



Genetic Properties of Some Economic Traits in Isfahan Native Fowl Using Bayesian and REML Methods

Salehinasab M¹, Latifi M², Zerehdaran S³ & Alijani S²

¹Department of Animal Genetic and Breeding, Faculty of Animal Science, Gorgan University of Agricultural Sciences and Natural Resources, Gorgan, Iran

²Department of Animal Science, College of Agriculture, Tabriz University, Tabriz, Iran

³Department of Animal Science, College of Agriculture, Ferdowsi University of Mashhad, Mashhad, Iran

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Corresponding author

Saeed Zerehdaran
zereh2s@yahoo.com

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Abstract

The objective of the present study was to estimate heritability values for some performance and egg quality traits of native fowl in Isfahan breeding center using REML and Bayesian approaches. The records were about 51521 and 975 for performance and egg quality traits, respectively. At the first step, variance components were estimated for body weight at hatch (BW_0), body weight at 8 weeks of age (BW_8), weight at sexual maturity (WSM), egg yolk weight (YW), egg Haugh unit and eggshell thickness, via REML approach using ASREML software. At the second step, the same traits were analyzed via Bayesian approach using Gibbs3f90 software. In both approaches six different animal models were applied and the best model was determined using likelihood ratio test (LRT) and deviance information criterion (DIC) for REML and Bayesian approaches, respectively. Heritability estimates for BW_0 , WSM and ST were the same in both approaches. For BW_0 , LRT and DIC indexes confirmed that the model consisting maternal genetic, permanent environmental and direct genetic effects was significantly better than other models. For WSM, a model consisting of maternal permanent environmental effect in addition to direct genetic effect was the best. For shell thickness, the basic model consisting direct genetic effect was the best. The results for BW_8 , YW and Haugh unit, were different between the two approaches. The reason behind this tiny differences was that the convergence could not be achieved for some models in REML approach and thus for these traits the Bayesian approach estimated the variance components more accurately. The results indicated that ignoring maternal effects, overestimates the direct genetic variance and heritability for most of the traits. Also, the Bayesian-based software could take more variance components into account.

Introduction

Breeding programs and genetic improvement composition of commercial chickens (Muir *et al.*, 2008). Having an accurate (co) variance

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components and consequent genetic parameters for every animal breeding program is very important. Researchers have used several statistical methods 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) and the second one is Bayesian method using Gibbs sampling (BAGS) technique (Yousefizonuz *et al.*, 2013).

Based on the history of maximum likelihood approach expressed by Sanchez *et al.*, (2003) this method was first used in the human genetics (Elston and Stewart, 1971). However, its adaptation to animal genetics has required approximations. Animal pedigree generally contains many loops due to the use of multiple matings, hence ignoring dependencies between families is one of those approximations (Le Roy *et al.*, 1989). While all relationships within a pedigree can be taken into account using a Monte Carlo Markov Chain (MCMC) algorithm (Gelfand and Smith, 1990), such as the Gibbs sampler (GS), generally in a Bayesian inference framework (Bayesian-GS) (Sanchez *et al.*, 2003).

Taking the uncertainty about parameters into account is possible in Bayesian methods because these methods consider the marginal posterior density of those parameters (Gianola and Fernando, 1986; Wang *et al.*, 1993 and Sorenson *et al.*, 1994). Although the Bayesian methods provide an attractive theoretical framework for this problem, Schenkel *et al.*, (2002) advocated the practical benefits in prediction accuracy and precision are not clear.

Unver *et al.* (2002) compared REML, MIVQUE (minimum variance quadratic unbiased estimation) and Bayesian approaches. There were no substantial differences in heritability estimates among these methods when the sire model was used, but it was not the case with the dam model in their research. They also found different estimates with GIBBS sampling compared with other methods. They said that there are advantages in GIBBS method for variance component estimation that makes this method preferable. Achieving point estimates are possible using GIBBS sampling, furthermore having confidence intervals for the posterior distribution of the variance component without approximations or normality assumption is another advantage (Unver *et al.*, 2002).

Sanchez *et al.* (2003) conducted a study in order to compare estimation of breeding values and fixed effects using Bayesian and empirical BLUP estimation under selection on parents and missing pedigree information. They found that Bayesian and BLUP estimation did not differ over the range of simulated situations. In other words, the two methods showed the same ability to rank animals.

Nariç *et al.* (2011) estimated genetic parameters for some egg traits in Japanese quail using different methods including REML, Gibbs Sampling, ML and MIVQUE. In their research, the smallest error variance was obtained with Gibbs sampling, which also gave the most unbiased results. They said that it is appropriate to use the variance-covariance components, which were obtained via Gibbs sampling approach, in the mixed model equation in the estimation of breeding values.

Wolc *et al.* (2009) indicated that the REML and Bayesian methods gave very similar estimates in the case of the usual variance components for means of the traits. Rosa *et al.* (2003) stated that the Bayesian methodology can be used for thick-tailed distributions such as the *t* distribution considerably. Wolc *et al.* (2009) pointed out that REML method is also advantageous because of short computing time. Low dependence on starting values is another advantage of this method. On the other hand, parallel estimation of breeding values for mean and variance is possible using REML procedure. They stated that this method could be useful for breeders of any species for which uniformity of product or more generally level of variation in studied traits is of economic importance.

Browne and Draper (2006) conducted a simulation study in order to examine the performance of likelihood-based and Bayesian methods of fitting variance components. Their likelihood approach was based on maximum and restricted maximum likelihood and their Bayesian methods used Markov chain Monte Carlo (MCMC) estimation. They found that both likelihood-based and Bayesian approaches can produce approximately unbiased estimates. Furthermore, in the case of small samples they pointed out both approaches had difficulty achieving nominal coverage.

Duangjinda *et al.* (2001) using simulated data found that under phenotypic selection, variance estimates using REML and Bayesian analysis were empirically unbiased.

To our knowledge, no research was done with the purpose of investigating the difference between REML and Bayesian approach at the level of real phenotypic data. So the objective of the current study was to estimate heritability values based on best models using REML and Bayesian methods and to compare the results of methods in the population of Isfahan native fowl.

Materials and Methods

The records of the economic traits were collected from native fowl in Isfahan breeding center. This center has been established in 1980 and started its activity by collecting native fowl from far rural areas. Native fowl were selected based on their phenotypic characteristics. Performance traits were recorded during 14 generations. These traits include body weight at hatch, 8 and 12 weeks of age (BW_0 , BW_8 and BW_{12}), age (ASM) and weight (WSM) at sexual maturity, number of eggs during the first 12 weeks of laying period (EN) and average egg weight at 28th, 30th and 32nd weeks (EW). Some of these traits including BW_0 , BW_8 and WSM were used in the analyses. The number of records for these traits was about 51521.

Egg quality traits were also measured on eggs of 1020 birds (one egg per bird) from generation 15 in the spring of 2012. The eggs were labeled to identify the parents and transferred to the laboratory. Egg quality traits were recorded during 6 days. Abnormal eggs were eliminated. The remained eggs were broken and subsequently, yolk and albumen were carefully separated and yolk weight (YW) was measured. The shell thickness (ST) was measured by a Shell Thickness Meter (calibrated in mm) at the pointed end, equator and blunt end of shells and the average value were used for analyses.

Then Haugh unit (HU) was calculated using the following formula:

$$HU = 100 (\text{Log AH} - 1.7 \text{EW}^{0.37} + 7.57)$$

These 3 traits together with performance traits were used in the analyses.

Statistical analyses

The UNIVARIATE and GLM procedures of the SAS software (SAS Institute, 2001) were used in order to achieve the descriptive statistics, and to assess the significance of fixed effects.

The variance components and the heritability values were estimated by different animal

models first using restricted maximum likelihood method via ASREML software (Gilmour *et al.*, 2000) and then using Bayesian method via GIBBS3F90 software (Misztal, 1999). In each Bayesian analysis, 500000 rounds of Gibbs sampling were conducted. The first 50000 rounds were discarded as a burn-in period, and the thinning interval was constant at 100 cycles.

Fixed effects were a combination of generation and hatch (45 levels), birth year (13 levels) and sex (2 levels) for BW_0 , BW_8 and WSM, and hatch (4 levels) and day of recording (6 levels) for YW, HU and ST.

Six univariate animal models were used as following:

$$\text{Model 1: } y = Xb + Z_1a + e$$

$$\text{Model 2: } y = Xb + Z_1a + Wc + e$$

$$\text{Model 3: } y = Xb + Z_1a + Z_2m + e \quad \text{Cov}_{am} = 0$$

$$\text{Model 4: } y = Xb + Z_1a + Z_2m + e \quad \text{Cov}_{am} \neq 0$$

$$\text{Model 5: } y = Xb + Z_1a + Z_2m + Wc + e \quad \text{Cov}_{am} = 0$$

$$\text{Model 6: } y = Xb + Z_1a + Z_2m + Wc + e \quad \text{Cov}_{am} \neq 0$$

In these models, y is the vector of observations, b is the vector of fixed effects; a is the vector of random direct additive genetic effects, m is the vector of random maternal additive genetic effects, c is the vector of random maternal permanent environmental effects, e is the vector of random residual effects, and X , Z_1 , Z_2 , and W are the incidence matrices relating the observations to the fixed, direct genetic, maternal additive genetic and maternal permanent environmental effects, respectively.

Models in REML method were compared using likelihood ratio test (LRT) to find the best model for each trait. LRT can be described as:

$$\chi^2 = 2 \log_e L(F) - 2 \log_e L(R)$$

Where $L(F)$ is the likelihood of the full model and $L(R)$ is the likelihood of the reduced model.

If the difference among models is not significant, the most simple model (model consisting of direct genetic effects) is recommended as the most appropriate model (Dabson, 1991). For Bayesian method, the deviance information criterion (DIC) was used for determining the best model. The idea is that the model with the smallest DIC should be selected as the best model.

Results and Discussion

Descriptive statistics and the results obtained from the test of significance for all traits are presented in Table 1.

Table 1. Descriptive statistics and test of significance of fixed effects for studied traits

Trait	N	Mean	CV (%)	Birth Year	Sex ¹	GH ²	Hatch	DR ³
BW ₀ (gr)	51521	37.72	9.06	*** ⁴	0.55***	***	-	-
BW ₈ (gr)	45517	842.58	18.46	***	147.48***	***	-	-
WSM (gr)	20000	1883.38	10.49	***	-	***	-	-
YW (gr)	939	16.36	7.06	-	-	-	***	*
HU	951	71.87	12.07	-	-	-	**	*
ST (mm)	975	0.38	7.43	-	-	-	ns	ns

BW₀ = body weight at hatch, BW₈ = body weight at 8 weeks of age, WSM = weight at sexual maturity, YW = yolk weight, HU = Haugh unit, ST = shell thickness

¹ The difference between male and female for each trait was shown as sex effect

² GH is the combination of generation and hatch effects

³ Day of recording

⁴ Because of large effects of birth year and GH, only the significance level was shown

***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, ns: non-significant

Table 2. The best models, direct and maternal genetic heritabilities and the proportion of maternal permanent environment to phenotypic variance (c^2) with their standard errors for studied traits based on REML method

Trait	Best model	h^2_{direct}	h^2_{maternal}	c^2
BW ₀	5	0.05 ± 0.01	0.30 ± 0.02	0.25 ± 0.02
BW ₈	5	0.24 ± 0.01	0.01 ± 0.01	0.04 ± 0.01
WSM	2	0.35 ± 0.02	--	0.03 ± 0.01
YW	1	0.11 ± 0.05	--	--
HU	1	0.24 ± 0.07	--	--
ST	1	0.37 ± 0.07	--	--

BW₀ = body weight at hatch, BW₈ = body weight at 8 weeks of age, WSM = weight at sexual maturity, YW = yolk weight, HU = Haugh unit, ST = shell thickness

Model 1 = the model consisting direct genetic effect

Model 2 = the model consisting direct genetic and maternal permanent environmental effects

Model 5 = the model consisting direct and maternal genetic effects and maternal permanent environmental effect

The best model for each trait, direct and maternal heritabilities and the proportion of maternal permanent environmental effects to phenotypic variance based on REML approach are shown in Table 2.

There were some differences in variance components and the heritability estimates for the studied traits across models based on REML approach. The genetic part of maternal effects was observed only for BW₀ and BW₈. For these two traits, the genetic and permanent environmental effects of the dam were significant and log likelihood was significantly increased in model 5 compared to models 1, 2, 3 and 4. Despite many efforts, the convergence of model 6 could not be achieved for these two traits.

Estimated maternal heritabilities were 0.30 and 0.01 for BW₀ and BW₈, respectively. In the study of Le Bihan-Duval *et al.* (1998) 3% to 8% of the phenotypic variation of BW in broilers was attributed to maternal environmental effects.

Maternal heritability (h^2_m) and the proportion of permanent environmental variance to phenotypic variance (c^2) for BW₀ (0.30 and 0.25,

respectively) were higher than BW at 8 weeks of age (0.01 and 0.04, respectively), while its direct heritability (0.05) was lower than BW at 8 weeks of age (0.24).

In a study done by Hartmann *et al.* (2003), estimated direct (0.01) and maternal heritability (0.50) in chick weight of a white Leghorn line were very close to the present results.

Dana *et al.* (2010) used an animal model consisting of direct genetic and common environmental effects for BW traits in Horro chicken of Ethiopia. The value of direct heritability for BW₀ in their study was higher than the present results. This may be due to ignoring the maternal genetic effects in their analyses.

Hartmann *et al.* (2003), in a study on white Leghorn line, found that the maternal heritability for chick body weight is intermediate while the direct heritability is close to 0. They pointed out that maternal part plays an important role in the variation of chick weight.

As it was shown in Table 2, only environmental part of maternal effects is important for WSM in Isfahan native fowl.

Ghorbani *et al.* (2012) found that model including genetic and environmental maternal effects is the best model for WSM.

For YW, HU and ST, running all models except model 1 was not successful. So it cannot be told that maternal genetic and environmental effects were not important for these traits. However, model 1 was introduced as the best model for these traits in Table 2. Hartmann *et al.* (2003), estimated direct and maternal genetic effect of YW based on REML approach in a white Leghorn line 0.43, but the maternal genetic effect was not significant for this trait.

The results suggest that models consisting of maternal additive genetic and permanent environmental effects fitted better for BW_0 , BW_8

and WSM. Perhaps for YW, HU and ST, more effort to reach the convergence is needed.

Grosso *et al.* (2010) reported that economic traits are widely affected by maternal effects and there are various sources of these effects including genetic or environmental differences between mothers and the combination of the genetic and environmental differences. Considering maternal effects in the analysis decreases the bias in estimation of genetic variance (Meyer, 1997).

The best model for each trait, direct and maternal heritabilities and the proportion of maternal permanent environmental effects to phenotypic variance based on Bayesian approach are shown in Table 3.

Table 3. The best models, direct and maternal genetic heritabilities and the proportion of maternal permanent environment to phenotypic variance (c^2) with their standard errors for studied traits based on Bayesian method

Trait	Best model	h^2_{direct}	h^2_{maternal}	c^2
BW_0	5	0.04 ± 0.01	0.29 ± 0.02	0.27 ± 0.02
BW_8	6	0.27 ± 0.02	0.02 ± 0.00	0.04 ± 0.02
WSM	2	0.34 ± 0.01	--	0.08 ± 0.02
YW	2	0.03 ± 0.01	--	0.73 ± 0.04
HU	2	0.23 ± 0.06	--	0.07 ± 0.03
ST	1	0.38 ± 0.07	--	--

BW_0 = body weight at hatch, BW_8 = body weight at 8 weeks of age, WSM = weight at sexual maturity, YW = yolk weight, HU = Haugh unit, ST = shell thickness

Model 1 = the model including direct genetic effects

Model 2 = the model including direct genetic and maternal permanent environmental effects

Model 5 = the model including direct and maternal genetic effects and maternal permanent environmental effects

Model 6 = the model including direct and maternal genetic effects and maternal permanent environmental effects with cov ≠ 0 between direct and maternal genetic effects

All models were successfully run via Gibbs3f90 software. For BW_0 , WSM and ST, the results were in agreement with REML approach. Sanchez *et al.* (2003) found the same similarity between these two approaches for detecting major genes affecting body composition, carcass, meat quality and the number of false teats in a Chinese-European pig line.

For BW_8 , YW and HU, Bayesian approach could take more variance components into account and so the heritability estimates were slightly different.

Based on Bayesian approach, the most comprehensive model (model 6) was the best for BW_8 . Regarding YW and HU the model consisting of maternal permanent environmental effects in addition to direct genetic effects (model 2) was the best. Direct heritability estimates in Bayesian approach were 0.27 (*vs.*

0.24 in REML approach), 0.03 (*vs.* 0.11 in REML approach) and 0.23 (*vs.* 0.24 in REML approach) for BW_8 , YW and HU, respectively. Browne and Draper (2006) pointed out that the likelihood-based methods are considerably faster computationally than MCMC. It was shown in our analyses, too.

Generally speaking, REML and Bayesian-GS approaches gave rather consistent results for all traits in our study. Heritability estimates were also approximately similar with both methods. However, Bayesian approach was more practical when the model consists of more components and it had no obstacle about convergence. The results confirm the conclusion of Sanchez *et al.* (2003). They pointed out that ML can be considered as a reliable approach while Bayesian-GS makes more comprehensive analyses possible.

Conclusion

The present study indicated that some economic traits (BW_0 , BW_8 , WSM, YW and HU) in Isfahan native fowl were significantly influenced by maternal effects. Hence, it is necessary to include additive genetic and maternal genetic and permanent environmental effects in the estimation of breeding values for these traits, in this population of native fowl.

The results showed that the estimates obtained from both REML and Bayesian approaches were very close to each other for the most of the traits, but for some models in REML-based software, convergence couldn't be achieved. So, the best model was introduced based on the comparison among models that were converged. There was also no significant difference between two approaches, but the time and efforts that were spent were different.

Since the REML approach is much less time-consuming than the Bayesian-GS, it is an appropriate model when the investigators are short of time, but we suggest applying a Bayesian-GS method in order to better characterization of economic traits.

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