Genetic Evaluation of Litter Size Traits in Pannon White Rabbits

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Summary

In this study 21060 kindling records (collected between 1992 and 2016) of 4926 Pannon White (PW) does inseminated with 1414 PW mating bucks were analysed. Genetic components and genetic trends for the number of kits born alive (NBA), number of kits born dead (NBD) and the total number of born kits (TNB) were estimated using the four single trait animal models. Heritability estimates were low for all traits. For NBA and TNB they ranged between 0.06-0.07±0.01. For NBD they were close to zero (0.019-0.020±0.004). The ratios of the permanent environmental to the phenotypic variances ranged between 0.07-0.1±0.01 for NBA, 0.009-0.013 ±0.004 for NBD and 0.07-0.10±0.01 for TNB. Analysing the models' fit showed that bias values were practically zero for all traits and models. After selecting the best fitted model (containing parity, age of the doe and year-month of kindling) it was extended with dominance effects. As a result, heritability estimates decreased to 0.06±0.01 for NBA, 0.02±0.01 for NBD and 0.06±0.01 for TNB. The ratio of the permanent environmental effects to the phenotypic variances also decreased to 0.08±0.01 for NBA, 0.008±0.005 for NBD and 0.08±0.001 for TNB. Ratios of the dominance effects were larger than those of the heritability estimates for NBA (0.09±0.01) and TNB (0.08±0.01). On the contrary for NBD ratio of the dominance effects was smaller than the heritability estimates (0.01±0.002). Confounding was found among additive genetic, permanent environmental and dominance effects. Inclusion of dominance effects also reduced genetics trends (0.027 vs 0.026, 0.0003 vs -0.0004 and 0.0258 vs 0.0255 for NBA, NBD and TNB, respectively). Spearman rank correlation coefficients between breeding values of the additive and dominance models were high for all traits (0.99). However, some re-ranking was observed among the top ranked animals for all litter size traits.

Key words

rabbit, litter traits, dominance effects, genetic trends

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Introduction

Meat production of multiparous species (like rabbits and pigs) is generally based on three-way cross, where in the first step two maternal lines (selected for litter traits) are crossed, and then in the second cross a sire line (selected mostly for average daily gain) is used (Baselga, 2004). Among the reproductive traits the number of kits born alive has the largest economic value (Cartuche et al., 2014) and this trait can be increased annually by 0.12 kits (Lenoir and Garreau, 2009) using BLUP methodology (Henderson, 1975). Although BLUP models have been applied in rabbit breeding for decades (Estany et al., 1989), the structures of these models show no change and they are considering only the additive genetic components. Other effects like non-additive genetic components are mainly ignored. The reason for this practice can simply be that the models containing dominance effects require not only large datasets but also large amount of full-sibs that are mainly available in multipara species (Li et al., 2017). The objectives of this study were twofold. The first objective was to estimate the genetic parameters and to predict the breeding values for litter size components: number of kits born alive (NBA), number of kits born dead (NBD) and total number of kits born (TNB) in the closed population of Pannon White rabbits using several animal models (based on the available environmental factors) in order to detect the structures of the "best" models. The second objective was to evaluate the best models extended with dominance effects on the stability of genetic parameters and on the predicted breeding values.

Materials and methods

Data information

In the course of this study kindling records (collected between 1992-2016 at the experimental rabbit farm of the Kaposvár University) of the Pannon White (PW) rabbit breed was analysed. General development and management of the Pannon rabbit breeds was described by Matics et al. (2014). The present analysis was based on 21060 kindlings of 4926 PW does inseminated with the individual sperm of 1414 PW bucks. The analyzed reproductive traits were NBA, NBD and TNB. Due to the fact that records showed highly unbalanced frequencies for latter kindlings, parities were combined into four categories (parities 1, 2, 3–10, >10). Descriptive statistics of the examined traits are also presented in Table 1.

Models

Applying single-trait repeatability animal models, genetic parameters, breeding values and genetic trends of NBA, NBD and TNB were estimated by the BLUP and REML methods using the PEST (Groeneveld, 1990) and VCE6 software (Groeneveld et al., 2008). Based on the available environmental factors, four different models were tested for all traits (Table 2) to estimate additive, permanent environmental, residual variances and to predict breeding values. The general structure of these models was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zp} + \mathbf{Wa} + \mathbf{e}$$

where: $\mathbf{y}$ - vector of phenotypic observations; $\mathbf{b}$ - vector of fixed effects; $\mathbf{p}$ - vector of permanent environmental effects; $\mathbf{a}$ - vector of additive genetic effects; $\mathbf{e}$ - vector of residuals: $\mathbf{X, Z,}$

Table 1. Descriptive statistics for the analysed traits and age of the does

Trait	N	Mean	Std	Min	Max
NBA	21060	8.54	3.04	1	19
NBD	21060	0.43	1.10	0	15
TNB	21060	8.97	3.07	1	19
Age	21060	361	197	131	1658

Std: standard deviation; NBA: number of kits born alive; NBD: number of kits born dead; TNB: and total number of born kits; Age: age of the does at kindling.

Table 2. Fixed factors of applied models

Fixed effects	Level	Models			
		1	2	3	4
Parity	4	x	x	x	x
Age	941	-	x	-	x
Year_month	253	x	x	-	-
Year_season	98	-	-	x	x

Parity: parity number; Age: age of the does at kindling; Year_month: year and month of kindling; Year_season: year and season of kindling

$\mathbf{W}$ - incidence matrices linking phenotypic records to respective effects. In order to compare the goodness of fit of the models the PREDICTION procedure of PEST (Groeneveld, 1990) was applied to calculate the mean squared error (MSE), Bias and correlation between the observed and predicted values of the female rabbits with records:

$$MSE = \frac{1}{n}\sum(\hat{y}_i - y_i)^2$$

$$BIAS = \frac{1}{n}\sum(\hat{y}_i - y_i)$$

$$Correlation = r_{\hat{y}_i y_i} = \frac{Cov(\hat{y}_i, y_i)}{\sqrt{Var(\hat{y}_i) \times Var(y_i)}}$$

Where $\hat{y}_i$ and y_i are the predicted and observed phenotypic vales. The prediction for a given kindling record of a given rabbit doe is accomplished summing all its BLUES and BLUP.

The squared differences between the observed and predicted values based on the four models were compared by means of one-way ANOVA (R Core Team, 2012). Genetic trends were determined by fitting the average predicted breeding values of the animals born in the same year on the years of birth using linear regression. The obtained slopes were compared as described by Mead et al. (1993).

After determining the best fitted models, dominance was included in these models via the family class effect following the work of Hoeschele and VanRaden (1991):

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zp_e} + \mathbf{Wa} + \mathbf{Uc} + \mathbf{e}$$

where: $\mathbf{c}$ - vector of family class effects - dominant effect, $\mathbf{p_e}$ - vector of permanent environmental effects, $\mathbf{U}$ - incidence matrices linking phenotypic records to family effects. The other effects were the same as explained for the basic models. In addition

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to estimated variance components, dominance variance was calculated as $V_D = 4V_C$. Contributions of additive (h^2), dominance (d^2), and permanent environmental (p^2) variance to total phenotypic variance ($V_P = V_{Pe} + V_A + V_D + V_E$) were also calculated. V_E had to be corrected by $3/4\ V_D$ because of the use of V_D instead of V_C.

Results and discussion

Means of TNB and NBA (Table 1) were higher than the reported values of other studies (Al-Saef et al., 2008; Rastogi et al., 2000) which result is favourable as PW was never selected for litter size traits. On the contrary, comparing between Pannon White rabbits and the maternal lines showed less superior performances for these traits (Ragab and Baselga, 2011). It can be considered that NBD for this line was about twice lower than in other breeds selected at the Kaposvár University (Nagy et al., 2013; Nagy et al., 2014).

Variance components and variance ratios

Estimates of additive genetic variances, permanent environmental and residual variances and ratios (compared to the phenotypic variance) are given in Tables 3 for all three litter size traits. Heritability estimates were low for NBA and TNB and close to zero for NBD. These estimates were in accordance with the heritability estimates of the relevant literature (Moura et al., 2001; García and Baselga, 2002a; García and Baselga, 2002b; Mantovani et al., 2008; Nagy et al., 2013; Nagy et al., 2014). Although the different applied models did not result in substantially different heritability estimates, adding age (models 2 and 4) they consistently reduced residual variance components of the examined traits. Several reasons could explain various heritabilites reported by the different studies, like genetic differences between the analysed rabbit breeds, observed environments and the different structures of the applied animal models. Nevertheless, most studies used only one model for genetic parameter estimation, therefore no tendency could be detected between the used model structure and the received heritability estimates. The estimates for the ratios of the permanent environmental variance to the phenotypic variance were low for NBD and moderate for NBA and TNB (Table 3) and they exceeded those of the additive genetic effects for NBA and TNB, whereas the opposite was true for NBD. Our results were in the range of 0.03-0.18 for NBA; 0.01-0.07 for NBD and 0.07-0.13 for TNB as reported by the different authors (García and Baselga, 2002a; Garcia and Baselga, 2002b; Ragab et al., 2011; Nagy et al. 2011; Nagy et al., 2013; Nagy et al., 2014). Nevertheless, it must be emphasized that there is no clear tendency in the literature whether the additive genetic or the permanent environmental variances provide larger part of the phenotypic variances of NBA, NBD and TNB, respectively.

Genetic trends

Genetic trends can be seen in Tables 4. Based on the results the genetic trends were significantly lower for the models containing age of NBA and TNB, whereas that of NBD presented an opposite trend. Mean of these trends were 0.04 for NBA, closer to 0 for NBD and 0.04 for TNB, respectively, for the applied four models. It can be noted that the studied breed was never selected for litter size composite traits. Furthermore, the obtained average genetic trend for NBA was higher than the reported value (0.001) for the Egyptian line (Hanaa et al., 2014) and was similar to those observed by Moura et al., 2001 for multi-purpose line. Nevertheless, the obtained trend of the PW breed was lower than those reported by several other studies (Garreau et al. 2005; García and Baselga 2002a; García and Baselga 2002b; Lenoir and Garreau 2009) where the annual genetic trends were 0.11-0.21 kits for TNB and 0.11-0.23 kits for NBA. The values characterizing the models' fit are provided in Tables 4. It can be seen that BIAS was practically zero for all traits and models. According to the MSE values and the correlation coefficients between the observed and predicted litter size traits in Table 4, models containing age showed a better goodness of fit than others. Statistically significant differences were found for NBA and TNB (p<0.0001) by comparing squared differences between the observed and predicted values based on the four models. On

Table 3. Estimated variance components of number of kits born alive (NBA), kits born dead (NBD) and total number of born kits (TNB)

Traits	Model	V_A	h^2	V_{Pe}	p^2	V_E	e^2
NBA	1	0.59 ± 0.02	0.07 ± 0.01	0.62 ± 0.02	0.07 ± 0.01	7.66 ± 0.02	0.86 ± 0.01
	2	0.54 ± 0.02	0.06 ± 0.01	0.81 ± 0.02	0.10 ± 0.01	7.16 ± 0.02	0.84 ± 0.01
	3	0.60 ± 0.02	0.07 ± 0.01	0.61 ± 0.02	0.07 ± 0.01	7.73 ± 0.02	0.86 ± 0.01
	4	0.57 ± 0.02	0.07 ± 0.01	0.80 ± 0.02	0.09 ± 0.01	7.21 ± 0.02	0.84 ± 0.01
NBD	1	0.022 ± 0.004	0.019 ± 0.004	0.015 ± 0.004	0.013 ± 0.004	1.146 ± 0.008	0.969 ± 0.004
	2	0.023 ± 0.004	0.020 ± 0.004	0.012 ± 0.005	0.010 ± 0.004	1.151 ± 0.008	0.970 ± 0.004
	3	0.023 ± 0.004	0.019 ± 0.004	0.013 ± 0.005	0.011 ± 0.004	1.161 ± 0.008	0.970 ± 0.004
	4	0.024 ± 0.004	0.020 ± 0.004	0.010 ± 0.004	0.009 ± 0.004	1.167 ± 0.008	0.971 ± 0.003
TNB	1	0.63 ± 0.02	0.07 ± 0.01	0.65 ± 0.02	0.07 ± 0.01	7.80 ± 0.02	0.86 ± 0.01
	2	0.58 ± 0.02	0.07 ± 0.01	0.86 ± 0.02	0.10 ± 0.01	7.27 ± 0.02	0.83 ± 0.01
	3	0.64 ± 0.02	0.07 ± 0.01	0.64 ± 0.02	0.07 ± 0.01	7.88 ± 0.02	0.86 ± 0.01
	4	0.61 ± 0.02	0.07 ± 0.01	0.84 ± 0.02	0.10 ± 0.01	7.33 ± 0.02	0.83 ± 0.01

Model 1: with additive, parity, permanent environmental and year-month effects; Model 2: as in model 1, plus age effects; Model 3: with additive, parity, permanent environmental and year-season effects; Model 4: as in model 3, plus age effects; V_A, V_{Pe} and V_E are additive, permanent environmental, and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P)

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Table 4. Estimated genetic trends and parameters evaluating the models' fit for number of kits born alive (NBA), number of kits born dead (NBD) and total number of born kits (TNB)

Traits	Model	Genetic trends	MSE	BIAS	r
NBA	1	0.049[a] ± 0.004	6.99	-5.9E-05	0.52
	2	0.027[b] ± 0.004	6.15	-5.9E-05	0.59
	3	0.050[a] ± 0.004	7.11	-5.9E-05	0.52
	4	0.029[b] ± 0.004	6.24	-5.9E-05	0.59
NBD	1	0.00014[c] ± 0.0003	1.10	1.76E-05	0.32
	2	0.00034[d] ± 0.0002	1.06	2.68E-05	0.36
	3	0.00007[d] ± 0.0003	1.13	1.79E-05	0.30
	4	0.00019[c] ± 0.0003	1.08	2.54E-05	0.34
TNB	1	0.0486[m] ± 0.004	7.10	-5.9E-05	0.53
	2	0.0258[n] ± 0.004	6.23	-5.8E-05	0.60
	3	0.0499[m] ± 0.004	7.23	-5.8E-05	0.52
	4	0.0283[n] ± 0.004	6.34	-5.8E-05	0.59

[abcdmn] Estimated genetic trend with different letter (superscript) were significantly different for NBA, NBD and TNB; MSE: mean squared error, r: correlation between the observed and predicted values

Table 5. Estimated variance components and variance ratios based on the extended models for number of kits born alive (NBA), number of kits born dead (NBD) and total number of kits born (TNB)

Traits	V_A	h^2	V_{Pe}	p^2	V_D	d^2	V_E	e^2
NBA	0.49±0.09	0.06±0.01	0.64±0.10	0.08±0.01	0.19±0.27	0.09±0.01	7.15±0.07	0.84±0.01
NBD	0.02±0.01	0.02±0.01	0.009±0.005	0.008±0.005	0.003±0.009	0.01±0.002	1.15±0.01	0.97±0.01
TNB	0.53±0.09	0.06±0.01	0.70±0.11	0.08±0.01	0.17±0.27	0.08±0.01	7.27±0.08	0.84±0.01

V_A, V_{Pe}, V_D and V_E are additive, permanent environmental, dominance, and residual variances, respectively; h^2 is narrow sense heritability (V_A/V_P); p^2 is the contribution of permanent environmental variance to phenotypic variance (V_{Pe}/V_P); d^2 is the contribution of dominance variance to phenotypic variance (V_D/V_P); e^2 is the contribution of residual variance to phenotypic variance (V_E/V_P)

the contrary non-significant differences were observed for NBD (p=0.8). Based on the MSE and BIAS estimating the goodness of fit for different models, model 2 was selected for NBA and TNB as the "best" model. For the sake of simplicity, model 2 was also chosen for NBD. Unfortunately, there was no similar evaluation available in the recent literature. However, Nagy et al. (2011) also applied MSE and correlation coefficients between the observed and predicted NBA and TNB for comparing repeatability and multivariate models in the Pannon White and Ka rabbits, whose repeatability model had the same structure as model 2 of the present study.

Dominance effects

Three selected models for litter size traits as the best fitted models were extended with dominance effects. Estimates of variance components relative to the phenotypic variance for additive genetic, permanent environment, dominance effects and residual of NBA, NBD and TNB are presented in Table 5. It can be seen that the values of the additive genetic and permanent environmental variances of analysed traits considerably decreased comparing to model 2 in Table 3. These reductions signalled confounding between dominance and those mentioned effects for all litter traits. The current trends of confounding were similar to that of previous studies (Nagy et al., 2013; 2014). Due to the slightly decreased additive genetic variances of the extended models, the annual genetic trends (0.026, -0.0004 and 0.0255) of NBA, NBD and TNB declined compared to the estimates of model 2 (Table

4). It was argued that ignoring to calculate dominance effect from animal models resulted from the technical and computational difficulties faced to analyse large dataset in herds (Toro and Varona, 2010). Based on estimated breeding values (with and without dominance effects) of NBA, NBD and TNB, their correlation coefficients are around 0.99 for all traits that is very high rank and there are 94 animals in common by selecting 100 best animal based on those models. Although single trait models presented high breeding value stability, some re-ranking may occur among the top ranked animals (Nagy et al., 2013; 2014).

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