INTRODUCTION

Egg production in laying hens is a process of pronounced cyclic nature and eggs are laid at intervals of around 24 to 27 hours or more, depending on age (Akbas et al. 2002). These cyclic processes result in the formation of the clutches of one or more eggs laid on consecutive days and each clutch is followed by one or more pause days. The length of a clutch varies little within a hen (Koops et al. 1992). Clutch size, like litter size, is a type of quantitative trait called meristic (Rowland et al. 1997) and quantitative trait methodologies can be applied to these kinds of traits (Crow et al. 2000).

Measurements that are taken along a trajectory of time can be modeled as a function of that trajectory by means of random regression models. The prime advantage of studying longitudinal records like CS using RRMs is its effectiveness for studying change (Van der Werf, 2001).

Hens with the same total or partial production, however, can exhibit different egg production curves (patterns) because of differences in persistency (Grossman et al. 2000). The effectiveness of selection can be improved by deeper
Analyze of Clutch Size Using Random Regression Models

understanding and more detailed analysis of the laying process (Koops et al. 1992). Therefore, the idea to use part-time records as separate or repeated measurement of egg production as proposed by Wolc et al. (2007), Wolc et al. (2009), Wolc et al. (2010), Wolc et al. (2011), Wolc et al. (2013), Farzin et al. (2010), Kranis et al. (2007), Anang et al. (2001) and Anang et al. (2002) leads to loss of pattern and characterization of egg production. The use of RRMs for the genetic evaluation of clutch size has not been reported and studies focusing especially on the order of polynomials can be performed using these models. The main objective of this study was to find the best random regression model and estimate the (co)variance components and variance ratios including heritability and ratio of animal permanent environmental variance to phenotypic variance of the clutch size as a new repeated record. To find the relative trajectory of variance components of CS according to the mean egg production of the flock, the hen-day curve was used.

MATERIALS AND METHODS

Egg production records were collected from 3156 birds comprising 10 generations of pedigreed birds from Iranian native fowl production center in Mazandaran province. Number of sires and dams were 81 and 516, respectively. After hatching, chicks were transferred to rearing barns. Every 10 hens were kept in one pen and hens laid in individual trap nests, and production was individually recorded on daily basis for 365 days. The records are consisted of a sequence of 365 binary records (0=no egg, 1=egg laid), with each record corresponding to a specific day of the whole production period. If a hen died during the laying period, the rest of its records after the date of the death were treated as missing values. Cracked eggs were counted as laid eggs.

Eggs laid on the floor were excluded, because they could not be assigned to a specific hen. The consecutive days of egg production without any delay is called CS. The first day of each clutch was assigned as test-day of that clutch. Data consists of 111,137 test-days CS which was extracted from daily egg production.

The trait analyzed in the current study was the CS which was extracted from eggs laid in trap nests over the period of 365 days. In order to edit and explore fixed effects on the trait R was used. The data were analyzed using the random regression model. All the analyses were performed using PXEM restricted maximum likelihood algorithm with the WOMBAT software (Meyer, 2006). Fifty alternative RRMs were analyzed.

All models include in their equation the same systematic effects; and temporary measurement errors were taken to be independently distributed with constant variance along days in production (DIP).

The analysis of CS was based on the following RRM:

$$Y_{ijk} = \text{Hatch}_i + \sum_{n=1}^{n_1} \beta_n X_{ijk} + \sum_{n=2}^{n_2} \alpha_n X_{ijk} + \sum_{n=3}^{n_3} Q_n X_{ijk} + \epsilon_{ijk}$$

Where:
- $Y_{ijk}$: $K^{th}$ test-day observation of the $j^{th}$ hen.
- Hatch$_i$: independent fixed effect of $i^{th}$ hatch.
- $\beta_n$: $j^{th}$ fixed regression coefficient.
- $\alpha_n$: $j^{th}$ random regression coefficient for additive genetic effect.
- $Q_n$: $j^{th}$ random regression coefficient for permanent environmental effect.
- $X_{ijk}$: covariate which is the value of Legendre polynomial on DIP.
- $\epsilon_{ijk}$: random residual effect.
- $n_1, n_2, n_3$: numbers of covariates, dependent on the order of Legendre polynomials.

The following structure of (co)variance matrices for random effects was assumed:

$$
\begin{pmatrix}
G & A \\
A^T & P
\end{pmatrix} = 
\begin{pmatrix}
G & A \\
A & P
\end{pmatrix}
$$

Where:
- $G$: genetic covariance matrix among random regression coefficients and the trait.
- $A$: additive numerator relationship matrix.
- $P$: permanent environmental covariance matrix among random regression coefficients and the trait.
- $E$: residual variance assumed to be constant throughout the period for simplification.
- \( \otimes \): kronecker product.

Following Kirkpatrick et al. (1990), regression coefficients were derived from Legendre polynomials. The use of Legendre polynomials for RRMs in monthly egg production was also recommended by Wolc et al. (2009). (Co)variance components for all models were estimated with the restricted maximum likelihood, employing PXEM algorithm, using WOMBAT program. Genetic and permanent environmental correlations were predicted for five values of the control variable, corresponding to lowest and highest value (d 116, d 407 respectively) and 3 approximately equidistant intermediate values (d 188, d 261, d 334; Meyer, 2006). Following Strabel et al. (2005), to compare the models, Bayesian Information Criteria (BIC), penalized-likelihood criteria, is used. Subsequently the lowest value of BIC was considered as best model (Venturini et al.
The starting point of each curve was defined to be 116 which is the age at 5% egg production of the flock. The hen-day rates of the flock were calculated for each day.

RESULTS AND DISCUSSION

Estimated BIC for 50 models fitted for the present records is shown in Figure 1. According to estimated BICs a model composed of the second order polynomial for ASM and 8th order polynomial for additive genetic and permanent environmental effect was found to be the most suitable for adjusting the present records. The results were similar to studies carried out by Pool et al. (1999) and Wolc et al. (2009) who reported that model adequacy was better for models with higher order polynomials.

The range of hen-day index was between 0.05 and 0.57 which is shown in Figure 2. The curve indicates that the production period is consisted of two consecutive egg production cycles which the first one is complete (d 116 to d 371) but the second one is about 30 days. The first cycle is consisted of two main parts including a fast rise from the age at 5% egg production of the flock to peak production (d 144) and a two-phase decrease from peak to the end of the cycle. This pattern of egg production agrees with the reports of Miyoshi et al. (1996) and is not a typical egg production curve. A typical egg production curve for a flock increases rapidly and then decrease at a constant rate to the end of the production period (Grossman, 2000) but in the current curve the decreasing part had a long slow decrease and then a short steep decrease. The duration of these three stages were 28, 210 and 17 days, respectively.

Phenotypic, permanent environmental and additive genetic variances of CS are shown in Figure 3. The highest phenotypic and permanent environmental variances of CS were at the first stage of the first cycle. The pattern of phenotypic variance at the starting point was similar to the results gained by Venturini et al. (2012) for monthly egg production but the highest additive genetic variance occurred in the second stage of the first cycle which is different from the results of mentioned study. The overall trend of phenotypic and permanent environmental variances was decreasing and the overall trend for additive genetic variance had two stages; 1) increasing from the beginning of the egg production period (d 116) to a peak (d 242), 2) decreasing from the peak to the end of the production period. Oscillatory nature of phenotypic, additive genetic and permanent environmental variances agreed with the results gained by Lukovic et al. (2003) on number of piglets born alive (NBA) which is another example of meristic trait. As mentioned by Lukovic et al. (2003) at the end of trajectory, decrease in phenotypic, additive genetic and permanent environmental variances probably were the consequence of small number of data. As proposed by Meyer (1998), some scaling of the observed ages can be considered, for instance, a logarithmic transformation should reduce the impact of few observations on very old individuals which is not applied to the current records. According to the changes of phenotypic, additive and permanent environmental variances, variations of phenotypic effects at the first stage of hen-day curve are because of permanent environmental effects. Heritability of CS was in the range of 0.033 to 0.199 (Figure 4) which was similar to the average estimated heritability obtained in the research conducted by Wolc et al. (2013) for pedigree model (0.2) and was somehow similar to the range of heritability estimated by Venturini et al. (2012) that was from 0.04 to 0.14. The lowest and the highest heritability estimates were at beginning and middle part of second phase of hen-day curve respectively (d 163, d 242) and this pattern of changes in heritability were different from results in Wolc et al. (2009) and Farzin et al. (2010) which highest heritability were at first month of egg

Figure 1 Bayesian information criteria (Y-axis) against order of fit for random regression effects (additive and permanent environmental effects) in X-axis, to check the adequacy of the models. BIC(0), BIC(1), BIC(2), BIC(3), BIC(4) stands for 1st, 2nd, 3rd, 4th order of fit for fixed regression effect (ASM), respectively

Figure 2 Hen-day against age of the flock in days

Figure 3 Hen-day against age of the flock in days

Figure 4 Heritability against age of the flock in days
production. The pattern of changes in heritability were also different from the results of study conducted by Kranis et al. (2006) which the random regression using second-order Legendre polynomial was fitted to five monthly egg production records in Turkey. According to results obtained by Kranis et al. (2006) the highest and the lowest estimates of heritability occurred in the first and second monthly egg production records, respectively. Changes of heritability over time may result from activation of different genes during production cycle. Early stages of production are under the influence of sexual maturity (Wolc et al. 2009) but from the point of peak production, genes related to persistency of egg production could be more influential (Minvielle et al. 2006).

The ratio of permanent environmental variance to phenotypic variance was in the range of 0.01 to 0.264 (Figure 5). The overall trend of the ratio was decreasing which agreed with the results gained by Kranis et al. (2007). At the beginning of the curve there was a rapid downward and upward change which is occurred around the peak production to d 185. Next, the ratio had a slow decrease to the end part of the first cycle. At the end of the curve which is simultaneous to the beginning of the second cycle of egg production the curve had smooth decreasing oscillations. As Lukovic et al. (2004) shown although the overall trend of the ratio was increasing but smooth oscillations have been observed.

The estimated genetic correlations for five values of the control variables, corresponding to lowest and highest values (d 116, d 407, respectively), and three approximately equidistant intermediate values (d 188, d 261, d 334) are presented in Figure 6. For the most adequate model, the range of genetic correlations for five values of the control variables including d 116, d 188, d 261, d 334 and d 407 were 0.258 to 0.99, 0.294 to 0.99, -0.018 to 0.99, -0.058 to 0.99 and -0.18 to 0.99 respectively. The correlations for d116 and d188 were all positive. The lowest correlations are found for d 407. The genetic correlations for three middle values including d 188, d 261 and d 344 were dominantly greater than 0.5. As the distance between the age of 116 and the consecutive ages increased the genetic correlations decreased rapidly and this pattern continued to the peak production of the first cycle and then the correlations had a slow increasing trend up to the beginning of the second cycle. The beginning of the first and second cycle of egg productions had high genetic correlations which is the indicator of common gene activations. The genetic correlations for the age of 188 decreased as the distant between consecutive days increased. The slope of the curve for the ages after d 188 was less than the ages before this point which means that changes in genetic correlations for the days after the point of d 188 were less than the days before this point. The correlations between this point and the beginning of the second cycle were high. Changes of the genetic correlations for the age of 261 as the middle point of the whole egg production period, had a slow decrease as the distance between consecutive points increased and these patterns were consistent in two opposite directions; 1) from this point to the peak production of the first cycle and 2) from this point to the beginning of the second cycle. The correlations between this point and the beginning of the first and second cycle decreased fast. The correlations for the ages of 334 and 407 as two end point of the curve had the same patterns as d 116 and d 188 but in the reverse direction.

The genetic correlations for partial egg production which are conducted by Venturini et al. (2012) and Wolc et al. (2007) were in the ranges of 0.1 to 0.99 and -0.177 to 0.99, respectively and the results of the current study were similar to Wolc et al. (2007) and different from Venturini et al. (2012). The overall pattern of changes of genetic correlations in the current study indicated that as the distance between adjacent ages increased the genetic correlations decreased and patterns agreed with the results obtained by
Komprij et al. (2013) for milk traits in Slovenian dairy sheep including milk yield, fat content and protein content, Lukovic et al. (2007) for litter size in pig, Wolc et al. (2007) for monthly egg production, Akbas et al. (2004) for quail body weights and Jensen (2001) for milk yield in dairy cattle. Despite the fact that at the time of this study, no research has been done on the architecture of CS as a time-dependent trait, the patterns of genetic correlations for five values of the control variables indicated probably the same genetic architecture for beginning point of the two consecutive egg production cycles and different genetic architecture for the point of peak production and the beginning of the two consecutive cycles. Estimates of permanent environmental correlations are also given in figure 6.

The range of permanent environmental correlations for five control variables including 116, 188, 261, 334 and 407 were -0.492 to 0.99, -0.371 to 0.99, -0.15 to 0.99, 0.146 to 0.99 and -0.594 to 0.99, respectively. The permanent environmental correlations were dominantly positive for the first three points and were all positive for d 334. Permanent environmental correlations for three middle control variables including 188, 261 and 334 had wild oscillations in peak of the first egg production cycle. As reported by Wolc et al. (2009) the range of permanent environmental correlations for partial egg production were from -0.12 to 0.99 which in the lower bound was different from the estimations in the current study. Wild oscillations for correlations between the first (d 116) and the last (d 407) control variable lasted for the whole egg production period. As Arango et al. (2004) mentioned the apparent weakness of the model for fitting the trait might be due to 1) a lack of mathematical flexibility to model the trait adequately with orthogonal polynomials; 2) the small number of records at different control variables; and 3) the general property of the estimation of regression coefficients. Rawlings et al. (1998) indicated that even with polynomial models of higher order and associated smaller residual sum of squares, in specific ages might exhibit wild oscillations.

CONCLUSION

Egg production curve of Iranian native fowl is not a typical egg production curve. Using random regression model appears promising and could be recommended for estimation of variance components of CS. Although none of the studies on random regression modeling used CS as repeated measurements, the results obtained by the current study proposed that the model composed of the second order polynomial for ASM and 8th order polynomial for additive genetic and permanent environmental effect was the most suitable for estimation of variance components in the current dataset. Selection applied in the CS can result in gains for adjacent ages. However, as the distance in time between consecutive ages increase, the selection becomes less efficient. Because the genetic correlations for d261 was dominantly greater than 0.5, the selection made on the basis of d242, where highest heritability was estimated, is useful.

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REFERENCES

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