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ANIMAL PRODUCTION

Genotypic parameters for egg production in pure breed hens by using random regression model

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ABSTRACT: *This study aimed to test different genotypic and residual covariance matrix structures in random regression models to model the egg production of Barred Plymouth Rock and White Plymouth Rock hens aged between 5 and 12 months. In addition, we estimated broad-sense heritability, and environmental and genotypic correlations. Six random regression models were evaluated, and for each model, 12 genotypic and residual matrix structures were tested. The random regression model with linear intercept and unstructured covariance (UN) for a matrix of random effects and unstructured correlation (UNR) for residual matrix adequately model the egg production curve of hens of the two study breeds. Genotypic correlations ranged from 0.15 (between age of 5 and 12 months) to 0.99 (between age of 10 and 11 months) and increased based on the time elapsed. Egg production heritability between 5- and 12-month-old hens increased with age, varying from 0.15 to 0.51. From the age of 9 months onward, heritability was moderate with estimates of genotypic correlations higher than 90% at the age of 10, 11, and 12 months. Results suggested that selection of hens to improve egg production should commence at the ninth month of age.*
Key words: *Barred Plymouth Rock, heritability, laying rate, White Plymouth Rock.*

Parâmetros genotípicos para produção de ovos em raças puras utilizando metodologia de modelos mistos

RESUMO: *Objetivou-se testar diferentes estruturas de matrizes de (co)variâncias genotípicas e residuais em modelos de regressão aleatória para modelar a produção de ovos do 5º ao 12º mês de idade de poedeiras das raças Plymouth Rock Barrada e Plymouth Rock Branca, bem como estimar a herdabilidade no sentido amplo e as correlações ambientais e genotípicas. Foram avaliados seis modelos de regressão aleatória e, para todos os modelos, foram testadas 12 estruturas das matrizes genotípicas e residuais. O modelo de regressão aleatória com intercepto linear com estrutura de (co)variância desestruturada (UN) para a matriz de efeitos aleatórios e correlação desestruturada (UNR) para a matriz de resíduos, modela adequadamente a curva de produção de ovos das aves das duas raças estudadas. As correlações genotípicas variaram de 0.15 (entre o 5º e o 12º mês) a 0.99 (entre o 10º e o 11º mês), aumentando conforme a proximidade entre os meses. As herdabilidades para a produção de ovos entre o 5º e o 12º mês de idade aumentam com o avanço da idade, variando de 0.15 a 0.51. A partir do nono mês de idade a herdabilidade é moderada com estimativas de correlações genotípicas superiores a 90% nos meses 10, 11 e 12. Sugere-se a seleção das poedeiras através de critérios fenotípicos a partir do 9º* mês de *idade das aves.*
Palavras-chave: *Plymouth Rock Barrada, herdabilidade, taxa de postura, Plymouth Rock Branca.*

INTRODUCTION

Search for new methodologies that may improve the selection of laying hens is important to achieve maximum egg production, since estimates of genetic and phenotypic parameters are the main tools to reach this maximum in the population, enabling better selection of laying strains.

The most significant economic traits are of a polygenic nature; and therefore, in breeding programs, animals are evaluated based on their performance. The phenotypic value of a given trait is the result of genetic heritage (genotype) of the animal in addition to environmental effects and the effects of the genotype/environment interaction. This suggested that the phenotypic value of the animal does not directly showed its genetic potential, as it is always influenced by the environment and the genotype/environment interaction (FALCONER, 1981). Thus, egg production is a quantitative trait influenced by genetics and environment.

The mixed model methodology proposed by HENDERSON (1949) was used to evaluate the traits of economic importance that are expressed in individuals over time such as milk production (DORNELLES et al., 2015), growth in beef cattle

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(TINEO et al., 2016; LOPES et al., 2016), and egg production (CRUZ et al., 2016). These models allows to adjust the random production curve of each animal, expressed as deviation from the mean curve of the population or group of animals (BONAFÉ et al., 2011). The regressions are adjusted depending on the production period using ordinary polynomials, or other linear functions, and model trajectories for the population mean (fixed regressions) and for each animal (random regressions). Additionally, it provides estimates of genetic parameters at any point along the egg production curve in the interval in which the measurements have been obtained. The prediction of these values for egg production is of great economic importance, and should be considered when selecting laying hens (VENTURINI, 2012).

The aim of this study was (1) to define the random regression model that best fits the observed data of egg production of Barred Plymouth Rock and White Plymouth Rock hens between 5 and 12 months of age; (2) to test different structures of genotypic covariance matrices (random effect matrix G) and residuals (R); and (3) to estimate broad-sense heritability, and environmental and genotypic correlations.

MATERIALS AND METHODS

This study was conducted using egg production data from Barred Plymouth Rock (BPR) and White Plymouth Rock (WPR) hens raised during the year of 2010 in the Laboratory of Poultry of the Animal Science Department of Federal University of Santa Maria. Poultry were bred in a 210-m^2 experimental aviary, in laying cages (L 0.33 × W 0.45 × H 0.40m) housing two hens each, received water and food *ad libitum*, identical environmental management procedures, and an increasing lighting program of up to 17h of light per day.

Percentage of eggs produced per cage was evaluated from 151 BPR (n = 1.120) and 134 WPR hens (n = 1.045), between age of 5 and 12 months. Estimate of egg production curve was obtained through a mixed model defined by the equation:

$$Y_{ij} = \text{breed} + \sum_{m=0}^{kb-1} \beta_m \phi_m(t_i) + \sum_{m=0}^{ka-1} \alpha_{jm} \phi_m(t_{ij}) + E_{ij};$$

where Y_{ij} is the production of eggs in the ith period, by the jth hen; β_m are the regression coefficients used to model the mean trajectory of the population; $\phi_m(t_i)$ is the regression function of order k_b that describes the mean population curve according to the age at production (t_i); $\phi_m(t_{ij})$ is the regression function that describes the trajectory of each hen j according to its age in months (t_i) for random genotypic effects; α_{jm} are the genotypic random regressors for each hen; k_b and k_a are the orders of the polynomials used for the purposes described above; and E_{ij} is the random error associated with the age (i) of a particular hen (j).

Initially, the second and third order polynomial models were tested to estimate the mean trajectory of the population (fixed curve). Random effects were tested using the following polynomial regression models: (1) linear with intercept, (2) linear without intercept, (3) quadratic with intercept, (4) quadratic without intercept, (5) cubic with intercept, and (6) cubic without intercept.

For all random regression models described above, 12 genotypic variance and covariance (G) matrices were tested: variance component (VC), compound symmetry (CS), unstructured (UN), first - order autoregressive (AIR[1]), first - order heterogeneous autoregressive (ARH[1]), heterogeneous compound symmetry (CSH), toeplitz (TOEP), first - order auto regressive moving average (ARMA[1,1]), first - order and dependence (ANTE[1]), unstructured correlation (UNR), banded main diagonal (UN[1]), and Huynh-Feldt (H-F). To determine the optimal structure of the G matrix, the VC matrix was maintained as the covariance (R) matrix, which assumes variance homogeneity, that is, the residual variances are the same throughout the egg-laying period. The mixed procedure of SAS® software (SAS Institute Inc., Cary, NC, USA 2010) was used for these analyses.

The best G matrix structure was selected based on the Akaike information criterion (AIC) (AKAIKE, 1974), the Bayesian information criterion (BIC) (SCHWARZ, 1978), the restricted log likelihood (-2LMR), the mean squared residue (MSR), and a graphical display. It is worth noting that lower -2LMR, AIC, BIC, and MSR values are preferred. After selection of the best G matrix structure, the G matrix was fixed and the 12 covariance matrices for residual effects (R matrix) were tested.

The estimate of the broad-sense heritability (h^2_a) for each month (t) of egg production was calculated as follows: $h^2_{a(t_i)} = \frac{\hat{g}_{t_i}}{\hat{g}_{t_i} + \hat{\sigma}^2_e}$, where $\hat{g}_{t_i}$ is the genotypic variance in the month t_i and $\hat{\sigma}^2_e$ is the residual variance. The estimates of genotypic correlation between measurements in different months of laying (t_i and t_j) were defined by the equation $\hat{g}t_i t_j = \frac{\hat{g}t_i t_j}{\sqrt{\hat{g}t_i t_j * \hat{g}t_i t_j}}$. The estimates of genotypic covariance for the month t were described as $\hat{g}t_i t_j = Z'_{t_i} K_a Z_{t_j}$, where i = 5, 6,...,12 and j = 5, 6,...,12 months of age; K_a is the covariance matrix between the random genotypic regression coefficients; and Z is the age matrix in months, in which each row represents an age and the number of columns is equal to the polynomial adjustment order used to calculate the variances $t_i = t_j$.

Genotypic value of hens for egg production at different age were estimated as follows: $VG = \bar{X}_p + h_a^2(X_i - \bar{X}_p)$, where $\bar{X}_p$ is the phenotypic mean of all hens belonging to the same breed estimated by the fixed curve andis the phenotypic value of each hen. After that the ranking correlation (Spearman) of hens at different age were estimated.

RESULTS AND DISCUSSION

The fixed curve was modeled by second and third order polynomial regressions using 12 matrix structures of the random variance and covariance matrix (G), maintaining the residual effects matrix (R) always equal to the VC. For all 24 combinations R–G that converged, the best values of -2LMR, AIC, BIC, and MSR were obtained when the third order polynomial regression was used to model the fixed curve. VENTURINI et al. (2012) used random regressions to assess the production of eggs in laying hens and defined the fixed trajectory of the curve by a cubic Legendre polynomial.

Regarding the best structure of the covariance matrix for random effects (G), lower values of -2LMV, AIC, BIC, and residuals were observed for the UN matrix in random quadratic regression models with intercepts (model 3), followed by the cubic model without intercept (model 6) (Table 1). According to FLORIANO et al. (2006), several methods were developed to facilitate the choice of the covariance structure that best explains the variability behavior and correlation between repeated measures, with AIC and BIC being the main selection criteria, as they depend on

Table 1 - Restricted log likelihood (-2LMV), Akaike information criterion (AIC), Bayesian information criterion (BIC), residuals, and parameter numbers of the models (NP) for different structures of the random covariance (G) matrix, with residual covariance (R) matrix equal to VC and the fixed curve modeled by third order (cubic) polynomial regression.

----------Structures---------		Models[1]	----------Statistical criteria----------				
R	G		NP	-2LMV	AIC	BIC	Residual
VC	UN	1	4	7854	7862	7877	160
VC	UN	2	2	7996	8000	8007	201
VC	UN	3	7	7765	7779	7805	137
VC	UN	4	4	7917	7925	7939	172
VC	UN	6	7	7788	7802	7827	142
VC	VC	1	3	7980	7986	7997	196
VC	VC	2	2	7996	8000	8007	201
VC	VC	4	3	7994	8000	8011	199
VC	CS	1	3	7995	8001	8012	200
VC	AR(1)	1	3	7995	8001	8012	200
VC	ARH(1)	1	4	7854	7862	7877	160
VC	CSH	1	4	7854	7862	7877	160
VC	TOEP	1	3	7995	8001	8012	200
VC	TOEP	2	2	7996	8000	8007	201
VC	ANTE(1)	1	4	7854	7862	7877	160
VC	ANTE(1)	2	2	7996	8000	8007	201
VC	ANTE(1)	4	4	7917	7925	7939	172
VC	UNR	1	4	7854	7862	7877	160
VC	UNR	2	2	7996	8000	8007	201
VC	UN(1)	1	4	7980	7986	7997	196
VC	UN(1)	2	2	7996	8000	8007	201
VC	UN(1)	4	4	7994	8000	8011	199
VC	H-F	1	4	7854	7862	7877	160
VC	H-F	4	5	7917	7925	7939	172

[1]Random regression models: 1 = linear with intercept, 2 = linear without intercept, 3 = quadratic with intercept, 4 = quadratic without intercept, 5 = cubic with intercept, and 6 = cubic without intercept.

the likelihood ratio value of the model, the number of observations, and the parameters used.

In this study, the best covariance structure for residual effects (R) was assessed. For this assessment, the UN structure for the G matrix and the quadratic model with intercept, the cubic model without intercept, and the linear model with intercept were used (Table 2). In Table 2, the models that had the lowest -2LMV and AIC values were: linear with the intercept G=UN and R=UNR; linear with intercept G=UN and R=ANTE (1). The BIC identified ANTE (1) as best structure of R matrix, followed by ARH (1).

The model that used the UNR structure for R matrix was not pointed as the best for BIC. To calculate the BIC, beyond LMV, the number of parameters of the model multiplied by the natural logarithm of total records, resulting in more rigorous penalty compared to AIC which considers only the number of parameters. This may be the explanation for the R=UNR model have been the third in this criterion, since it has a higher number of parameters when compared to the other two models (38 vs 15 and 18 parameters).

In carrying out the graphic display of the observed and estimated production of eggs for each animal it was observed that the linear model with intercept G=UN and R=UNR was the best fit for the production curve of eggs per animal, with 83% and 87% efficiency for BPR and WPR hens, respectively, while the other models did not reach 76% efficiency, independent of breed (model with intercept G=UN and R=ANTE(1), and quadratic model with intercept G=UN and R=ARH(1)).

In the figure 1 it can be observed the curve estimated by linear model with intercept G=UN and R=UNR for four different animals in each breed. With this information is possible to identify the animals that have curves over the average of the breed (fixed), such as the Plymouth Rock White animals 6119 and 6132 (Figure 1A) and the Barred Plymouth Rock animals 6030 and 6212 (Figure 1B).

Environmental correlation estimates between different months of egg production were low, ranging from 0.21 to 0.24 (Table 3). Genotypic correlation estimates ranged from 0.15 to 0.99, with the largest estimates observed between proximal months (Table 3), that is, the best animals in month 5 may not be the best in months 10, 11, and 12.

The broad sense heritability estimates for egg production in hens aged between 5 and 12 month ranged from 0.15 to 0.51 (Table 3). These values set a limit to the narrow-sense heritability

Table 2 - Restricted log likelihood (-2LMV), Akaike information criterion (AIC), Bayesian information criterion (BIC), residuals, and parameter numbers of the models (NP) for different structures of the residual covariance (R) matrix, with random covariance (G) matrix equal to UN and the fixed curve modeled by third order (cubic) polynomial regression.

----------Structures----------		Models[1]	------Selection Criteria------			
R	G		NP	-2LMV	AIC	BIC
VC	UN	1	4	7854	7862	7877
VC	UN	3	7	7765	7779	7805
VC	UN	6	7	7788	7802	7827
AR(1)	UN	1	5	7794	7804	7823
AR(1)	UN	3	8	7740	7756	7785
AR(1)	UN	6	8	7759	7775	7804
ARH(1)	UN	1	12	7559	7583	7627
ARH(1)	UN	3	15	7540	7570	7625
TOEP	UN	6	7	7788	7802	7827
ARMA(1,1)	UN	1	6	7774	7786	7808
ARMA(1,1)	UN	3	9	7722	7740	7773
UNR	UN	1	39	7415	7493	7635
CSH	UN	1	12	7622	7646	7690
CSH	UN	3	15	7563	7593	7648
ANTE(1)	UN	1	18	7473	7509	7574
UN(1)	UN	1	39	7622	7644	7685
UN(1)	UN	3	42	7563	7591	7642

[1]Random regression models: 1 = linear with intercept, 2 = linear without intercept, 3 = quadratic with intercept, 4 = quadratic without intercept, 5 = cubic with intercept, and 6 = cubic without intercept.

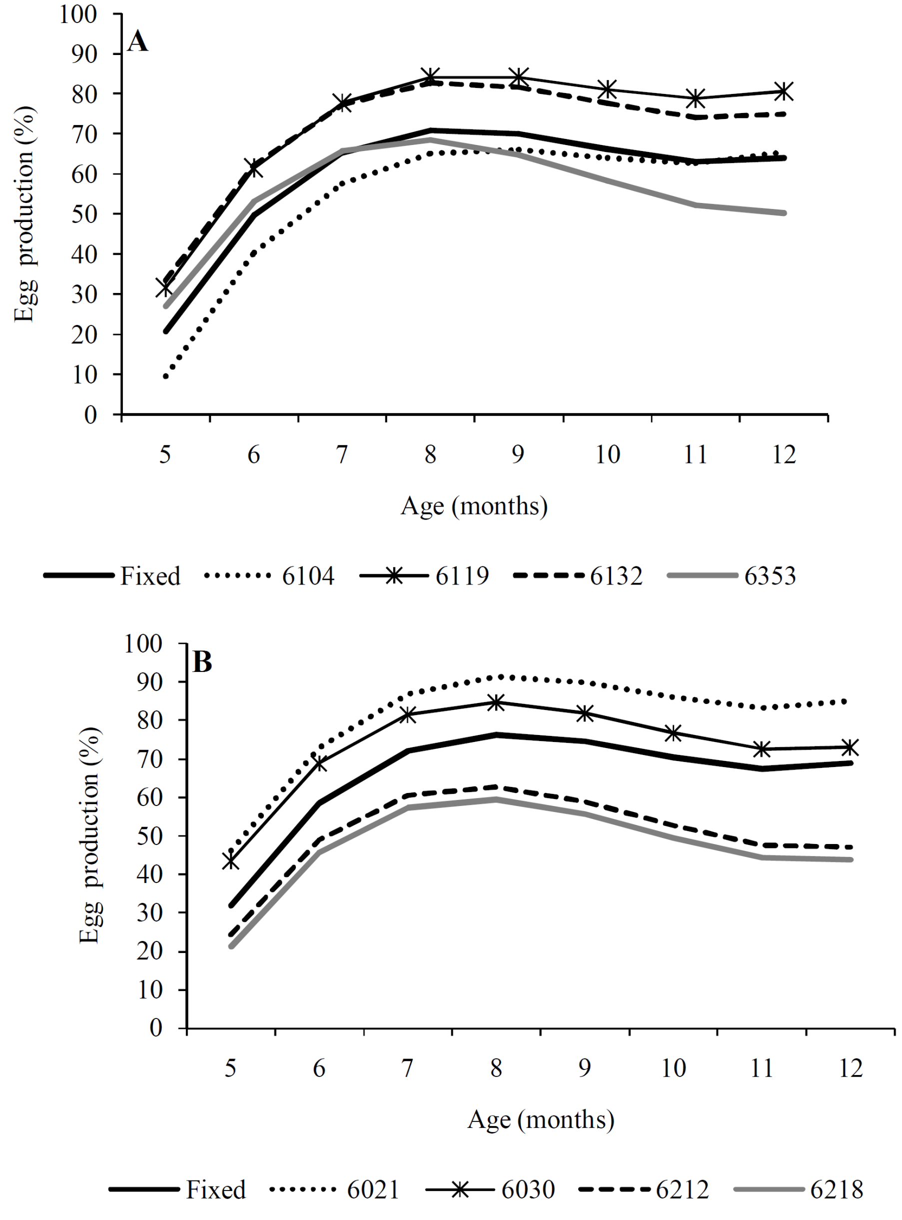

Figure 1 - Estimated curve for the 6304, 6119, 6132 and 6353 animals of the Barred Plymouth Rock race (A) and the animals 6021, 6030, 6212 and 6218 of the race White Plymouth Rock (B) by means of the linear random regression model with intercept, using the (co)variance structures UN and UNR to estimate the matrix G and R, respectively. The fixed curve was estimated by race using the cubic polynomial regression.

value, which considers only additive genetic variance. Heritability estimates were obtained in determined times; however, random regression models allowed to estimate the heritability at any point within the study period.

Results indicated that higher environmental influences were seen at the beginning of the laying period and decrease over time; therefore, phenotypic selection should not be made in the initial months. From the age of 9 months on ward, the heritability

Table 3 - Broad-sense heritability (diagonal) of egg production, environmental (below the diagonal) and genotypic (above the diagonal) correlations between the eggs produced by hens obtained at different stages of the egg production curve.

Months	5	6	7	8	9	10	11	12
5	0.15	0.97	0.88	0.73	0.56	0.39	0.26	0.15
6	0.24	0.24	0.97	0.87	0.73	0.59	0.47	0.37
7	-0.19	-0.02	0.23	0.97	0.88	0.78	0.68	0.60
8	0.07	-0.07	0.18	0.35	0.97	0.91	0.85	0.78
9	-0.12	-0.04	-0.21	-0.14	0.42	0.98	0.95	0.90
10	0.01	-0.04	-0.06	-0.15	0.70	0.49	0.99	0.97
11	0.09	-0.08	0.09	0.04	0.09	0.14	0.42	0.85
12	-0.21	0.13	-0.08	-0.30	-0.08	-0.05	0.07	0.51

value was considered moderate (0.42), with high correlation estimates with the age of 10 (0.98), 11 (0.95), and 12 (0.90) months. ANANG et al. (2000) reported high heritability for monthly egg production in Leghorn hens, which ranged from 0.18 to 0.47, and suggested that egg production should be evaluated between the age of 5 and 10 months. SAVEGNAGO et al. (2011) analyzing the 17 to 30 week old laying rate of White Leghorn laying hens selected by seven generations for egg production observed a heritability of 0.15. TONGSIRI et al. (2014) working with birds of the 11th generation of hens selected from the Plymouth Rock White and Rod Island Red breeds observed a heritability of 0.30 and 0.33 respectively for the characteristic egg production at 17 weeks of age. SHADPARVAR & ENAYATI (2012), analyzing data from six generations of Mazandaran native laying hens selected at the eighth week of age, reported a heritability of 0.156 for the number of eggs produced, and reported a negative correlation for egg numbers and the age of the first egg.

High heritability for egg number (from 0.25 to 0.34) was also reported by NIKNAFS et al. (2012), WOLC et al. (2012) and QADRI et al. (2013) who reported egg production estimates for up to the age of 40 weeks. LUO et al. (2007) estimated that egg production heritability varied from 0.16 (26 to 27 weeks of age) to 0.54 (62 weeks of age), which values are corroborated by the results reported in the present study.

The ranking correlation estimates of hens' classification at different ages revealed low correlation of hens genotypic values between the initial and final months. The highest heritability value (0.51) was observed at the age of 12 months; therefore, higher response to the phenotypic selection is expected at this age.

Correlations of genotypic values between the ages of 9 and 12 months were 0.94 for WPR and 0.96 for BPR hens (Table 4), that is, selecting 20% of the best egg production hens in the ninth and twelfth month, 78 and 81% of the selected hens for BPR and WPR breeds, respectively will be the same.

Table 4 - Correlations between the genotypic values of eggs produced by Barred Plymouth Rock (above the diagonal) and White Plymouth Rock (below the diagonal) hens of different ages.

Age (months)	5	6	7	8	9	10	11	12
5		0.97	0.89	0.78	0.66	0.55	0.45	0.37
6	0.97		0.97	0.90	0.81	0.73	0.65	0.58
7	0.89	0.97		0.98	0.93	0.87	0.80	0.75
8	0.79	0.92	0.98		0.98	0.95	0.91	0.87
9	0.69	0.85	0.94	0.98		0.99	0.97	0.94
10	0.61	0.78	0.89	0.96	0.99		0.99	0.98
11	0.53	0.72	0.85	0.94	0.98	0.99		0.99
12	0.47	0.67	0.82	0.91	0.96	0.99	0.99	

CONCLUSION

The random regression linear intercept model with Unstructured (UN) covariance structure for the random effects matrix (G) and Unstructured Correlations (UNR) for residuals matrix (R) adequately model the egg production curve of Barred Plymouth Rock and White Plymouth Rock hens.

Egg production heritability estimates from the age of 9 months onward are moderate and the estimates of genotypic correlations between 9 with the age of 10, 11, and 12 months are above 90%. Therefore, the phenotypic selection of Barred Plymouth Rock and White Plymouth Rock hens beginning at the age of 9 months is suggested, with the aim to anticipate the selection of hens for egg production, to decrease the range of generations, increase annual gain, and reduced production costs.

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