study, selection for low RFI could reduce FI without significant changes in EM, while selection on FCR will increase EM. Our results provide valuable insight into genetic basic of feed efficiency traits in the laying period and could assist in designing selection programs for improvement of feed efficiency in egg-type chickens.

ACKNOWLEDGMENTS

The authors gratefully acknowledge staffs at Jiangsu Institute of Poultry Science for their technical assistance. The work was supported in parts by the National High Technology Development Plan of China (2013AA102501), China Agriculture Research Systems (CARS-41), Program for Changjiang Scholars and Innovative Research in University (IRT1191), and National Scientific Supporting Projects of China (2011BAD28B03).

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