Heritability of egg production in laying hens under cumulative, multitrait and repeated measurement animal models

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ABSTRACT: Six generations of three layer lines (13 770 recorded individuals of A22 line, 13 950 of A88, 9 351 of K66) were used to estimate genetic effects on egg production under cumulative, multitrait and repeatability models. Variance components were estimated by the AI-REML algorithm. The heritability of cumulative records ranged from 0.08 to 0.1. For the repeated measurements model the following genetic parameters were obtained: heritability 0.02–0.03, repeatability 0.04–0.38. The first two months of egg production were found to differ from the other periods: heritability was relatively high ($h^2 > 0.35$) and low or negative correlations with the other periods were found. Heritability was low ($h^2 < 0.1$) from the peak production until the end of recording and the consecutive periods were highly correlated. Further studies on monthly records are suggested.

Keywords: egg production; laying hens; cumulative model; monthly records

Although nowadays a higher pressure is given on the quality rather than on the quantity of a product due to consumer demands, egg production still remains the most important trait in layer selection programs. Consistent selection led to doubtless progress that was achieved in this trait. For example in Germany the average number of eggs laid per hen annually more than doubled between 1950 and 1990 (Hartmann, 1992), in 2004 an average layer in Canada laid 231 eggs (Agriculture Division Statistical Bulletin, 2004). Progress was also achieved in the Polish population with the average of 198 eggs per hen in the same year, but over 300 eggs from birds at a test station (Wężyk, 2003).

Models of genetic evaluation and trait definitions have varied over time. Selection was primarily based on phenotypes, then selection indexes were introduced. Variance components were estimated using ANOVA based methods and later on they were replaced by REML methodology based on animal model. The effectiveness of selection can be improved by deeper understanding and more detailed analysis of the laying process. In selection programs egg production is usually recorded as a single measurement – initial egg production until the specific age of an individual. This approach is advantageous due to both the short generation interval and its relative numerical simplicity. However, several studies suggest that gene expression varies with age (Szczerbińska, 1997; Lijedahl et al., 1999; Ledur et al., 2002). Therefore the initial egg production may not necessarily be the same trait as the production at the end of the laying cycle. Some of the studies suggest a low (Anang et al., 2000a) or even negative genetic correlation between early and late records (Preisinger and Savas, 1997). Therefore the idea to use part-period records as separate or repeated measurements of egg production appeared. This study aims to estimate heritability and repeatability of monthly egg production and to compare the estimates with classical cumulated record.

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MATERIAL AND METHODS

The initial egg production of three lines in six generations kept at Poultry Research Branch at Zakrzewo was recorded. Pedigree recording started in the generation previous to the one in which the first data was collected. Laying hens were kept in single cages with automatically controlled environmental factors e.g. light, temperature, humidity, and feeding. The data on 37 071 hens were analyzed. Two Rhode Island White lines (13 770 recorded individuals of A22 line and 13 950 of A88) were selected for egg production and shell colour whereas the Rhode Island Red line (K66 with 9 351 hens) was selected for egg weight and shell colour. The base populations consisted of 1 226, 688, 551 individuals and pedigree files included 18 909, 18 207, 13 155 birds for A22, A88, K66 lines, respectively. The data was analyzed within lines. The first nine months of egg production were recorded. A brief statistical description of the analyzed populations is given in Table 1. An average egg production in the studied lines was similar and equal to about 200 eggs per hen in the first nine months of lay. After a reduction in the flock size in the fourth generation the population rebuilt in the fifth generation performed significantly worse. Daily egg production was cumulated into monthly records starting at the day when it exceeded 5%. The egg production recording to a fixed day punishes the birds from later hatches because they showed highly significantly lower average production than those from the first hatch. The differences in recording duration were taken into account by including the hatch-year effect in the model.

Three animal models were used to estimate genetic parameters.

For cumulated egg production (model I):

$$y = Xb + Z_1a + e$$

where:

y = vector of observations
b = vector of fixed effects of hatch-year classes
a = vector of random additive genetic effects
e = vector of random errors
X = known design matrix of fixed effects
Z_1 = known design matrix of random additive genetic effects

For monthly egg production: multitrait animal model (model II):

$$y^* = (X \otimes \mathrm{I})b^* + (Z_1 \otimes \mathrm{I})a^* + e^*$$

where:

y^* = vector of observations on t traits
b^* = vector of fixed effects
a^* = vector of random additive genetic effects
e^* = vector of random errors
X, Z_1 = as in the previous model

Repeatability model (model III):

$$y^* = Xb^* + Z_1a^* + Z_2p^* + e^*$$

where:

p^* = vector of random permanent environmental effects
Z_2 = known design matrix for permanent environmental effects
Other symbols were denoted as in the previous models

Corrected repeatability model (model IV):

$$y^* = Xb^* + Z_1a^* + Z_2p^* + e^*$$

where:

b^* = vector of fixed effects of hatch-year classes and month of lay classes
Other symbols were denoted as in the previous models

The Average Information approach (Johnson and Thompson, 1995) to Derivative Free Restricted Maximum Likelihood algorithm was used to estimate genetic parameters. Genetic correlations were estimated under multitrait model. The variance component estimation was carried out using the DFREML package (Meyer, 2001).

Table 1. Average egg production of the studied populations within generations

Generation	A22			A88			K66		
	n	mean	SD	*n*	mean	SD	*n*	mean	SD
1	2 060	222.67	49.45	2 889	205.98	36.53	1 921	197.46	38.05
2	3 196	214.99	48.23	3 020	199.40	43.51	2 018	220.40	31.41
3	2 095	228.82	53.12	1 891	212.02	35.46	1 864	225.19	35.86
4	1 741	210.83	37.54	1 582	203.85	35.28	1 323	226.97	34.78
5	2 533	190.48	55.47	1 991	181.88	41.31	1 487	208.71	35.25
6	2 145	171.83	42.47	2 217	185.20	37.92	738	173.34	56.81

Table 2. Average monthly egg production in the studied populations

Line	1st Month		2nd Month		3rd Month		4th Month		5th Month	
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
A22	8.62	7.63	25.58	5.62	27.59	4.12	27.28	4.43	26.69	4.90
A88	9.35	7.52	25.69	5.67	27.25	4.73	26.75	5.17	25.74	5.86
K66	13.72	6.71	27.36	4.58	27.21	4.93	26.77	5.20	26.03	6.05

Line	6th Month		7th Month		8th Month		9th Month	
	mean	SD	mean	SD	mean	SD	mean	SD
A22	25.01	5.58	21.21	7.57	20.43	8.48	18.03	10.25
A88	24.05	6.61	21.52	8.20	19.53	9.14	18.33	9.63
K66	25.07	6.26	24.66	6.65	23.06	7.18	21.51	8.11

Table 3. Residual variance estimates under different models

Line	Cumulative model	Multitrait model	Repeatability model	Corrected repeatability model
A22	1 289.2	16.1–51.7	72.8	35.3
A88	1 277.4	20.9–60.4	85.6	40.9
K66	1 999.6	19.5–52.7	41.5	22.7

Heritability was estimated as the ratio of additive genetic variance to total variance whereas repeatability as the sum of additive genetic and permanent environmental variances divided by phenotypic variance.

RESULTS AND DISCUSSION

Heritability estimates are shown in Figure 1. The estimates of residual variance for different models are given in Table 3. However, the direct comparison of these values is not possible. For the cumulative model heritability was estimated on a low level of about 0.1. The estimates found in the literature often vary in a wide range depending on the population, time and model. In experimental lines not selected for egg production heritability of this trait may reach almost 0.5 (Anang et al., 2000a) whereas in commercial lines it is often less than 0.2 (Zięba, 1990; Preisinger and Savas, 1997). In long-term selection studies it was also shown that realised heritability may change over generations (Sharma et al., 1998). Low heritability estimates may result from a reduction in genetic variance due to selection but also from the overestimation of error variance due to the high skewness of traits. It should be noted that some authors (Ünver et al., 2004) reported an increase in heritability for transformed data. However, transformation aimed at the improvement of trait normality does not often change the estimated genetic parameters (Anang

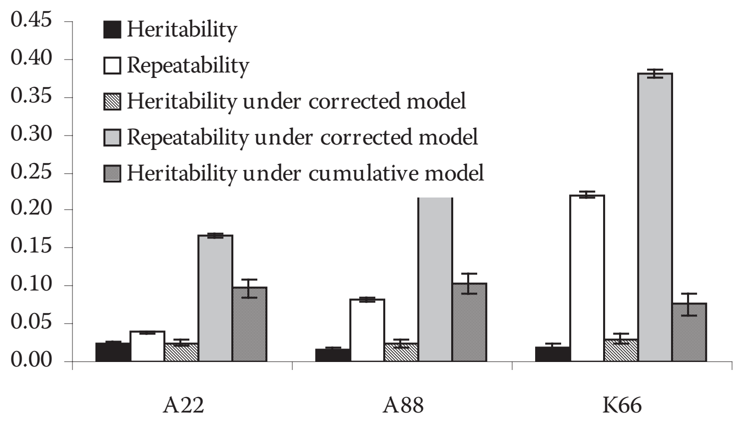

Figure 1. Genetic parameters under repeatability and cumulative model

Table 4. Coefficients of phenotypic (below diagonal) and genetic (above diagonal) correlations between egg production in the part-period and heritabilities (diagonal) for A22 line

Month	1	2	3	4	5	6	7	8	9
1	0.3697 ± 0.0191	0.7328	–0.1776	–0.1264	–0.1410	0.0894	0.1567	0.0488	–0.0504
2	0.3274	0.0955 ± 0.0119	0.2081	0.1820	0.1093	0.2612	0.3773	0.2051	0.1155
3	0.0334	0.3709	0.0288 ± 0.0076	0.9445	0.5098	0.1739	0.2707	0.3230	0.2486
4	0.0426	0.2708	0.5890	0.0174 ± 0.0063	0.7080	0.4512	0.6256	0.7627	0.5804
5	0.0440	0.2374	0.4330	0.5973	0.0369 ± 0.0082	0.8337	0.8086	0.9181	0.7265
6	0.0484	0.2014	0.3188	0.3805	0.5308	0.0429 ± 0.0086	0.8960	0.8785	0.8034
7	0.0532	0.1422	0.2056	0.2479	0.3162	0.5011	0.0603 ± 0.0099	0.8562	0.7040
8	0.0572	0.1230	0.1829	0.2125	0.2724	0.3595	0.6186	0.0537 ± 0.0092	0.9150
9	0.0205	0.0782	0.1207	0.1471	0.1884	0.2424	0.4378	0.6614	0.0496 ± 0.0089

Standard errors of correlation coefficients ranged from 0.04 to 0.16

Table 5. Coefficients of phenotypic (below diagonal) and genetic (above diagonal) correlations between egg production in the part-period and heritabilities (diagonal) for A88 line

Month	1	2	3	4	5	6	7	8	9
1	0.3860 ± 0.0196	0.7008	–0.0479	–0.1345	–0.0561	0.0145	0.0882	0.0707	–0.1449
2	0.3511	0.1084 ± 0.0129	0.5367	0.2678	0.2145	0.2255	0.2653	0.2052	–0.0531
3	0.0330	0.4329	0.0323 ± 0.0081	0.8151	0.6220	0.4836	0.6897	0.6600	0.4313
4	0.0353	0.3160	0.6268	0.0440 ± 0.0090	0.9433	0.8140	0.8672	0.9016	0.7172
5	0.0286	0.2712	0.4884	0.6898	0.0585 ± 0.0101	0.9503	0.8932	0.9125	0.7571
6	0.0421	0.2448	0.4147	0.5245	0.6745	0.0688 ± 0.0108	0.8345	0.8325	0.7158
7	0.0377	0.2138	0.3343	0.4056	0.4845	0.6503	0.0677 ± 0.0106	0.9910	0.7709
8	0.0270	0.1862	0.3055	0.3697	0.4247	0.5228	0.7179	0.0678 ± 0.0106	0.8327
9	–0.0205	0.1274	0.2610	0.3183	0.3735	0.4538	0.5854	0.7334	0.0605 ± 0.0101

Standard errors of correlation coefficients ranged from 0.02 to 0.11

Table 6. Coefficients of phenotypic (below diagonal) and genetic (above diagonal) correlations between egg production in the part-period and heritabilities (diagonal) for A88 line

Month	1	2	3	4	5	6	7	8	9
1	0.4280 ± 0.0245	0.2600	0.1522	0.2037	0.2679	0.1481	0.0864	0.0547	–0.1430
2	0.2806	0.0565 ± 0.0133	0.8407	0.7876	0.6014	0.6084	0.6533	0.6903	0.5118
3	0.1214	0.5796	0.0464 ± 0.0118	0.8074	0.6076	0.6318	0.5915	0.6545	0.2694
4	0.1065	0.4540	0.6563	0.0289 ± 0.0096	0.9395	0.9161	0.8370	0.7920	0.4428
5	0.0789	0.3624	0.5179	0.6942	0.0303 ± 0.0102	0.8524	0.7122	0.6626	0.2413
6	0.0610	0.3161	0.4513	0.5812	0.7508	0.0399 ± 0.0114	0.9053	0.7893	0.5130
7	0.0467	0.2750	0.4032	0.5144	0.6272	0.7984	0.0496 ± 0.0121	0.8992	0.7023
8	0.0330	0.2442	0.3561	0.4495	0.5388	0.6673	0.7818	0.0427 ± 0.0114	0.8111
9	0.0267	0.2105	0.2975	0.3825	0.4480	0.5451	0.6462	0.7696	0.0715 ± 0.0142

Standard errors of correlation coefficients ranged from 0.07 to 0.18

et al., 2000a). Moreover, the breeding values on a transformed scale have no biological meaning and are difficult to interpret (Savas et al., 1999). The idea to use monthly egg production as repeated measurements originates from the analysis of Test Day Records in dairy cattle. The trials to implement it in the analysis of poultry data have been made in the last years (Anang et al., 2001; Nurgiartiningsih et al., 2005). Average monthly records are given in Table 2. The peak production was achieved in the second (K66 line) or the third (A22 and A88 lines) month of lay on the level of over 90%. On the phenotypic level the variance was high at the beginning of laying period, it decreased to minimum in the peak production and was increasing until the end of recording. The heritability of monthly egg production under the multitrait model is given in Tables 4–6. The standard errors of the estimates ranged from 0.006 to 0.025. The ratio of genetic variance to phenotypic variance was relatively high (above 35% in all lines) in the first month of lay and substantially decreased in further periods. The tendency is in agreement with the reports from literature (Preisinger and Savas, 1997; Anang et al., 2000a). Although in the ninth month of lay phenotypic variance exceeded the level of the first month, the increase in genetic variance was proportionally lower so that the heritability was not increased. Genetic correlations between the first two periods and the other months were low and even negative between the first month and more distant periods (Tables 4–6). For other periods the correlations decreased as the interval between periods increased. Preisinger and Savas (1997) suggested modelling the first periods as a separate trait. The heritability from repeated measurements model was lower in all lines than that obtained for cumulated production and did not exceed 3% for both the corrected and uncorrected model. The repeatability differed among lines, it was low in both Rhode Island White lines (0.04 and 0.08 for A22 and A88, respectively) but higher in K66 line (0.22). When the effect of the period of lay was included in the model, the repeatability was increased, however the estimates of heritability were not considerably affected. In the study of Anang et al. (2001) heritability and repeatability under a comparable model were equal to 0.06 and 0.07, respectively. Low values of heritability make further searching for new models and new definitions of egg production traits necessary. Anang et al. (2000b) concluded that genetic evaluation based on the average monthly production could be better than the use of cumulative production. The use of fixed or random regression models might be more promising methods of choice.

CONCLUSION

Heritability of egg production changes during the laying period therefore single measurement of cumulated egg production may not be sufficient enough to give an adequate description of the trait.

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