

Bayesian Inference of Genetic Parameters for Reproductive and Performance Traits in White Leghorn Hens

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ABSTRACT

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This study estimated the genetic parameters for reproductive and performance traits and determined which ones can be used as selection criteria for egg production in laying hens using the Bayesian inference. The data of 1894 animals from three generations of White Leghorn laying hens were analyzed for fertility (FERT), hatchability (HATC), and birth rate measurements at 60 weeks of age (BIRTH), body weight at 16 and 60 weeks of age (BW16 and BW60), age at sexual maturity (ASM), egg height/width ratio, weight, and density at 28, 36, and 40 weeks of age (RHW28, RHW36, RHW40, WEGG28, WEGG36, WEGG40, DENS28, DENS36, and DENS40, respectively) traits. The genetic parameters were estimated by the Bayesian inference method of multi-trait animal model. The model included the additive and residual genetic random effects and the fixed effects of generation. The *a posteriori* mean distributions of the heritability estimates for reproductive traits ranged from 0.14 ± 0.003 (HATC) to 0.22 ± 0.005 (FERT) and performance from 0.07 ± 0.001 (RHW28) to 0.42 ± 0.001 (WEGG40). The *a posteriori* mean distributions of the genetic correlation between reproductive traits ranged from 0.18 ± 0.026 (FERT and HACT) to 0.79 ± 0.007 (FERT and BIRTH) and those related to performance ranged from -0.49 ± 0.001 (WEGG36 and DENS36) to 0.75 ± 0.003 (DENS28 and DENS36). Reproductive and performance traits showed enough additive genetic variability to respond to selection, except for RHW28. This trait alone would have little impact on the genetic gain because environmental factors would have a higher impact compared to those from the additive genetic factors. Based on the results of this study, the selection applied on the BIRTH trait can be indicated to improve FERT and HATC of eggs. Furthermore, the use of the WEGG40 could improve egg quality in this population.

Keywords: egg production; fertility; genetic correlation; hatchability; heritability

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The continuous monitoring of economically important traits through genetic parameter estimates in poultry production aims to ensure the production of high quality eggs and their products to meet the requirements of the global consumers. The breeding of laying hens begins with selecting the best animals for reproduction, directed at improving traits that can increase the profit of the commercial activity of egg production.

Reproductive and performance traits, such as egg weight, egg production, age at sexual maturity, body weight, fertility, and hatchability are important traits to be considered in breeding programs of laying hens (Rozempolska-Rucinska et al. 2011; Venturini et al. 2012; Icken et al. 2013). These traits are directly associated with the production and product integrity during shipping and storage of eggs. The knowledge of the genetic parameters of economically important traits in laying is relevant to breeding programs because direct the selection to be practiced. The genetic and phenotypic parameters estimates are the main tools for choosing the selection method and the traits that should be considered as selection criteria for obtaining genetic gains in egg production.

The REML (restricted maximum likelihood) and Bayesian methods have been applied extensively in animal breeding to estimate (co)variance components and genetic parameters. The Bayesian methodology provides a solution for the finite sample size problem, because an exact *a posteriori* distribution exists for each large or small data set from which inferences can be drawn. When a large data set is analyzed, *a priori* information tends to be subjugated by the likelihood function in the establishment of the *a posteriori* distribution. In this case, the parameter estimates are close to those obtained by frequentist methods based in likelihood functions. However, this may not be true when the sample size is limited because the maximum likelihood procedure only presents well-defined properties when the sample size is large enough (van de Schoot et al. 2015).

Several studies (Hanna et al. 2014; van de Schoot et al. 2015; Jamrozik et al. 2016) have demonstrated that the Bayesian methodology can be used to solve problems related to the genetic evaluation of animals, linear or nonlinear, even when there is uncertainty about genetic parameters. This methodology can provide considerable genetic gains when applied to species to be genetically

improved, given the importance of the estimation of the genetic parameters for performance and reproductive traits. There are few studies approaching the Bayesian inference to estimate genetic parameters for performance characteristics and reproduction in laying hens. The aim of this study was to estimate genetic parameters for performance and reproductive traits using the Bayesian methodology to identify the traits that could be used as selection criteria to improve egg production.

MATERIAL AND METHODS

Experimental population. The phenotypic observations of 1894 animals from three generations (2009–2011) were used in this study. This dataset was from a pure line of White Leghorn hens, called “CC”, which were developed by the Poultry Breeding Programme from Embrapa Swine and Poultry National Research Center, Concordia, Brazil. The CC is mainly selected for egg production, egg weight, feed conversion, hatchability, sexual maturity, fertility, viability, egg quality, and reduced body weight (Venturini et al. 2013). The pedigree file contained 2262 birds. The pedigree data structure of the generations studied for performance traits consisted of 117 sires mated with 468 hens in a hierarchical scheme (at least 4 females per male) by means of artificial insemination and 72 sires mated with 181 hens in a hierarchical scheme (at least 2 females per male) by means of artificial insemination for reproductive traits. Unregistered sires and dams were excluded from the data set.

Phenotypic traits and fixed effects. A total of 15 performance and reproductive traits of laying hens were evaluated in this study, as described below:

Reproductive traits. Fertility (FERT): the ratio between the number of fertile eggs and the total number of eggs set; hatchability (HATC): the ratio between the chicks hatched and the number of fertile eggs; birth rate (BIRTH): the ratio between the number of chicks hatched and the total number of eggs set.

Performance traits. Body weight (BW, in g) measured individually at 16 and 60 weeks of age (BW16 and BW60); age at sexual maturity (ASM, in days); egg height : width ratio (RHW), egg weight (WEGG, in g) and density (DENS, in g/ml)

measured at 28, 36, and 40 weeks of age (RHW28, RHW36, RHW40, WEGG28, WEGG36, WEGG40, DENS28, DENS36, and DENS40, respectively).

Analyses using the Least Squares method were performed beforehand using the GLM procedure of the SAS software (Statistical Analysis System, Version 9.2) to ascertain the influence of the fixed effects of generations (3 levels). The generation data were distributed in 119 records in 2009, 253 in 2010, and 124 in 2011 for reproductive data and in 379 records in 2009, 254 in 2010, and 770 in 2011 for performance data. These fixed effects were significant ($P < 0.05$) for the 15 traits studied. The descriptive statistics on the traits of performance and reproduction involved in the study (Table 1) were obtained through the MEANS procedure of the SAS (Version 9.2).

Genetic parameters. Variance components were estimated using the Bayesian inference method on a multi-trait animal model involving all 15 traits, via Gibbs using GIBBS2F90 software (Misztal 2004). The general model included the fixed effect from generation (3 levels) and the random direct additive genetic and residual effects. The general mixed model for all traits was:

$$y = X\beta + Za + e$$

where:

y = vector of observations for each trait

X = incidence matrix for fixed effects related to β

β = vector of fixed effect (generations)

Z = incidence matrix for random additive effects related to a

a = vector of random additive genetic direct effect

e = vector of residual effects.

The assumptions for the model were:

$$E(y) = X\beta; \text{Var}(a) = A \otimes S_a \text{ and } \text{Var}(e) = I \otimes S_e$$

where:

S_a = additive covariance matrix

S_e = residual covariance matrix

A = numerator additive genetic relationship matrix

I = identity matrix

\otimes = direct product or Kronecker product between matrices

A total of 1 500 000 Gibbs sampling rounds were completed, with a burn-in period of 500 000 iterations and a thinning interval of 200 iterations, totalling 5000 samples. These criteria were applied

Table 1. Number of animals (n), means (M), standard deviation (SD), minimum (Min) and maximum (Max) values, coefficients of variation (CV), and confidence interval at 95% (CI 95%) of the reproductive and productive traits of laying hens

Trait	n	M	SD	Min	Max	CV (%)	CI95%
FERT	496	79.27	23.78	0.00	100.00	29.99	77.18–81.36
HATC	496	74.91	28.5	0.00	100.00	38.04	72.40–77.42
BIRTH	496	54.41	30.83	0.00	94.44	56.66	51.70–57.12
BW16	1398	1196.81	130.23	674.00	1620.00	10.88	1189.98–1203.64
BW60	1398	1933.28	245.92	1230.00	2836.00	12.72	1920.39–1946.17
WEGG28	1398	54.55	4.60	37.00	74.00	8.43	54.31–54.79
WEGG36	1398	58.33	5.51	5.00	76.00	9.44	58.04–58.62
WEGG40	1398	59.86	5.63	40.00	83.00	9.40	59.56–60.16
RHW28	1398	1.29	0.09	1.10	4.30	6.97	1.29–1.29
RHW36	1398	1.31	0.11	1.10	5.13	8.39	1.30–1.32
RHW40	1398	1.32	0.11	1.15	5.13	8.33	1.31–1.33
DENS28	1398	4.73	1.25	1.00	9.00	26.42	4.66–4.80
DENS36	1398	4.32	1.28	0.00	8.00	29.62	4.25–4.39
DENS40	1398	4.08	1.36	1.00	8.00	33.25	4.01–4.15
ASM	1398	145.74	10.61	125.00	189.00	7.28	145.18–146.30

FERT = fertility, HATC = hatchability, BIRTH = birth rate measurements at 60 weeks of age, BW16 (60) = body weight at 16 (60) weeks of age, WEGG28 (36, 40) = egg weight at 28-(36-, 40-)week-old hens, RHW28 (36, 40) = egg height/width ratio at 28-(36-, 40-)week-old hens, DENS28 (36, 40) = egg density at 28-(36-, 40-)week-old hens, ASM = age of sexual maturity

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using a statistical Bayesian output analysis package described by Smith (2005) in the R program (R Development Core Team, 2008), and the genetic parameters were presented as the mean of the *a posteriori* samples.

RESULTS

The *a posteriori* measurements (mean, mode, and median) of the heritability estimates for each trait were similar, suggesting that their distributions were approximately symmetrical (Table 2).

The heritability of the traits showed extreme estimates (minimum and maximum), but these occurred in small proportion (less than 5%) and did not affect the position measurements. The amplitudes of the 95% confidence intervals for the estimates were small, and the Monte Carlo standard errors were below 0.03 (Table 2).

The means of *a posteriori* heritability estimates for the reproductive traits (Table 3) ranged from 0.14 ± 0.003 (HATC) to 0.22 ± 0.005 (FERT). For the performance traits (Table 2), the means of the *a posteriori* heritability estimates ranged from

0.07 ± 0.001 (RHW28) to 0.42 ± 0.001 (WEGG40). Genetic correlations between reproductive traits (Table 3) ranged from 0.18 ± 0.026 for FERT and HATC to 0.79 ± 0.007 for FERT and BIRTH. However, the means of the *a posteriori* estimate of the genetic correlation for FERT and HATC, although positive, was small compared to other estimates.

For the performance traits, the genetic correlation ranged from 0.55 ± 0.004 for WEGG8 and DENS36 to 0.95 ± 0.000 for RHW36 and RHW40 (Table 3). The BW16 trait had a high and positive genetic correlation with the BW60 (0.68 ± 0.002), WEGG36 (0.57 ± 0.004), WEGG40 (0.70 ± 0.001), RHW36 (0.67 ± 0.002), and RHW40 (0.69 ± 0.004) traits and a negative genetic correlation with ASM (-0.18 ± 0.004) (Table 4). In this study, the genetic correlations observed between ASM and WEGG28 (-0.30 ± 0.003), WEGG36 (-0.20 ± 0.004), and WEGG40 (-0.13 ± 0.003) traits showed that selection for poultry with heavier weights would favour the earliest poultry, but with heavier eggs. Environmental correlations for BW16 and WEGG36, ASM and WEGG28, ASM and WEGG36, ASM and WEGG40, ASM and RHW40, and RHW28 and WEGG36 presented opposite signs to the

Table 2. Descriptive statistics *a posteriori* of heritability estimates (h^2) for reproductive and productive traits of laying hens

Trait	Mean	Median	Mode	Min	Max	CI 95%
FERT	0.22	0.21	0.20	0.00	0.45	0.21–0.22
HATC	0.14	0.13	0.11	0.00	0.45	0.13–0.14
BIRTH	0.21	0.21	0.20	0.03	0.59	0.21–0.22
BW16	0.37	0.31	0.31	0.26	0.48	0.36–0.37
BW60	0.31	0.31	0.31	0.26	0.48	0.31–0.32
ASM	0.34	0.34	0.34	0.20	0.49	0.33–0.34
WEGG28	0.36	0.36	0.36	0.22	0.52	0.35–0.36
RHW28	0.07	0.07	0.07	0.03	0.20	0.07–0.08
DENS28	0.31	0.31	0.32	0.16	0.50	0.31–0.32
WEGG36	0.34	0.34	0.34	0.20	0.50	0.34–0.35
RHW36	0.20	0.19	0.19	0.09	0.35	0.19–0.20
DENS36	0.36	0.36	0.36	0.20	0.54	0.35–0.36
WEGG40	0.42	0.42	0.42	0.28	0.56	0.41–0.42
RHW40	0.20	0.20	0.20	0.11	0.35	0.20–0.21
DENS40	0.32	0.32	0.31	0.15	0.48	0.31–0.32

FERT = fertility, HATC = hatchability, BIRTH = birth rate measurements at 60 weeks of age, BW16 (60) = body weight at 16 (60) weeks of age, ASM = age of sexual maturity, WEGG28 (36, 40) = egg weight at 28-(36-, 40-)week-old hens, RHW28 (36, 40) = egg height/width ratio at 28-(36-, 40-)week-old hens, DENS28 (36, 40) = egg density at 28-(36-, 40-)week-old hens, Min = minimum value, Max = maximum value, CI 95% = confidence interval at 95%

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Table 3. Genetic (above the diagonal) and environmental correlations (below the diagonal) with their Monte Carlo standard errors (in parentheses) between reproductive and productive traits of laying hens

Productive traits												
	BW16	BW60	ASM	WEGG28	RHW28	DENS28	WEGG36	RHW36	DENS36	WEGG40	RHW40	DENS40
BW16		0.68 (0.002)	-0.18 (0.004)	0.42 (0.002)	0.48 (0.001)	-0.01 (0.003)	0.57 (0.004)	0.67 (0.002)	-0.07 (0.003)	0.70 (0.001)	0.69 (0.004)	0.07 (0.004)
BW60	0.48 (0.000)		0.07 (0.003)	0.17 (0.003)	0.10 (0.011)	0.01 (0.004)	0.38 (0.004)	0.24 (0.007)	-0.05 (0.004)	0.32 (0.003)	0.18 (0.006)	0.05 (0.005)
ASM	-0.10 (0.015)	0.13 (0.001)		-0.30 (0.003)	0.00 (0.012)	0.30 (0.004)	-0.20 (0.004)	0.00 (0.006)	0.25 (0.004)	-0.13 (0.003)	-0.09 (0.006)	0.36 (0.004)
WEGG28	0.34 (0.001)	0.26 (0.001)	0.17 (0.001)		0.59 (0.013)	-0.35 (0.003)	0.91 (0.002)	0.22 (0.005)	-0.55 (0.004)	0.81 (0.001)	0.15 (0.005)	-0.34 (0.004)
RHW28	0.14 (0.001)	0.14 (0.001)	0.01 (0.001)	0.27 (0.002)		0.00 (0.011)	0.63 (0.012)	0.47 (0.017)	-0.09 (0.011)	0.63 (0.010)	0.41 (0.017)	-0.07 (0.010)
DENS28	-0.16 (0.001)	-0.02 (0.001)	0.08 (0.001)	-0.17 (0.001)	0.15 (0.001)		-0.26 (0.004)	-0.14 (0.004)	0.75 (0.003)	-0.21 (0.003)	-0.16 (0.004)	0.68 (0.004)
WEGG36	-0.35 (0.001)	0.26 (0.001)	0.18 (0.012)	0.56 (0.001)	0.16 (0.002)	-0.09 (0.001)		0.19 (0.006)	-0.49 (0.001)	0.92 (0.003)	0.14 (0.002)	-0.28 (0.001)
RHW36	-0.01 (0.001)	0.02 (0.001)	0.04 (0.001)	0.14 (0.001)	0.07 (0.002)	-0.01 (0.000)	-0.07 (0.001)		-0.07 (0.002)	0.35 (0.001)	0.95 (0.000)	-0.10 (0.002)
DENS36	-0.12 (0.001)	-0.07 (0.002)	0.05 (0.001)	-0.03 (0.001)	-0.07 (0.001)	0.34 (0.001)	-0.09 (0.001)	0.02 (0.002)		-0.43 (0.001)	-0.05 (0.002)	0.68 (0.001)
WEGG40	0.37 (0.001)	0.33 (0.001)	0.16 (0.000)	0.62 (0.001)	0.15 (0.002)	-0.10 (0.001)	0.67 (0.001)	0.14 (0.001)	-0.05 (0.001)		0.36 (0.000)	-0.14 (0.001)
RHW40	-0.03 (0.001)	0.05 (0.001)	0.05 (0.001)	0.15 (0.001)	0.06 (0.002)	0.03 (0.000)	-0.12 (0.001)	0.92 (0.000)	0.05 (0.002)	0.21 (0.001)		-0.06 (0.002)
DENS40	-0.08 (0.001)	-0.07 (0.001)	-0.01 (0.001)	-0.03 (0.001)	-0.03 (0.001)	0.25 (0.001)	-0.09 (0.001)	-0.02 (0.002)	0.39 (0.001)	-0.15 (0.001)	-0.01 (0.001)	
Reproductive traits												
	FERT				HATC				BIRTH			
FERT					0.18 (0.026)				0.79 (0.007)			
HATC	-0.09 (0.004)								0.71 (0.014)			
BIRTH	0.60 (0.001)				0.70 (0.002)							

BW16 (60) = body weight at 16 (60) weeks of age, ASM = age of sexual maturity, WEGG28 (36, 40) = egg weight at 28-(36-, 40-)week-old hens, RHW28 (36, 40) = egg height/width ratio at 28-(36-, 40-)week-old hens, DENS28 (36, 40) = egg density at 28-(36-, 40-)week-old hens, FERT = fertility, HATC = hatchability, BIRTH = birth rate measurements at 60 weeks of age

genetic correlations with magnitudes ranging from -0.35 ± 0.001 (BW16 and WEGG36) to 0.92 ± 0.000 (RHW36 and RHW40) (Table 3).

DISCUSSION

The total phenotypic data number was 1894 animals. After data consistency the number of remaining samples from reproductive and performance traits was 496 and 1398, respectively, being sufficient to describe the posterior distribution of the parameters estimated based on CI95% (Table 1).

The heritability estimates and the genetic and environmental correlations (Tables 2 and 3) showed that the size of the Gibbs chain used in this study was sufficient for the convergence analysis and, therefore, the estimates obtained for the genetic and environmental parameters were reliable.

The heritability estimates reported in the literature ranged from 0.055 ± 0.004 to 0.53 ± 0.01 for reproductive traits (Rozempolska-Rucinska et al. 2013; Silva et al. 2013; Jafarnejad et al. 2017) and 0.24 ± 0.00 to 0.53 ± 0.06 for performance traits (Niknafs et al. 2012; Shadparvar and Enayati 2012; Kjaer 2016; Jafarnejad et al. 2017). These varia-

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tions observed in the literature for the estimates of genetic parameters may be explained by factors, such as the population genetic background resulting from using different breeds and crossings, as well as the methodology used. However, in this study, the mean heritability estimate for reproductive and performance traits (Tables 2) indicated that there was sufficient phenotypic variance due to additive effects of genes. Thus, genetic improvement through selection of individuals with superior phenotype would be possible for most of the traits studied in this population, with the exception of RHW28, because the heritability estimates were close to zero. Thus, phenotypic selection for RHW28 would be inefficient because the environmental factors have a greater influence than the additive genetic factors. RHW is a very good indicator of size uniformity of the eggs (Rajaravindra et al. 2014) and the results of this study show that from the 36th week the eggs become more uniform, so RHW28 was different from RHW36 and RHW40. According to Tumova and Gous (2012), RHW changed with hen age, with eggs becoming longer with advancing age.

The selection applied to the FERT and BIRTH reproductive traits in this population would be highly efficient because their heritability estimates were higher than the HATC (Table 2). However, it is noteworthy that FERT and HATC decrease with increasing age being that HATC increases up to 26 weeks of laying and decreases with the laying poultry age (Alsobayel and Albadry 2012). Also, BIRTH is an easy trait to measure in the hatchery compared to FERT, considering that an increase in BIRTH would be enough to increase FERT and HATC. Based on the genetic correlations between them (Table 3), if the purpose of selection includes improving reproductive rates, we recommend using BIRTH trait as a selection criterion to improve the reproduction rates of this population of laying hens.

The genetic correlations for the performance traits (Table 3) obtained in this study varied when compared to the results found in the literature, which range from -0.32 ± 0.08 to 0.18 ± 0.05 (Shadparvar and Enayati 2012; Abou Khadiga et al. 2016; Jafarnejad et al. 2017). In this study, the genetic correlation estimates for body weight and egg weight at different ages were all positive, indicating a linear relationship between the genes involved in the expression of both traits (Table 3). According to

Niknafs et al. (2012), if selection is applied over body weight and egg traits, reduction in the number of eggs could occur, but this would be compensated by the increase in egg weight. However, generally, the productive chain of commercial eggs aims to increase the number of eggs to achieve greater profitabilities. From this idea, selection could be conducted to decrease body weight since the number of eggs and body weight have negative genetic correlation. However, the breeding programs of laying hens constantly seek for standardization of egg production (uniformity, quality, and weight) since higher quality standards lead to greater financial profitability than the number of eggs.

The genetic correlations of BW16 with ASM and ASM with WEGG traits measured at different ages were negative with moderate magnitudes (Table 3). These results indicate that selecting to increase BW16 would decrease ASM, i.e., heavier poultry reaches ASM earlier, and the selection to reduce ASM would result in heavier eggs. Similar result was reported by Jafarnejad et al. (2017) who observed negative genetic correlation (-0.32 ± 0.08) between body weight at 12 weeks and ASM. The selection to reduce ASM should be performed seeking adjust precocity and uniformity eggs, because ASM can harm the egg density and consequently egg weight, due to their genetic correlations (Table 3). Therefore if the selection pressure is performed to reduce the ASM, DENS may also be reduced, resulting in WEGG loss, leading to increased embryo mortality and thus, a drop in HATC.

The genetic correlations between BW16 and WEGG36, ASM and WEGG28, ASM and WEGG36, ASM and WEGG40, ASM and RHW40, and RHW28 and WEGG36 had opposite signs to the environmental correlations (Table 3). This result indicates that the environment acts contrary to the genotypes and depending on the magnitude, the selection efficiency may be compromised. Falconer and Mackay (1996) reported that sign differences between the genetic and environment correlations can be attributed to heritable and environment variability that affect two traits through different physiological mechanisms.

CONCLUSION

Based on results, it can be concluded that selection applied to body weight at 16 weeks of age can

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be indicated to improve body weight at 60 weeks of age, age of sexual maturity, and egg weight and height/width ratio. In addition, the fertility improvement would bring about better results of hatchability and mainly birth rate.

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REFERENCES

- About Khadiga G., Mahmoud B.Y.F., El-Full E.A. (2016): Genetic evaluation of early egg production and maturation traits using two different approaches in Japanese quail. *Poultry Science*, 95, 774–779.
- Alsobayel A.A., Albadry M.A. (2012): Effect of age and sex ratio on fertility and hatchability of Baladi and Leghorn laying hens. *Journal of Animal and Plant Sciences*, 22, 15–19.
- Falconer D., Mackay T. (eds) (1996): *Introduction to Quantitative Genetics*. Longmans Green, Harlow, UK.
- Hanna L.L.H., Garrick D.J., Gill C.A., Herring A.D., Sanders J.O., Riley D.G. (2014): Comparison of breeding value prediction for two traits in a Nellore-Angus crossbred population using different Bayesian modeling methodologies. *Genetics and Molecular Biology*, 37, 631–637.
- Icken W., Thurner S., Heinrich A., Kaiser A., Cavero D., Wendl G., Fries R., Schmutz M., Preisinger R. (2013): Higher precision level at individual laying performance tests in noncage housing systems. *Poultry Science*, 92, 2276–2282.
- Jafarnejad A., Kamali M.A., Fatemi S.J., Aminafshar M. (2017): Genetic evaluation of laying traits in Iranian indigenous hens using univariate and bivariate animal models. *Journal of Animal and Plant Sciences*, 27, 2017–2020.
- Jamrozik J., Koeck A., Kistemaker G.J., Miglior F. (2016): Multiple-trait estimates of genetic parameters for metabolic disease traits, fertility disorders, and their predictors in Canadian Holsteins. *Journal of Dairy Science*, 99, 1990–1998.
- Kjaer J.B. (2016): Divergent selection on home pen locomotor activity in a chicken model: selection program, genetic parameters and direct response on activity and body weight. *PLoS ONE*, 12, e0182103.
- Misztal I. (2004): GIBBS2F90 Manual. Available at <http://nce.ads.uga.edu/~ignacy/numpub/blupf90/docs/blupf90.pdf> (accessed Sep 10, 2017).
- Niknafs S., Nejati-Javaremi A., Mehrabani-Yeganeh H., Fatemi S.A. (2012): Estimation of genetic parameters for body weight and egg production traits in Mazandaran native chicken. *Tropical Animal Health Production*, 44, 1437–1443.
- Rajaravindra K.S., Rajkumar U., Rekha K., Niranjana M., Reddy B.L.N., Chatterjee R.N. (2014): Evaluation of egg quality traits in a synthetic coloured broiler female line. *Journal of Applied Animal Research*, 43, 10–14.
- Rozempolska-Rucinska I., Zieba G., Lukaszewicz M., Ciechomska M., Witkowski A., Slaska B. (2011): Egg specific gravity in improvement of hatchability in laying hens. *Journal of Animal and Feed Sciences*, 20, 84–92.
- Rozempolska-Rucinska I., Zieba G., Lukaszewicz M. (2013): Heritability of individual egg hatching success versus hen hatchability in layers. *Poultry Science*, 92, 321–324.
- Shadparvar A.A., Enayati B. (2012): Genetic parameters for body weight and laying traits in Mazandaran native breeder hens. *Iranian Journal of Applied Animal Research*, 2, 251–256.
- Silva L.P., Ribeiro J.C., Crispim A.C., Silva F.G., Bonafe C.M., Silva F.F., Torres R.A. (2013): Genetic parameters of body weight and egg traits in meat-type quail. *Livestock Science*, 153, 27–32.
- Smith B.J. (2005): *Bayesian Output Analysis Program (BOA) Version 1.1. User's Manual*. Available at <http://www.publichealth.uiowa.edu/boa/BOA.pdf> (accessed Sep 9, 2017).
- Tumova E., Gous R.M. (2012): Interaction of hen production type, age, and temperature on laying pattern and egg quality. *Poultry Science*, 91, 1269–1275.
- van de Schoot R., Broere J.J., Perryck K.H., Zondervan-Zwijnenburg M., van Loey N.E. (2015): Analyzing small data sets using Bayesian estimation: the case of posttraumatic stress symptoms following mechanical ventilation in burn survivors. *European Journal of Psychotraumatology*, 6, 25216.
- Venturini G.C., Grossi D.A., Ramos S.B., Cruz V.A.R., Souza C.G., Ledur M.C., El Faro L., Schmidt G.S., Munari D.P. (2012): Estimation of genetic parameters for partial egg production periods by means of random regression models. *Genetics and Molecular Research*, 11, 1819–1829.
- Venturini G.C., Savegnago R.P., Nunes B.N., Ledur M.C., Schmidt G.S., El Faro L., Munari D.P. (2013): Genetic parameters and principal component analysis for egg production from White Leghorn hens. *Poultry Science*, 92, 2283–2289.

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