

## ESTIMATION OF MATERNAL EFFECTS ON THE NORTH-IRANIAN NATIVE CHICKEN TRAITS USING BAYESIAN AND REML METHODS

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### ABSTRACT

In the present research, direct and maternal genetic parameters were estimated for 4 productive and reproductive traits of Iranian native chickens. Six different animal models with restricted maximum likelihood (REML) and Bayesian procedure were applied to estimate genetic parameters. The chickens were investigated considering their phenotypic and genotypic trend after 19 generation selection. Estimated direct and maternal heritability is based on best models using REML methods: 0.55, 0.01 for average egg weight; 0.22, 0.009 for body weight at 8 weeks old; 0.15, 0.02 for egg number and 0.39, 0.045 for age at sexual maturity, respectively. The estimated values of these parameters using Bayesian approach for studied traits are based on best model: 0.54, 0.034 for average egg weight, 0.23 and 0.044 for body weight at 8 weeks old, 0.15, 0.02 for egg number and 0.41, 0.048 for age at sexual maturity, respectively. In this study, the results obtained from the statistical REML method are similar to that of Bayesian approach, but there are differences between the traits regarding the selection of best model due to different ways of models' evaluation. The result of genetic trend regarding average egg weight, body weight at 8 weeks old, egg number and age at sexual maturity were -0.100 (g), 5.650 (g), 0.721 (number) and -1.558 (day), respectively. Correlation of the direct and maternal genetic effects ( $r_{am}$ ) for studied traits was estimated. Consequently, a negative correlation between maternal and direct additive genetic effects was observed.

**Key words:** genetic parameters; native chicken; maternal effects; REML; Bayesian

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### INTRODUCTION

In recent decades, breeding programs and genetic gain have an important effect on the genetic composition of commercial chickens (Muir *et al.*, 2008). But the question striking to mind is what would be the future of genetic diversity of pure commercial line. Muir *et al.* (2008) showed that 50 % or more of the genetic diversity in ancestral breeds is absent in commercial pure line. This absence resulted from high number of non-corporate breeds. These studies indicate an important role of native chicken in satisfying future genetic diversity needs. The first goal of the Mazandaran breeding center was to conserve the native chicken's gene pool and the second one was to increase the production ability of this breed for that environmental condition in developing

the rural industry. It is important to have an accurate (co) variance component and consequent genetic parameters for every animal breeding program. To achieve this aim, several statistical methods have been used during the four past decades. Two powerful statistical methods are still being widely used for different animal breeding researches. The first one is Restricted Maximum Likelihood (REML) using popular algorithm average information REML (AI-REML; Misztal, 2008) and the second one is a Bayesian method using Gibbs sampling (BAGS) technique. The BAGS method has been widely used in different animal breeding programs (Wing, 1993a, 1994b; Jensen, 1994; Sorenson, 1994; Van Tassel and Van Vleck, 1996). Direct and maternal genetic effects are genetically correlated. The maternal effect influenced the progeny phenotype due to genetic and environmental

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differences between dams (Grosso *et al.*, 2010). There is a very high genetic correlation between the maternal effect on chick weight and the direct effect on egg weight (Hartman *et al.*, 2003). In another study by Saatci (2006) strong correlation was detected between direct genetic effect of egg traits and maternal genetic effect of BW trait. Several studies have reported estimates of (co) variance components, additive and maternal genetic parameters considering productive and reproductive traits of native chicken (Kamali *et al.*, 2007; Seraj *et al.*, 2006; Xu *et al.*, 2011). The aim of this research was to estimate the genetic parameters and correlation between direct and maternal genetic effect with different animal models using both REML and Bayesian methods. An additional aim was to calculate predicted genetic trend following selection over 19 generations.

## MATERIAL AND METHODS

### Birds and data

Mazandaran province in the north of Iran has mostly a rainy and humid climate. In this research, data on 74500 Iranian native hens which belong to the breeding center of Mazandaran native chickens from founder generation (G0) to generation 19 (G19) were used to estimate (co) variance component and genetic parameters of productive and reproductive traits. All laying chickens were selected from a small population, with an individual phenotypic value of body weight in 8 weeks (BW8) of age and egg number (EN) during the first 12 weeks of the laying period. For first generation, the eggs were collected from rural areas without any background of birds and were hatched to compose the basic population. Parents were selected on the basis of BW8 and the production of their sisters. All birds were reared on the floor for 8 weeks. Following that, a number

of laying native chickens were selected according to their body weights, transferred into the individual cages and their production traits were recorded. The selection intensities were 40 % for hens and 5 % for cocks during the breeding process. The collected data from the individuals included Body Weight at 8 weeks of age (BW8), Egg Number during the first 12 weeks of the laying period due to the average period of Mazandaran native fowl is 12, so that during the selection only 12 weeks of laying period were monitored Average Egg Weight (AEW) at 28, 30 and 32, weeks old of chickens and Age at Sexual Maturity (ASM). The data file of animal consists of sire, dam number, generation, hatch number and sex (for BW8 trait), number of productivity days as a covariate (for EN trait) and information about other traits.

### Statistical analysis

The statistical description of the traits is summarized in Table 1. Because of missing observation, the number of observations was different between traits. The Proc Univariate was used for editing data to remove outlier values. The GLM procedure of SAS software (SAS, 2003) was used to test the significance of the fixed effects of generation (in 19 levels), hatch number (maximum 6 levels in each generation) and sex (in 2 levels) in the model. As shown in Table 1, fitting these fixed effects in a model as contemporary group effects of generation - hatch (GH) for AEW, ASM and EN and generation - hatch - sex (GHS) for BW8 have significant ( $P < 0.0001$ ) effects in studying these traits. The effect of days in production (DP) was fitted in the model considering EN trait. It should be noted that egg laying period was different among hens; therefore this effect was included in the model as a covariate. For estimation of (co) variance components and genetic parameters six different animal models were used as follows (Meyer, 1998):

**Table 1: Basic data statistics**

Trait	N	Mean	SD	Min	Max	C.V %
AEW	44183	47.67	4.98	26.50	83.2	10.32
BW8	73726	574.72	166.89	400	1400	17.56
EN	31967	36.65	15.49	15	95	38.61
ASM	42919	163.56	16.72	120	235	1.35

Number of observations (N), calculated mean (Mean), Standard deviation (SD), Coefficient of variation (C.V), Minimum (Min), Maximum (Max) Value of traits and of traits AEW= average egg weight (g), BW8 = body weight at 8 weeks of age (g), EN = egg number and (ASM) age at sexual maturity (day) in 19 generation of selection

$y = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{e}$		Model (1)
$y = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Wc} + \mathbf{e}$		Model (2)
$y = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{e}$	cov (a,m) = 0	Model (3)
$y = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{e}$	cov (a,m) $\neq$ 0	Model (4)
$y = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{Wc} + \mathbf{e}$	cov (a,m) = 0	Model (5)
$y = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{Wc} + \mathbf{e}$	cov (a,m) $\neq$ 0	Model (6)

The first model is a simple animal model including only additive animal genetic effects as random effects. Model 2 included the maternal permanent environmental effect as additional random effects which had no relationship with the other effects. Model 3 included maternal genetic effects as a second random genetic effect having no covariance between the direct and maternal effects, i.e.  $\sigma_{am} = 0$ . In the model 4, the covariance between them is not set to zero. In the model 5 and 6, both the permanent environmental and maternal genetic effects were considered. The differences between model 5 and 6 are in ignoring and considering covariance between direct and maternal effects, respectively. In these models,  $\mathbf{y}$  = the vector of observations,  $\mathbf{b}$  = vector of fixed effects including (generation, hatch number of all traits and days in product (DP) as a covariate of EN only),  $\mathbf{a}$  = vector of direct genetic effects,  $\mathbf{m}$  = vector of maternal genetic effects, and  $\mathbf{e}$  = vector of residual effects and  $\mathbf{X}$  = incidence matrix relating to the observation obtained from fixed effects.  $\mathbf{Z}_1$ ,  $\mathbf{Z}_2$  and  $\mathbf{W}$  are incidence matrices relating observation to the above mentioned random vectors ( $\mathbf{a}$ ,  $\mathbf{m}$ , and  $\mathbf{c}$ , respectively). The covariance structure of the full model ( $M_6$ ) will be as follows:

$$V = \begin{bmatrix} a \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 \\ 0 & 0 & I\sigma_c^2 & 0 \\ 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix},$$

Where,  $\sigma_a^2$  = direct additive genetic variance,  $\sigma_m^2$  = the maternal additive genetic variance,  $\sigma_{am}^2$  = covariance between, direct and maternal genetic effects,  $\sigma_c^2$  = maternal permanent environmental variance,  $\sigma_e^2$  = residual variance. The basic assumptions in these models were:  $E[\mathbf{y}] = \mathbf{Xb}$ ;  $E[\mathbf{a}] = 0$ ;  $E[\mathbf{c}] = 0$  and  $E[\mathbf{e}] = 0$ . Total phenotypic variance ( $\sigma_p^2$ ) was estimated as the while cumulating all (co) variance components. Direct heritability ( $h^2$ ), maternal genetic heritability ( $h_m^2$ ) and proportion of maternal permanent environmental variance to phenotypic variance ( $c^2$ ) were calculated. In Table 2 more information is included to make the statistical importance of effects more clearly.

Total heritability resulting from incorporating direct-maternal genetic covariance and variance from heritable maternal effects was calculated using the formula

$$h_{tot}^2 = (\sigma_a^2 + 0.5 * \sigma_m^2 + 1.5 * \sigma_{am}^2) / \sigma_p^2 \quad \text{Willham (1972).}$$

Estimation of (co) variance components in the first step was done by REML using an average information algorithm by AI-REMLF90 Misztal (1999b) software. The convergence criterion was set at  $10^{-10}$  for most of the analyses. To test the significance of the random maternal (genetic and permanent environmental) effects in REML method, the likelihood ratio test with k degree of freedom was used, where k is set to the number of additional factors in the complete model of Dobson (1990).

$$\chi_k^2 = 2 \log(L) - 2 \log(L(R)),$$

where L (F) = the likelihood of full model, and L (R) the likelihood of reduced model. In the second step, BAGS method was applied by GIBBS3F90 Misztal (1999a) software. In each analysis, 500000 rounds of Gibbs sampling were conducted. The first 50000 steps were discarded as a burn-in period, and the thinning interval was constant at 100 cycles. The deviance information

**Table 2: Univariate animal model for Mazandaran chicken**

Factor	Type <sup>a</sup>	Trait <sup>b</sup>			
		AEW	BW8	EN	ASM
Generation	F	×	×	×	×
Hatch	F	×	×	×	×
Sex	F	-	×	-	-
Days in production	C	-	-	×	-
Additive animal genetic effect	A	×	×	×	×
Additive maternal genetic effect	A	×	×	×	×
Maternal permanent effects	R	×	×	×	×

<sup>a</sup> Type of factor: F, fixed factor, R, random factor, A, random factor with covariance matrix, C, covariable

<sup>b</sup> Traits: see footnotes for Table 1.

criterion (DIC) was used for model compared with BAGS methods. The idea is that models with smaller DIC should be preferred to models with larger DIC. The phenotypic and genetic trend of studied traits was estimated by regression of Least Square Means (LSM) and an average of breeding values of birds on generation in nineteen generations of selection, respectively.

## RESULTS AND DISCUSSION

There were different estimation of (co) variance components and genetic parameters considering different models. Results of Restricted maximum likelihood and Bayesian approach using Gibbs sampling regarding AEW, BW8, EN and ASM are shown in Tables 3 and 4, respectively. Estimated direct heritability of AEW using REML method was 0.55 based on the best model (model 6), compared to the BAGS method in which this value was 0.54. From all of the models, model 4 was regarded as a good model. Based on model 6 with REML method, estimates of  $c^2$  and  $h_m^2$  were 0.03, 0.01 respectively.

Using Bayesian method estimated  $h_m^2$  proved to be 0.34. According to these methods total heritability was 0.48 and 0.47 for REML and Bayesian method, respectively. As shown in Table 3, estimated  $h^2$ ,  $c^2$ ,  $h_m^2$  and  $r_{am}$  in BW8 by REML method were 0.22, 0.041, 0.009 and -0.52 respectively. According to the model 4 as the best model used in Bayesian method  $h^2$ ,  $h_m^2$  and  $r_{am}$  of BW8 were 0.23, 0.044, -0.17 respectively. Estimated total heritabilities regarding REML and Bayesian methods of BW8 were 0.19 and 0.23 in that order. According to the same obtained results of EN based on model 6 as a good model in both REML and Bayesian methods estimation of direct heritability, proportion of maternal environmental variance to phenotypic variance ( $c^2$ ), maternal heritability ( $h_m^2$ ) and total heritability ( $h_t^2$ ) of EN were 0.15, 0.02, 0.02 and 0.10, respectively. The estimated correlation between direct additive genetic effect and maternal additive genetic effects ( $r_{am}$ ) of EN proved to be -0.74 using REML method and -0.77 using BAGS method. As shown in Table 4, estimation of direct and maternal heritability of ASM based on the best model (model 6) in REML method was 0.39 and

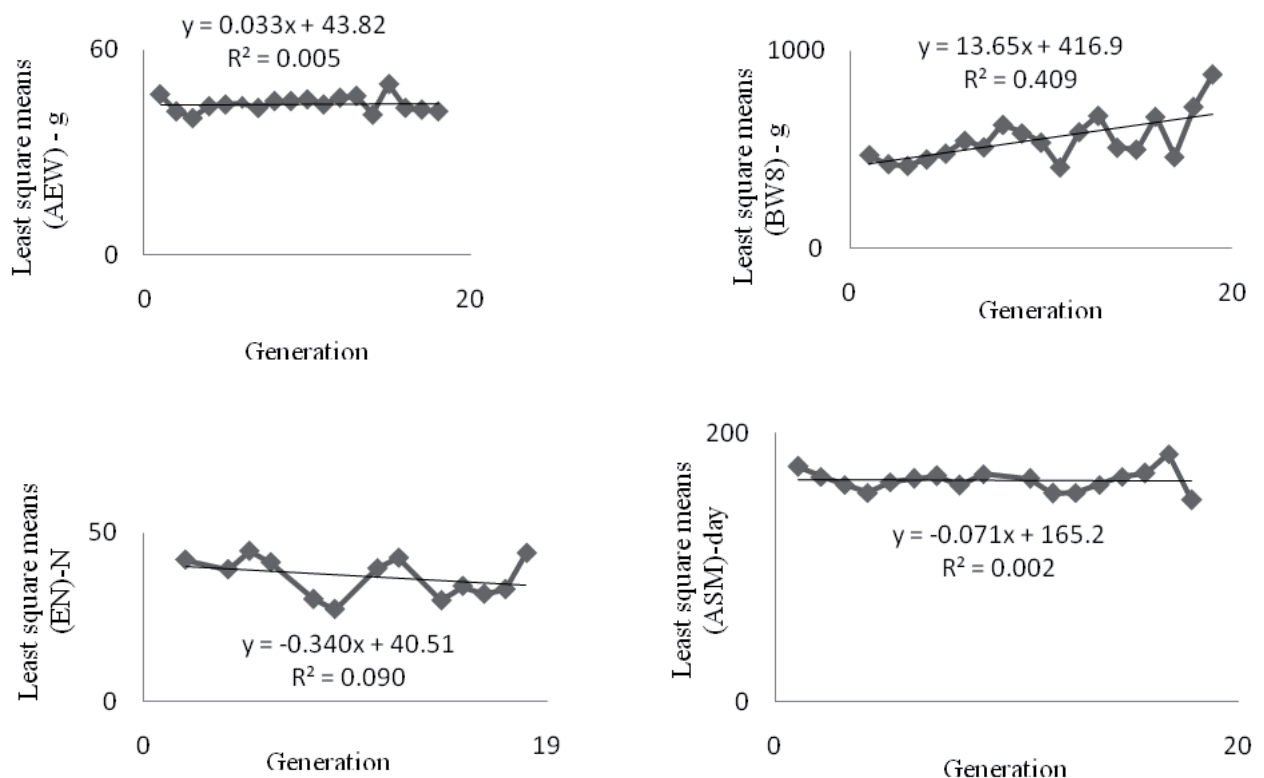


Fig. 1: Phenotypic trend of : (a) average egg weight (AEW), (b) body weight at 8 weeks of age (BW8), (c) egg number (EN) and (d) age at sexual maturity in 19 generations of selection

0.045 respectively. According to this model the estimated values for ( $c^2$ ), ( $r_{am}$ ) and ( $h^2$ ) were 0.054, -0.37 and 0.34 respectively. The estimated genetic parameters of ASM using Bayesian methods are shown in Table 4, direct heritability of ASM based on model 4 as a better model was 0.41 and the estimated maternal heritability of this trait was 0.048. The correlation between direct additive genetic effect and maternal additive genetic effects ( $r_{am}$ ) and total heritability were estimated to be -0.38 and 0.36 respectively. As shown in Figure 1, (a) to (d), the phenotypic trends were calculated considering studying traits. The least square means on generation number were 0.33 (g), 13.65 (g), -0.34 (num) and -0.71 (day) for AEW, BW8, EN and ASM respectively. As reported in Figure 2, (a) to (d), the genetic trend estimation of AEW, BW8, EN and ASM were -0.100, 5.65, 0.72, and -1.558, respectively. The genetic trend estimation showed a

significant and positive improvement in trait BW8 and EN and the genetic trend of AEW trait proved to be negative due to a negative correlation present between EN and AEW. According to negative genetic trend of ASM, the age of maturation in this breed decreased as well during the 19 generation selection. Considering these traits genetic trends indicate that selection would be effective. The means of the posterior distribution of additive genetic variance of average egg weight, body weight at 8 weeks, egg number and age at sexual maturity are shown in Figure 3 (a) to (d).

In the studies of Chamber *et al.* (1990) and Akbas *et al.* (2002), the maternal genetic effects were evaluated using different models with considering paternal and maternal half-sib and full-sib progeny. According to their reports, the highest value of direct heritability in maternal half-sib progeny was estimated by maternal effects. In

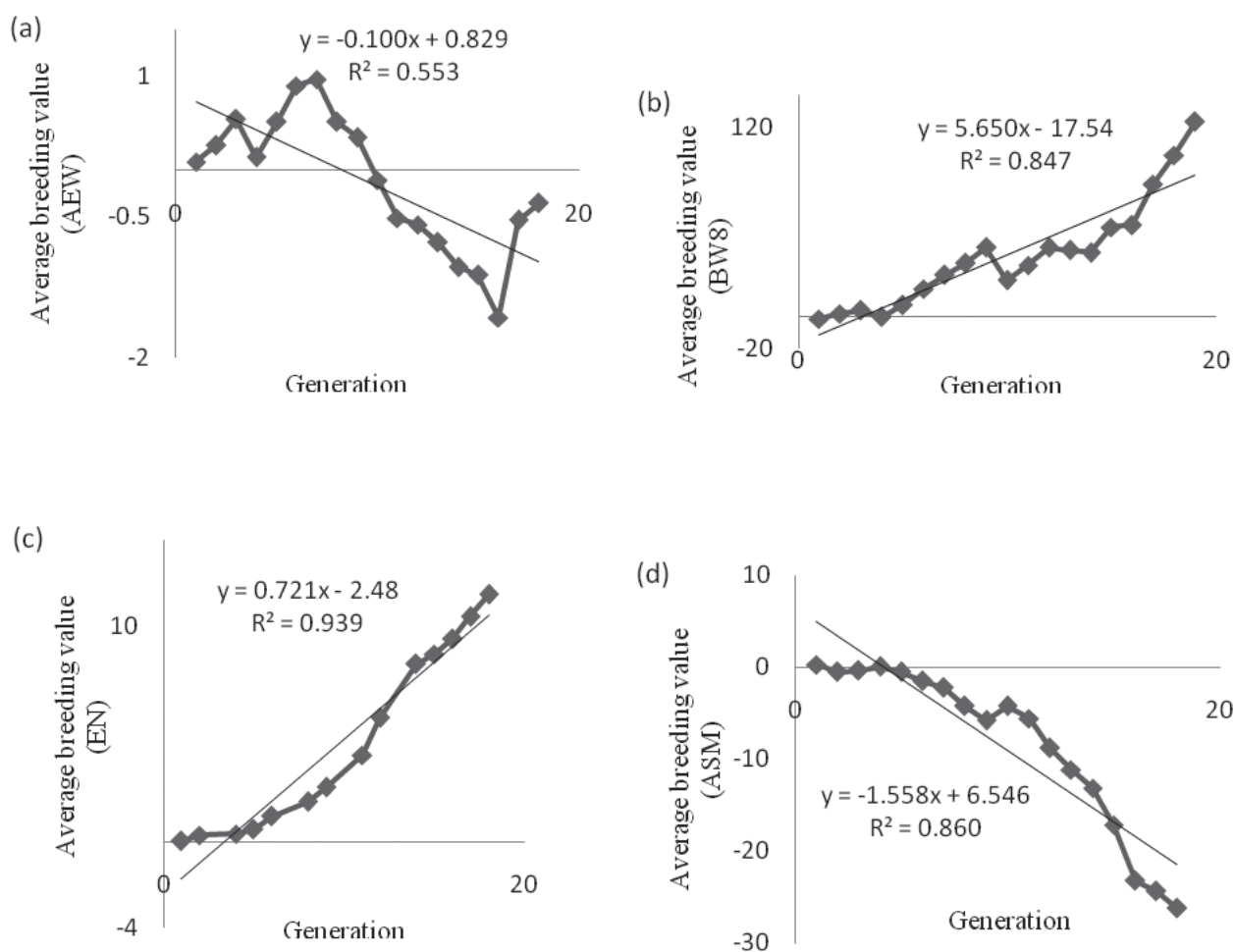
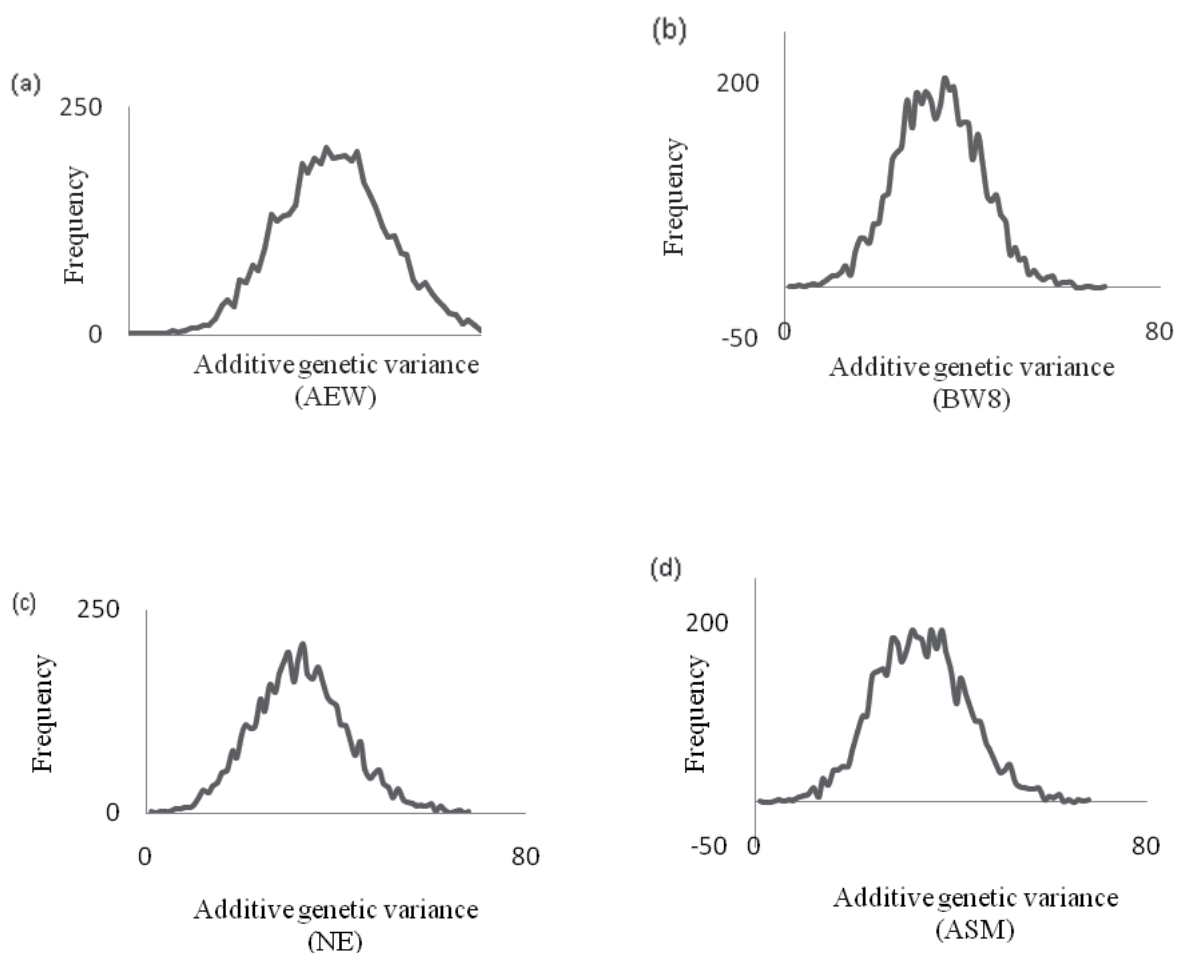


Fig. 2: Genetic trend of : (a) average egg weight (AEW), (b) body weight at 8 weeks of age (BW8), (c) egg number (EN) and (d) age at sexual maturity in 19 generations of selection

another study on Iranian native chicken by Seraj *et al.* (2007) it was revealed that maternal genetic and environmental effects considering the covariance of maternal and direct genetic effects proved to be important for body weight at 8 weeks, which are similar to our results. Fathi (2003) reported that estimated genetic parameters for six-week-old body weight using an animal model results in an overestimation of direct additive genetic variance and heritability if maternal additive genetic and environmental effects were ignored in the models. Our results indicate that estimated heritability decreased in complete model as compared with other simple models due to the negative covariance of maternal and direct genetic effects in studied traits. Consistent with the present finding, Rahman *et al.* (2010) reported that the analysis of day-old chick body weight and six-week-old body weight records on commercial broiler line and

the direct maternal 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. Koerhuis *et al.* (1996) allocated 2, 2, 3, and 4 % of observed phenotypic variance from egg weight, age at sexual maturity, egg number and six-week weight of a broiler line trait to maternal environmental effects, which are inconsistent with the results of the current research. In a study by Koerhuis *et al.* (1997) maternal heritability and maternal permanent environment as a proportional of phenotypic variance on six-week-old body weight of the chicks was estimated to be 2 - 4 and 5 - 6 percentages, respectively. The results of this study indicated that ignoring maternal effects in the model resulted in overestimating of additive genetic variance and direct heritability considering a body weight at 8 weeks-old traits. Regarding age at sexual maturity, average egg



**Fig. 3:** The posterior distribution of additive genetic variance for (a) average egg weight (AEW), (b) body weight at 8 weeks of age (BW8), (c) egg number (EN) and (d) age at sexual maturity

**Table 3: Estimation of (co) variance component and derived parameters for average egg weight and body weight at 8 weeks old**

Traits	Method	M	$h_a^2 \pm \text{S.E.}$	$c^2 \pm \text{S.E.}$	$h_m^2 \pm \text{S.E.}$	$r_{am}$	$h_t^2$	$-2\text{Log}L, DIC$
AEW	REML	1	$0.51 \pm 0.01$	-	-	-	-	258188
		2	$0.50 \pm 0.02$	$0.02 \pm 0.004$	-	-	-	229500
		3	$0.49 \pm 0.01$	-	$0.02 \pm 0.005$	-	0.50	204108
		4	$0.54 \pm 0.02$	-	$0.03 \pm 0.013$	-0.36	0.48	204078
		5	$0.49 \pm 0.02$	$0.01 \pm 0.005$	$0.01 \pm 0.005$	-	0.50	204082
		6*	$0.55 \pm 0.03$	$0.03 \pm 0.005$	$0.01 \pm 0.001$	-0.53	0.48	204040
	Bayesian	1	$0.50 \pm 0.02$	-	-	-	-	220675
		2	$0.48 \pm 0.02$	$0.03 \pm 0.007$	-	-	-	224878
		3	$0.49 \pm 0.02$	-	$0.02 \pm 0.009$	-	0.50	220092
		4*	$0.54 \pm 0.022$	-	$0.034 \pm 0.008$	-0.37	0.47	217927
		5	$0.48 \pm 0.02$	$0.02 \pm 0.005$	$0.01 \pm 0.007$	-	0.49	220442
		6	$0.55 \pm 0.01$	$0.03 \pm 0.006$	$0.01 \pm 0.007$	-0.50	0.49	219147
BW8	REML	1	$0.27 \pm 0.023$	-	-	-	-	899994
		2	$0.24 \pm 0.019$	$0.04 \pm 0.003$	-	-	-	813195
		3	$0.22 \pm 0.022$	-	$0.037 \pm 0.008$	-	0.24	813228
		4	$0.23 \pm 0.020$	-	$0.044 \pm 0.008$	-0.17	0.23	813222
		5	$0.19 \pm 0.023$	$0.040 \pm 0.005$	$0.003 \pm 0.006$	-	0.20	813087
		6*	$0.22 \pm 0.024$	$0.041 \pm 0.005$	$0.009 \pm 0.007$	-0.52	0.19	813070
	Bayesian	1	$0.27 \pm 0.018$	-	-	-	-	845754.4
		2	$0.25 \pm 0.022$	$0.044 \pm 0.008$	-	-	-	848357.0
		3	$0.22 \pm 0.022$	-	$0.037 \pm 0.006$	-	0.24	847529.2
		4*	$0.23 \pm 0.019$	-	$0.044 \pm 0.009$	-0.17	0.23	846372.4
		5	$0.19 \pm 0.017$	$0.038 \pm 0.009$	$0.007 \pm 0.009$	-	0.20	846784.7
		6	$0.22 \pm 0.021$	$0.040 \pm 0.007$	$0.011 \pm 0.008$	-0.52	0.19	847482.7

$h_a^2$  = direct heritability;  $c^2$  = proportion of maternal environmental variance to phenotypic variance;  $h_m^2$  = maternal heritability ;  $r_{am}$  = correlation between direct additive genetic effect and maternal additive genetic effects;  $h_t^2$  = total heritability;  $2\text{Log}L$  = log likelihood (in REML method); (M = models ).  $DIC$  = deviance information criterion (in Bayesian method); (\*) = best model

weight and egg number considering maternal effects in models without inclusion of covariance of maternal and direct genetic effects resulted in lower estimation of additive genetic variance and consequently direct heritability. Results obtained from univariate parameter estimation showed that in all of the studied traits there is a negative correlation between maternal and direct genetic effects. In the study of Robinson *et al.* (1993) the negative correlation between maternal genetic and direct effects were observed for body weight trait. They reported that this negative correlation can be resulted from ignoring the maternal effects during last generations and selection which is only based on direct additive animal genetics.

## CONCLUSION

(Co) variance components, estimated using two Bayesian and of REML methods, were almost the same. In best model selection using Bayesian method the best model resulted in the simple models with fewer effects. We assume that including maternal effect in statistical models is essential for estimation of genetic parameters; the models with covariance between the direct and maternal effects give more accurate result in most of the traits.

**Table 4: Estimation of (co) variance component and derived parameters for egg number and age of sexual maturity**

Traits	Method	M	$h_a^2 \pm$ S.E.	$c^2 \pm$ S.E.	$h_m^2 \pm$ S.E.	$r_{am}$	$h_t^2$	$-2\text{Log}L, DIC$
EN	REML	1	0.16 ± 0.011	-	-	-	-	283602
		2	0.13 ± 0.014	0.023 ± 0.00	-	-	-	242487
		3	0.12 ± 0.011	-	0.01 ± 0.007	-	0.13	224161
		4	0.15 ± 0.012	-	0.03 ± 0.009	-0.58	0.11	224135
		5	0.11 ± 0.014	0.02 ± 0.006	0.003 ± 0.008	-	0.12	224150
		6*	0.15 ± 0.013	0.02 ± 0.005	0.02 ± 0.008	-0.74	0.10	224119
	Bayesian	1	0.16 ± 0.012	-	-	-	-	257119.8
		2	0.13 ± 0.014	0.025 ± 0.00	-	-	-	228671.1
		3	0.12 ± 0.012	-	0.01 ± 0.005	-	0.13	241563.4
		4	0.16 ± 0.015	-	0.04 ± 0.001	-0.58	0.11	241389.0
		5	0.11 ± 0.014	0.02 ± 0.009	0.002 ± 0.006	-	0.12	241719.3
		6*	0.15 ± 0.013	0.02 ± 0.007	0.02 ± 0.003	-0.77	0.10	241012.5
ASM	REML	1	0.43 ± 0.014	-	-	-	-	271589
		2	0.38 ± 0.018	0.051 ± 0.008	-	-	-	229500
		3	0.38 ± 0.020	-	0.035 ± 0.006	-	0.40	216275
		4	0.42 ± 0.019	-	0.046 ± 0.006	-0.33	0.37	216271
		5	0.35 ± 0.016	0.042 ± 0.005	0.031 ± 0.007	-	0.37	216173
		6*	0.39 ± 0.021	0.055 ± 0.005	0.041 ± 0.005	-0.43	0.33	160538
	Bayesian	1	0.44 ± 0.018	-	-	-	-	233820.1
		2	0.36 ± 0.019	0.057 ± 0.008	-	-	-	233814.1
		3	0.37 ± 0.027	-	0.063 ± 0.008	-	0.40	234559.7
		4*	0.41 ± 0.024	-	0.048 ± 0.007	-0.38	0.36	229611.4
		5	0.35 ± 0.018	0.046 ± 0.009	0.031 ± 0.006	-	0.37	233494.7
		6	0.39 ± 0.021	0.054 ± 0.007	0.045 ± 0.005	-0.37	0.34	231385.7

$h_a^2$  = direct heritability;  $c^2$  = proportion of maternal environmental variance to phenotypic variance;  $h_m^2$  = maternal heritability;

$r_{am}$  = correlation between direct additive genetic effect and maternal additive genetic effects;  $h_t^2$  = total heritability;  $2\text{Log}L$  = log likelihood (in REML method); (M = models).  $DIC$  = deviance information criterion (in Bayesian method); (\*) = best model

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