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Effects of Maternal Factors on Day-old Chick Body Weight and Its Relationship with Weight at Six Weeks of Age in a Commercial Broiler Line

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ABSTRACT : The present study aimed to investigate the effects of maternal factors on body weight at hatching (day-old) and at six weeks of age in a commercial broiler line. A total of 6,765 records on body weight at day-old (BWTDO) and 115,421 records on body weight at six weeks of age (BWT6W), originated from a commercial broiler line during 14 generations, were used to estimate genetic parameters related to the effects of maternal traits on body weight of chicks immediately after hatch or six weeks thereafter. The data were analyzed using restricted maximum likelihood procedure (REML) and an animal model with DFREML software. Direct heritability (h^2_a), maternal heritability (h^2_m), and maternal environmental variance as the proportions of phenotypic variance (c^2) for body weight at day-old were estimated to be 0.050, 0.351, and 0.173, respectively. The respective estimated values for body weight at six weeks of age were 0.340, 0.022, and 0.030. The correlation coefficient between direct and maternal genetic effects for six-week-old body weight was found to be -0.335. Covariance components and genetic correlations were estimated using a bivariate analysis based on the best model determined by a univariate analysis. Between weights at hatching and at six week-old, the values of -0.07, 0.53 and 0.47 were found for the direct additive genetic variance, maternal additive genetic variance and permanent maternal environmental variance, respectively. The estimated correlation between direct additive genetic effect influencing weight at hatch and direct additive maternal effect affecting weight at six weeks of age was -0.21, whereas the correlation value of 0.15 was estimated between direct additive maternal effect influencing weight at hatch and direct additive genetic effect affecting weight at six-week-old. From the present findings, it can be concluded that the maternal additive genetic effect observed for weight at six weeks of age might be a factor transferred from genes influencing weight at hatch to weight at six-week-old. (**Key Words :** Broiler Line, Maternal Effects, Animal Model, Restricted Maximum Likelihood Procedure, Heritability, Genetic Variance)

INTRODUCTION

Heredity of economic and reproductive traits in living organisms results from genetic and environmental factors, with maternal and direct additive genetic effects being of great importance among the genetic factors. The importance or necessity of estimating the maternal effects and resulting consequences on chick body weight lies in the fact that these estimates are used to select the next generations of the female line (Szwacokowki et al., 2000). Maternal effects arise when the genetic and environmental characteristics of a mother influence the phenotype of her offspring, beyond the direct inheritance of alleles. These effects have long been recognized to be of great importance not only for early-life performance in most domestic species, but also for at least some further performance. However, there have been relatively few published papers on the estimation of maternal effects on body weights in poultry. Within the limited literature cited, Hartmann et al. (2003a) reported that the maternal heritability for chick weight was 0.50, whereas the direct heritability was close to zero in a White Leghorn line. Similar results, namely that maternal heritability (0.74, 0.26) is much more important than direct heritability (0.07, 0.16), have been reported for body weights at hatch in Japanese quails (Saatci et al., 2006) and in ostriches (Bunter and Cloete, 2004). Recent studies indicate that the body weight at hatch is greatly influenced by maternal additive genetic effect and is significantly positively correlated with additive genetic effect influencing albumen and yolk weight (Hartmann et al., 2003a,b). Also, mother genes are involved in determining egg weight, yolk weight, albumen weight, and percentage of albumen dry matter that greatly affect chick body weight at hatch

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(Hartmann et al., 2003b).

A number of studies have also estimated the magnitude of maternal effects on body weight at six weeks of age in broiler lines. Koerhuis and McKay (1996) and Le Bihan-Duval et al. (1998) indicated that maternal environmental effect on juvenile body weight in broiler chickens accounted for 4.14% and 3 to 8% of phenotypic variance, respectively. Also, a small but not-negligible maternal heritability (0.01 to 0.04) for body weight at six weeks of age has been reported by Koerhuis and Thompson (1997) and Navarro et al. (2006). Some studies have reported different results for the relationship between body weight at hatch and weight at slaughter. Powell (1965) studied the relationship between day-old chick weight and weight at slaughter, and reported a significant positive correlation between day-old weight and weight gain after hatching. Another study showed that one gram increase in egg weight resulted in 3.8 grams increase in slaughter weight for chicks from young mothers and 3.2 grams for those of aged hens (Prudfoot et al., 1982). Vieira and Moran (1998) found a negative correlation between these traits, while other studies such as Tona et al. (2004) found no significant relationship between day-old weight and weight at the end of the growth period except between weight above 7-10 day-old and weight at slaughter, where a positive correlation was reported.

To our knowledge, there is limited data reported to show the effect of maternal factors on phenotypic appearance of day-old body weight and its relationship with weight at six weeks of age in broiler lines. The objective of this study, therefore, was to compare estimates of genetic parameters using different animal models for body weight at hatch (day-old) and at six weeks of age in a commercial broiler line (Arian), and also to estimate the genetic correlations using the most appropriate model.

MATERIALS AND METHODS

Data

A total of 6,765 records on body weights at day-old (BWTDO) and 115,421 records on body weights at six weeks of age (BWT6W), originated from a commercial broiler (Arian) female line (Arian Co., Babol Kenar, Mazandaran, Iran), were obtained during 14 generations and used to estimate genetic parameters on the relationship between maternal factors and body weight at hatch and its relation with body weight at six-week-old broiler chicks. These chickens were the progeny of 1,377 sires and 10,650 dams. The studied line (Arian) consisted of four separate lines (2 male and 2 female lines), with one selection index based on multivariate models for each line. A coefficient was considered for each trait of interest based on an aggregate genotype model, with the higher coefficient values for reproductive traits (egg production, fertility, hatchability, etc.) in the female line. The structure of the data used is shown in Table 1.

Estimates of genetic parameters

(Co)variance components were estimated using "restricted maximum likelihood procedures (REML)"

Table 1. Structure of data set and descriptive statistics of performances of body weight in a broiler line

	Performance[1]	
	BWTDO	BWT6W
Total number of animals	115,782	115,782
Number of animals with records	6,765	115,421
Number of sires in total	1,377	1,377
With progeny in data	469	1,377
With own records	36	1,322
Average progeny records per sire	13.23	81.97
Number of dams in total	10,650	10,650
With progeny in data	2,914	10,650
With own records	347	10,362
Average progeny records per dam	2.22	10.52
Body weight		
Mean of total records during 14 generations (g)	42.33	1,704.96
Standard deviation (g)	4.06	233.66
Coefficient of variation (%)	8.60	9.51
Minimum weight over the generations (g)	28.00	500.00
Maximum weight over the generations (g)	58.00	2,665.00
Trend from the 1st to 14th generation (g)	32.21 to 41.53	1,232.3 to 2,193.5

[1] BWTDO = Day-old body weight (weight at hatch); BWT6W = Body weight at six weeks of age (42 d).

applied to univariate and bivariate animal models. Six different models (Table 2) were fitted to both BWTDO and BWT6W performances (Meyer, 1998). The univariate models run to evaluate the effects of maternal factors on body weight were as follow:

$y = Xb+Z_1a+e$ (M1)
$y = Xb+Z_1a+Wc+e$ (M2)
$y = Xb+Z_1a+Z_2m+e \quad COV(a, m) = 0$ (M3)
$y = Xb+Z_1a+Z_2m+e \quad COV(a, m) \neq 0$ (M4)
$y = Xb+Z_1a+Z_2m+Wc+e \quad COV(a, m) = 0$ (M7)
$y = Xb+Z_1a+Z_2m+Wc+e \quad COV(a, m) \neq 0$ (M8)

In these models, y and b are the vectors of observations and fixed effects (including generation, hatch number, sex and age of dam for both performance and age at weighing as a covariate for BWT6W only); terms a, c, m are all the random effects and are the vectors of additive genetic effects, maternal environmental effects, and maternal genetic effects, respectively; and **e** is the residual. X, Z_1, W and Z_2 are incidence matrices relating observations to the above vectors (b, a, c, and m, respectively). Cov (a, m) is the covariance between direct additive genetic and maternal effects. The convergence criterion was set at 10^{-8} for all of the analyses. A likelihood ratio test was $\log(\lambda) = L(b_2)-L(b_1)$, where L(b) is the likelihood function evaluated at the maximum likelihood estimator (b) (Dobson, 1990). The statistic $-2(\log L_2-\log L_1)$ has an x^2 distribution with degrees of freedom equal to the difference between the number of parameters for the two models being compared. The likelihood statistic was used to determine whether including additional random effects into the models significantly accounted for more variation (Morrell, 1998). The model which led to significantly higher likelihood was used to estimate the genetic and phenotypic correlations.

The bivariate analysis was conducted using DFREML software (Meyer, 1998) based on the most appropriate animal model obtained from univariate analysis. If all random effects are assumed to be significant, the statistical model for body weight at hatch and at six weeks of age will be as follow:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix}\begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix}\begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix}\begin{bmatrix} m_1 \\ m_2 \end{bmatrix} + \begin{bmatrix} W_1 & 0 \\ 0 & W_2 \end{bmatrix}\begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

Where, the indices 1 and 2 are related to body weights at hatch and at six weeks of age, respectively; y_i designates the vector of observations; b_i, the vector of fixed factors; a_i, the vector of direct additive genetic effect; m_i, the vector of maternal additive genetic effect; c_i, the vector of environmental effect; e_i, the vector of residual effect; and X, Z_1, Z_2 and W are incidence matrixes relating fixed, direct additive genetic, maternal additive genetic and maternal environmental effects to above vectors, respectively. Fixed factors include generation, hatching number, sex, and mother age.

RESULTS AND DISCUSSION

Univariate analysis

Univariate estimates of genetic parameters differed across models for BWTDO and BWT6W (Tables 2 and 3). For performance at both stages (hatch and six-week-old), Model 1 resulted in the higher estimates of direct heritability (0.735 for BWTDO and 0.439 for BWT6W). Inclusion of maternal (genetic and environmental) effects into the models (Models 2 to 8) caused a decrease in direct heritability estimates, and the value of log likelihood over Model 1 was significantly ($p<0.01$) increased. Based on the estimate values obtained for the log likelihood in different models, Models 7 and 8 can be considered as the most appropriate ones for BWTDO performance, but including the covariance of maternal and direct additive genetic effects into Model 8 for BWT6W caused a significant ($p<0.05$) increase in the log likelihood. On the other hand, Model 8 can be presented as the most appropriate model for estimation of variance components for BWT6W. Including maternal effects into the models (as in Model 8) is needed because the selection based on genetic evaluations requires accurate estimates of genetic and environmental parameters

Table 2. Estimates of (co)variance components and derived parameters for day-old body weight

Models	σ_a^2	σ_c^2	σ_m^2	σ_{am}	σ_e^2	σ_p^2	h^2_a±SE	c^2±SE	h^2_m±SE	r_{am}	Log L
M1	10.150	-	-	-	3.650	13.801	0.745±0.024		-	-	-11,259.84
M2	3.080	4.770	-	-	4.181	12.041	0.256±0.033	0.397±0.018	-	-	-10,901.50
M3	0.658	-	7.901	-	5.420	13.980	0.047±0.020	-	0.565±0.017	-	-10,842.44
M4	0.876	-	8.602	-0.851	5.312	13.950	0.063	-	0.617	-0.307	-10,840.88
M7	0.630	2.153	4.372	-	5.302	12.451	0.051±0.024	0.173±0.026	0.351±0.034	-	-10,820.83
M8	0.719	2.123	4.621	-0.242	5.260	12.471	0.058	0.170	0.370	-0.133	-10,820.65

h^2_a = Direct heritability; h^2_m = Maternal heritability; c^2 = Proportion of maternal environmental variance to phenotypic variance; r_{am} = Correlation between direct additive genetic effect and maternal additive genetic effect; σ^2_a = Direct additive genetic effect variance; σ^2_c = Maternal environmental effect variance; σ^2_m = Maternal additive genetic effect variance; σ_{am} = Covariance between direct additive genetic effect and maternal additive genetic effect; σ^2_e = Residual effect variance; σ^2_p = Phenotypic effect variance; Log L: Log likelihood.

Table 3. Estimates of (co)variance components and derived parameters for body weight at six weeks of age

Models	σ_a^2	σ_c^2	σ_m^2	σ_{am}	σ_e^2	σ_p^2	h^2_a±SE	c^2±SE	h^2_m±SE	r_{am}	Log L
M1	11,574.33	-	-	-	14,785.66	26,359.99	0.439±0.010	-	-	-	-632,869.01
M2	7,940.50	859.94	-	-	16,143.08	24,943.52	0.318±0.013	0.035±0.002	-	-	-632,706.41
M3	8,490. 90	-	1,159.29	-	15,947.37	25,597.55	0.332V0.013	-	0.045±0.011	-	-632,727.25
M4	8,686.49	-	1,231.59	-176.41	15,858.27	25,599.94	0.339	-	0.048	-0.054	-632,726.80
M7	7,657.97	625.42	414.91	-	16,267.37	24,965.67	0.307±0.013	0.025±0.004	0.017±0.011	-	-632,687.75
M8	8,468.02	736.80	549.55	-723.3	15,891.82	24,922.88	0.340	0.030	0.022	-0.335	-632,679.23

h^2_a = Direct heritability; h^2_m = Maternal heritability; c^2 = Proportion of maternal environmental variance to phenotypic variance; r_{am} = Correlation between direct additive genetic effect and maternal additive genetic effect; σ^2_a = Direct additive genetic effect variance; σ_c = Maternal environmental effect variance; σ^2_m = Maternal additive genetic effect variance; σ_{am} = Covariance between direct additive genetic effect and maternal additive genetic effect; σ^2_e = Residual effect variance; σ^2_p = Phenotypic effect variance; Log L = Log likelihood.

(Lee and Pollak, 1997a,b). In this regard, Lee and Pollak (1997b) stated that the additive direct and maternal genetic effects have been integral components in genetic evaluation of weaning weight in beef cattle. Recent researchers observed that the correlation estimate between additive direct and maternal genetic effects, ignoring sex by year interactions, was negative (-0.29) in Simmental beef cattle (Lee and Pollak, 1997b). In the same study, direct and maternal genetic variances were deflated when the covariance was ignored, leading to significantly lower estimates of heritability for both. This result indicates that if the fixed effects and their interactions are detected, then they are true effects, not spurious results due to an incorrect direct and maternal covariance (Lee and Pollak, 1997b). Therefore, removing interactions from the models used for estimating (co)variance components is a potential source of bias in estimations (Lee and Pollak, 1997a,b).

Consistent with the present finding, Fathi (2003) reported that the analysis of six-week-old body weight records using an animal model resulted in overestimation of direct additive genetic variance and direct heritability if maternal additive genetic effect and environmental maternal effect are not taken into account. The increase in the estimated heritability from 56.2 (Model 2) to 92% (Model 8) compared to Model 1 supports this point.

The estimated value and the sign of covariance for maternal and direct additive genetic effects did not have any significant effects on the estimated maternal and direct heritability values. As shown in Table 2, introducing this factor into the model only caused an increase in the estimated values of maternal and direct heritability compared to the scenarios in which these traits were not included in the model. The main reason for this could be the negative covariance of maternal and direct additive genetic effects which were -0.85 and -0.24 for Models 4 and 8, respectively.

Although Model 7 was an appropriate model for body weight at hatch, Model 8 can be considered as the most appropriate one for both body weights at hatching and at six-week-old. However, bivariate analysis was based on Model 8 due to the negative estimated value of correlation between maternal and direct additive genetic effects (-0.133). Under this model, the estimates of h^2, c^2, m^2 and r_{am} were 0.058, 0.170, 0.370 and -0.133 for BWTDO and 0.340, 0.030, 0.022 and -0.335 for BWT6W, respectively. The importance of maternal effects on estimates of body weight performance as evidenced in the present study was consistent with the reports by Koerhuis and Thompson (1997), Hartmann et al. (2003a), and Navarro et al. (2006). The later results indicate three points: firstly, examination of the results obtained from the running animal models shows a reduction in the heritability value from 25 (Model 4) to 34% (Model 7) as compared to Model 1. This indicates that the running simple animal model in which only direct additive genetic effect is taken into account, will lead to overestimation of the estimated direct heritability value; secondly, as shown in Table 3, consideration of covariance of maternal and direct additive genetic effect in the model resulted in a significant increase in the estimated value of log likelihood. Estimated values of maternal and direct heritability are considerably affected by the value and the sign of the covariance of maternal and direct additive genetic effects, as shown by Models 4 or 8. Therefore, selection of birds for body weight at six weeks of age based on direct breeding values may reduce the frequency of controlling genes for maternal capabilities; and thirdly, the results derived from Model 8 show the estimated values of 0.022 and 0.030 for maternal heritability and maternal environmental effect, respectively. As there is no relation between chicks and their mothers up to the six-week-old, it seems that these effects might be due to the correlation between maternal effects for body weight at hatch and at six weeks of age. As a conclusion, step by step introducing of affecter variables into the models make them an appropriate model for prediction of genetic components.

Bivariate analysis

Bivariate estimates of genetic parameters obtained using the most appropriate model (Model 8) for BWTDO and BWT6W are shown in Table 4. In general, the estimates of

Table 4. Estimation of variance and covariance components and genetic parameters for body weights at hatch and at six weeks of age with bivariate and univariate analyses

		σ_a^2	σ_c^2	σ_m^2	σ_{am}	σ_e^2	σ_p^2	h^2_a±SE	c^2±SE	h^2_m±SE	r_{am}
day-old body weight	Bivariate	0.65	2.08	4.74	-0.214	5.28	12.54	0.052±0.02	0.166±0.020	0.378±0.010	-0.122
	Univariate	0.72	2.12	4.62	-0.243	5.26	12.47	0.057±0.024	0.170±0.017	0.370±0.013	-0.133
body weight at six weeks of age	Bivariate	8,386.44	732.21	554.25	-696.58	15,929.96	26,291	0.337±0.013	0.029±0.005	0.022±0.009	-0.323
	Univariate	8,468.02	736.80	549.55	-723.30	15,891.82	24,923	0.340±0.014	0.030±0.003	0.022±0.010	-0.335

h^2_a = Direct heritability; h^2_m = Maternal heritability; c^2 = Proportion of maternal environmental variance to phenotypic variance; r_{am} = Correlation between direct additive genetic effect and maternal additive genetic effect; σ^2_a = Direct additive genetic effect variance; σ^2_c = Maternal environmental effect variance; σ^2_m = Maternal additive genetic effect variance; σ_{am} = Covariance between direct additive genetic effect and maternal additive genetic effect; σ^2_e = Residual effect variance; σ^2_p = Phenotypic effect variance.

genetic parameters were very similar to those obtained from the univariate analysis. The additive genetic correlation between BWTDO and BWT6W (Table 5) was negative and low (-0.07), indicating an increase in body weight at hatch will lead to no important alteration in chick body weight at six weeks of age. These estimates for correlations between maternal parameters were positive and high with a value of 0.47 for maternal environment and 0.53 for maternal additive genetic. The high maternal additive genetic correlation shows that these performances are influenced to some extent by similar maternal genes, and selection based on maternal breeding values of body weight at hatch will increase potential maternal abilities for chick body weight at older ages (Table 6). Using the bivariate analysis, the correlations between maternal and direct additive genetic effects for BWTDO and BWT6W performances were estimated to be -0.12 and -0.32, respectively. These estimates are similar to the respective values of the univariate analysis (0.13 and 0.34). The negative and low to moderate estimates of r_{a1m1} (-0.12) and r_{a2m2} (-0.32) were in agreement with those reported by Koerhuis and Thompson (1997). These findings may reflect a real genetic antagonism between performance traits and those traits related to hen maternal ability such as egg weight and egg compositions. The estimate of cross-correlation between direct additive genetic effects for BWTDO and maternal additive genetic effects for BWT6W (r_{a1m2}) was moderate and negative (-0.21). The later result shows that the selection based on the direct breeding value for increasing weight at hatch can decrease effects of maternal capabilities on weight at six weeks of age. This correlation coefficient between maternal additive genetic effects for BWTDO and direct additive genetic effects for BWT6W (r_{a2m1}) was low and positive (0.15), indicating that selection based on BWT6W may lead to an increase in maternal ability for BWTDO performance.

CONCLUSIONS

The results proved that ignoring maternal effects lead to the over-estimation of direct heritability for BWTDO and BWT6W. The magnitude of maternal heritability was substantial and greater than direct heritability for BWTDO. Also, maternal effects were still a significant source of

Table 5. Estimation of (co)variance and correlation coefficients between body weight at hatch and at six weeks of age with bivariate analysis based on the most appropriate model (Model 8)

Model	σ_{a12}	σ_{c12}	σ_{m12}	σ_{e12}	σ_{p12}	r_{a12}	r_{c12}	r_{m12}	r_{e12}	r_{p12}
Model 8	-5.50	18.29	27.23	30.96	83.69	-0.07	0.47	0.53	0.11	0.15

σ_{a12} = Genetic covariance between the 1st and 2nd traits; σ_{m12} = Maternal genetic covariance between the 1st and 2nd traits; σ_{c12} = Environmental covariance between the 1st and 2nd traits; σ_{e12} = Residual covariance between the 1st and 2nd traits; σ_{p12} = Phenotype covariance between the 1st and 2nd traits; r_{a12} = Correlation between direct genetic effects for the 1st and 2nd traits; r_{m12} = Correlation between maternal genetic effects for the 1st and 2nd traits; r_{c12} = Correlation between environmental maternal effects for the 1st and 2nd traits; r_{e12} = Correlation between residual effects for the 1st and 2nd traits; r_{p12} = Correlation between phenotype effects for the 1st and 2nd traits.

Table 6. (Co)variance and correlation coefficients between direct additive genetic effects and maternal additive genetic effects of two studied traits (body weight at hatch and at six weeks of age) alone or with each other based on Model 8

Model	σ_{a1m1}	σ_{a1m2}	σ_{a2m1}	σ_{a2m2}	r_{a1m1}	r_{a1m2}	r_{a2m1}	r_{a2m2}
Model 8	-0.21	-4.05	29.47	-696.58	-0.12	-0.21	0.15	-0.32

σ_{a1m1} = Covariance between direct and maternal genetic effects for the 1st trait; σ_{a1m2} = Covariance between direct genetic effect for the 1st trait and maternal genetic effect for the 2nd trait; σ_{a2m1} = Covariance between direct genetic effect of the 2nd trait and maternal genetic effect for the 1st trait; σ_{a2m2} = Covariance between direct and maternal genetic effects for the 2nd trait; r_{a1m1} = Correlation between direct and maternal genetic effects for the 1st trait; r_{a1m2} = Correlation between direct genetic effect of the 1st trait and maternal genetic effect for the 2nd trait; r_{a2m1} = Correlation between direct genetic effect of the 2nd trait and maternal genetic effect for the 1st trait; r_{a2m2} = Covariance between direct and maternal genetic effects for the 2nd trait.

variation for BWT6W, but their relative importance was markedly reduced. For performance at six-week-old, the influence of maternal effects could be a carry-over effect from BWTDO. The estimates of cross-correlations indicated that the selection based on direct additive genetic effect of BWTDO can lead to a decrease in maternal ability for body weight at six weeks of age.

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