

Genetic evaluation of litter size traits in Pannon Large rabbits*

Nguyen Thao Nguyen¹, János Farkas², Zsolt Szendrő¹, István Nagy^{1**}

¹ University of Kaposvár, Department of Animal Genetics and Biotechnology,
40. Guba S. Str., H-7400 Kaposvár, Hungary

² University of Kaposvár, Department of Informatics,
40. Guba S. Str., H-7400 Kaposvár, Hungary

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Genetic parameters and genetic trends for the number of kits born alive (NBA), number of kits born dead (NBD) and the total number of born kits were estimated in Pannon Large rabbits. Using the REML method 12 single trait models were examined. Heritability estimates were low for all traits and ranged between 0.07-0.08 (with standard errors 0.018-0.021) for NBA (5830 records), 0.01-0.02 (0.009-0.009) for NBD (6278 records) and 0.04-0.05 (0.015-0.018) for TNB (6278 records) from 1469 does. The ratios of the permanent environmental and the phenotypic variances exceeded of the heritability estimates and ranged between 0.11-0.16 (0.016-0.018) for NBA, 0.06-0.07 (0.014-0.015) for NBD and 0.11-0.17 (0.014-0.017) for TNB. When characterizing the goodness of models bias values were practically zero for all traits and models. After identifying the best fitted model (containing parity, age of the doe and year-month of kindling effects) it was extended with dominance effects. As a result, heritability estimates decreased to 0.06 (0.028) for NBA, 0.02 (0.012) for NBD and 0.02 (0.022) for TNB. The relative importance of the permanent environmental effects also decreased to 0.09 (0.031) for NBA, 0.05 (0.024) for NBD and 0.07 (0.028) for TNB. Ratios of the dominance effects exceeded those of the heritability estimates and amounted to 0.27 (0.024) for NBA, 0.05 (0.013) for NBD and 0.38 (0.025) for TNB. When compared to the additive model, the model including dominance showed some confounding with additive genetic and with permanent environmental effects and reduced calculated genetics trends (0.035 vs 0.03, -0.0017 vs -0.003 and 0.016 vs 0.01 for NBA, NBD and TNB, respectively). Spearman rank correlation coefficients between breeding values of the additive and dominance models were high for all traits (0.96-0.98). When dominance effects were included some re-ranking was observed among the top ranked animals for every trait.

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**Corresponding author: nagy.istvan@ke.hu

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It cannot be denied that sufficient reproductive performance is indispensable in animal breeding. However, reproductive traits are especially important in multiparous species such as the rabbit [Cartuche *et al.* 2014]. Reproductive performance is mainly characterized by litter size. In order to perform a successful breeding program enhancing reproductive performance, estimation of genetic parameters and prediction of breeding values are necessary. Since the first evaluation of rabbits' reproductive performance based on the Best Linear Unbiased Prediction (BLUP) [Estany 1988], several similar studies have been published [Rastogi 2000, García and Baselga 2002a, Piles *et al.* 2006, Nagy *et al.* 2011, Ragab *et al.* 2011] covering the most important breeds and hybrid lines. Nevertheless, when analysing model structures applied by these authors, besides the obvious random effects (animal and permanent environmental effects) we may see that the considered factors of these studies are highly heterogeneous (mating buck, physiological status, kindling month, kindling season, inbreeding coefficient of the dam, etc.). Scarcely studies presented model comparisons [Piles *et al.* 2006, Nagy *et al.* 2011], where repeatability and multi-trait models were compared. In most studies no extensive information is given to specify how the authors developed the structure of the model evaluating reproductive performance. Another important issue of genetic evaluation is to determine which genetic effects should be considered. In animal breeding mostly simplified models are applied taking into account only the additive genetic effects. However, as noted by [Toro and Varona 2010], we need to remember that ignoring non-additive genetic effects will produce less accurate estimates of breeding values and will have an effect on rankings. Technically it is now also possible to consider dominance effects; however, mainly due to the technical and computational difficulties [Toro and Varona 2010] dominance effects are usually ignored from animal models.

The objectives of this study were thus twofold. The first objective was to estimate the genetic parameters and 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 Large 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 effect of extending these models with dominance effects on the stability of genetic parameters and on the predicted breeding values.

Material and methods

The present study was conducted using Pannon Large (L) rabbits. The development of this synthetic rabbit breed was started at the Kaposvár University in 2004. The basis of selection was the Pannon White rabbit breed, also developed at the Kaposvár University. At the beginning Pannon White rabbit does were inseminated using other

rabbit lines showing high average daily gains (ADG). Then using the progenies a two-stage selection procedure was applied, which has not been changed ever since. During the first step the ADG between the ages of 5 and 10 weeks is recorded and the rabbits showing higher ADG values than their kindling batch are selected for the second selection step. In the course of the second step the thigh muscle volume (TMV) of the 10.5 week old rabbits is determined *in vivo* using Computer Tomography (CT). Rabbits with the best TMV are kept as breeding animals. The Pannon Large population has been officially recognized as a rabbit breed since 2013. A more detailed description of the development and management of the Pannon Large rabbit breed was given by Matics *et al.* [2014].

Data information

The present analysis was based on 6269 kindling records of 1469 Pannon Large does inseminated with the sperm of 686 bucks. Kindling records were collected between 2004 and 2015 at the experimental rabbit farm of the Kaposvár University. The total number of animals in the pedigree file was 3664. The analyzed traits included the number of kits born alive (NBA), number of kits born dead (ND) and total number of born kits (TNB). Due to the fact that records showed highly unbalanced frequencies for later kindlings, parities were combined into four categories (parities 1, 2, 3-10, >10). Descriptive statistics of the recorded traits are presented in Table 1.

Table 1. Descriptive statistics for analysed traits

Trait	N	Mean	SD	Minimum	Maximum
NBA	5830	8.58	3.19	1	19
ND	6278	1,20	2.41	0	18
TNB	6278	9.17	3.42	1	20

N – number of observations; SD – standard deviation; NBA – number of kits born alive; ND – number of kits born dead; TNB – total number of born kits.

Models

Applying single-trait animal models, genetic parameters, breeding values and genetic trends of NBA, NBD and TNB were estimated by the REML and BLUP methods using the PEST [Groeneveld 1990] and VCE6 software [Groeneveld *et al.* 2008]. Based on the available environmental factors, 12 different models were tested for all traits (Tab. 2) to estimate additive, permanent environmental, residual variances and breeding values. The general structure of these models followed that of models available in the relevant literature [Rastogi *et al.* 2000, Moura *et al.* 2001, Wolf and Wolfova 2012]:

$$y = Xb + Zp + Wa + e$$

where:

- y – vector of phenotypic observations;
- b – vector of fixed effects;
- p – vector of permanent environmental effects;
- a – vector of additive genetic effects;
- e – vector of residuals;

X, Z, 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. The squared differences between the observed and predicted values based on the 12 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]:

$$y = Xb + Zp_e + Wa + Uc + e$$

where: c – vector of family class effects - dominant effect; p_e – vector of permanent environmental effects; U – incidence matrices linking phenotypic records to family effects.

The other effects were the same as explained for the basic models. In addition 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 .

Table 2. Fixed factors of applied models

Fixed effects	Number of levels	Model												
		1	2	3	4	5	6	7	8	9	10	11	12	
Parity	4		X	X	X	X	X	X	X	X	X	X	X	X
Age	518	X	X											
Age_square	518			X		X								
Year	12		X	X	X	X			X					X
Month	12	X	X	X	X									
Season	4		X		X	X								
Year_month	101									X	X	X	X	X
Year_season	42												X	X

Parity – parity number; age – age of does at kindling; age_square – the squared age of does at kindling; year – year of kindling; month – month of kindling; season – season of kindling; year_month – year and month of kindling; year_season – year and season of kindling.

Results and discussion

Means and standard deviations of TNB and NBA (Tab. 1) showed similar values to those of other studies [Al-Saef *et al.* 2008, Nagy *et al.* 2013], which result is promising considering that in the present study a terminal rabbit line was used, previously never selected for litter size composite traits. On the contrary, when compared to Pannon Large rabbits the maternal lines showed superior performances for these traits [Ragab and Baselga 2011]. It needs to be stressed that NDB for Pannon Large rabbits was about two times higher than in other breeds [Nagy *et al.* 2013, Nagy *et al.* 2014].

Variance components and variance ratios

The magnitude and ratios (compared to the phenotypic variance) of additive genetic, permanent environmental and residual variance components are presented in Tables 3-5. The various heritability estimates were low for NBA and TNB ranging from 0.03 to 0.07 and close to zero for NBD ranging from 0.01 to 0.02. The different models did not result in substantially different heritability estimates, although it could be noted that adding age or agesquare in models 2, 3, 5, 6, 8, 9, 11, 12 consistently reduced residual variance components of NBA and TNB. The obtained NBA, NBD and TNB heritability estimates in this study were within the ranges (0.03-0.13 for NBA, 0.02-0.04 for NBD and 0.08-0.15 for TNB) reported in relevant literature [Moura *et al.* 2001, García and Baselga 2002b, Mantovani *et al.* 2008, Nagy *et al.*

Table 3. Estimated variance components for the number of kits born alive (NBA)

Model	V_A	h^2	V_{pe}	p^2	V_E	e^2
1	0.77±0.06	0.08±0.018	1.10±0.05	0.11±0.016	8.09±0.04	0.81±0.012
2	0.78±0.06	0.08±0.019	1.41±0.05	0.15±0.018	7.29±0.04	0.77±0.012
3	0.78±0.06	0.08±0.019	1.41±0.05	0.15±0.018	7.29±0.04	0.77±0.012
4	0.75±0.06	0.07±0.018	1.11±0.05	0.11±0.016	8.12±0.04	0.81±0.011
5	0.80±0.06	0.08±0.020	1.40±0.05	0.15±0.018	7.30±0.04	0.77±0.012
6	0.80±0.06	0.08±0.020	1.40±0.05	0.15±0.018	7.30±0.04	0.77±0.012
7	0.73±0.06	0.07±0.019	1.15±0.05	0.12±0.016	7.98±0.04	0.81±0.012
8	0.70±0.07	0.07±0.021	1.51±0.06	0.16±0.019	7.22±0.04	0.77±0.012
9	0.70±0.07	0.07±0.021	1.51±0.06	0.16±0.019	7.22±0.04	0.77±0.012
10	0.80±0.06	0.08±0.019	1.09±0.05	0.11±0.016	8.05±0.04	0.81±0.012
11	0.77±0.06	0.08±0.020	1.42±0.05	0.15±0.018	7.25±0.04	0.77±0.012
12	0.77±0.06	0.08±0.020	1.42±0.05	0.15±0.018	7.25±0.04	0.77±0.012

Model 1 – with additive, parity, permanent environmental, year and month effects. Model 2 – as in model 1, plus age effects. Model 3 – as in model 1, plus age square effects. Model 4 – with additive, parity, permanent environmental, year and season effects. Model 5 – as in model 4, plus age effects. Model 6 – as in Model 4, plus age square effects. Model 7 – with additive, parity, permanent environmental and year-month effects. Model 8 – as in model 7, plus age effects. Model 9 – as in model 7, plus age square. Model 10 – with additive, parity, permanent environmental and year-season effects. Model 11 – as in model 10, plus age effects. Model 12, as in model 10, plus age square 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).

Table 4. Estimated variance components for the number of kits born dead (NBD)

Model	V _A	h ²	V _{pe}	p ²	V _E	e ²
1	0.11±0.02	0.02±0.009	0.38±0.03	0.07±0.014	5.13±0.03	0.91±0.013
2	0.09±0.02	0.01±0.009	0.34±0.04	0.06±0.015	5.23±0.04	0.92±0.013
3	0.09±0.02	0.01±0.009	0.34±0.04	0.06±0.015	5.23±0.04	0.92±0.013
4	0.11±0.02	0.02±0.009	0.38±0.03	0.07±0.014	5.14±0.03	0.91±0.013
5	0.09±0.02	0.02±0.009	0.34±0.04	0.06±0.015	5.24±0.04	0.92±0.013
6	0.09±0.02	0.02±0.009	0.34±0.04	0.06±0.015	5.24±0.04	0.92±0.013
7	0.10±0.02	0.02±0.009	0.41±0.03	0.07±0.014	5.06±0.03	0.91±0.013
8	0.07±0.02	0.01±0.009	0.38±0.03	0.07±0.014	5.18±0.04	0.92±0.012
9	0.07±0.02	0.01±0.009	0.38±0.03	0.07±0.014	5.18±0.04	0.92±0.012
10	0.12±0.02	0.02±0.009	0.39±0.03	0.07±0.014	5.12±0.03	0.91±0.013
11	0.09±0.02	0.02±0.009	0.35±0.04	0.06±0.015	5.21±0.04	0.92±0.013
12	0.09±0.02	0.02±0.009	0.35±0.04	0.06±0.015	5.21±0.04	0.92±0.013

Explanation are given in Table 3.

Table 5. Estimated variance components, total number of born kits (TNB)

Model	V _A	h ²	V _{pe}	p ²	V _E	e ²
1	0.61±0.05	0.05±0.016	1.31±0.05	0.11±0.014	9.48±0.04	0.83±0.011
2	0.56±0.06	0.05±0.018	1.64±0.05	0.15±0.017	8.50±0.04	0.79±0.011
3	0.56±0.06	0.05±0.018	1.64±0.05	0.15±0.017	8.50±0.04	0.79±0.011
4	0.61±0.05	0.05±0.015	1.30±0.05	0.11±0.014	9.52±0.04	0.83±0.011
5	0.60±0.06	0.06±0.017	1.60±0.05	0.15±0.017	8.53±0.04	0.79±0.012
6	0.60±0.06	0.06±0.017	1.60±0.05	0.15±0.017	8.53±0.04	0.79±0.012
7	0.51±0.05	0.05±0.015	1.40±0.05	0.12±0.015	9.29±0.04	0.83±0.010
8	0.41±0.05	0.04±0.017	1.78±0.05	0.17±0.017	8.37±0.04	0.79±0.011
9	0.41±0.05	0.04±0.017	1.78±0.05	0.17±0.017	8.37±0.04	0.79±0.011
10	0.62±0.05	0.05±0.016	1.29±0.05	0.11±0.014	9.41±0.04	0.83±0.011
11	0.54±0.05	0.05±0.017	1.63±0.05	0.16±0.017	8.45±0.04	0.80±0.012
12	0.54±0.05	0.05±0.017	1.63±0.05	0.16±0.017	8.45±0.04	0.80±0.012

Explanation are given in Table 3.

2013, Nagy *et al.* 2014]. The variability in the heritability estimates of these studies may be caused by genetic differences between the analysed rabbit breeds. As it was observed by Rastogi *et al.* [2000], rabbit populations with heterogeneous history involving multiple breed introductions (e.g. in tropical environments) may show higher heritability values. Another source for different heritabilities might be connected with the different structures of the applied animal models. With some simplification model structures in different studies may be sorted into two main groups. One group may comprise the models containing very similar random (animal and permanent environmental effects) and fixed effects (year-month or year-season and parity) as in the present study [Rastogi *et al.* 2000, Moura *et al.* 2001, Al-Saef *et al.* 2008]. In the other group the so-called physiological status of the doe (when pregnant, the doe may be nulliparous, lactating or not lactating) is used instead of or together with the parity effect [García and Baselga 2002a, García and Baselga 2002b, Garreau *et al.*

2005, Piles *et al.* 2006, Lenoir and Garreau, 2009, Lenoir *et al.* 2011]. Apart from these random and fixed effects some authors also included maternal genetic effects [Moura *et al.* 2001], the mating buck as a random effect [Rastogi *et al.* 2000, Piles *et al.* 2006, Nagy *et al.* 2011], the inbreeding coefficient of the doe [Moura *et al.* 2001, Nagy *et al.* 2013] and the inbreeding coefficient of the litter [Nagy *et al.* 2013] as covariates. 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 (Tab. 3) and they exceeded those of the additive genetic effects. These estimates were within the range of values (0.03-0.18 for NBA; 0.01-0.07 for NBD and 0.08-0.13 for TNB) given by other previously mentioned 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]. However, based on the estimated variance components for NBA, NBD and TNB there was no clear tendency in the literature to show if the additive genetic or the permanent environmental effects represents a greater proportion of the phenotypic variance.

Genetic trends

When comparing the estimated genetic trends for the analysed traits (Tab. 6-8) it may be seen that they became significantly lower for the models containing age or age. Calculated mean genetic trends for the applied 12 models were 0.05 for NBA (Tab. 6), closer to 0 for NBD (Tab. 7) and 0.03 for TNB (Tab. 8), respectively. The values received for NBA are favourable, because the Pannon Large rabbit breed was never

Table 6. Estimated genetic trends and parameters evaluating the goodness of fit for models for the number of kits born alive

Model	Genetic trend	MSE	BIAS	r
1	0.081 ^a ±0.005	7.28	-0.0007	0.57
2	0.042 ^b ±0.006	5.87	-0.0005	0.67
3	0.042 ^b ±0.006	5.87	-0.0005	0.67
4	0.075 ^a ±0.005	7.32	-0.0007	0.57
5	0.043 ^b ±0.006	5.89	-0.0005	0.67
6	0.043 ^b ±0.006	5.89	-0.0005	0.67
7	0.074 ^a ±0.004	7.07	-0.0006	0.58
8	0.035 ^b ±0.005	5.72	-0.0004	0.68
9	0.035 ^b ±0.005	5.72	-0.0004	0.68
10	0.083 ^a ±0.004	7.21	-0.0007	0.58
11	0.040 ^b ±0.006	5.82	-0.0005	0.67
12	0.040 ^b ±0.006	5.82	-0.0005	0.67

^{ab}Estimated genetic trends with different letters (superscripts) were significantly different for NBA.. MSE – mean squared error. R – correlation between observed and predicted performances.

Table 7. Estimated genetic trends and parameters evaluating the goodness of fit for model for number of kits born dead

Model	Genetic trend	MSE	BIAS	r
1	-0.0019 ^c ±0.0007	4.81	0.00003	0.46
2	-0.0021 ^d ±0.00059	4.51	0.00001	0.49
3	-0.0021 ^d ±0.00059	4.51	0.00001	0.49
4	-0.0015 ^c ±0.00077	4.82	0.00002	0.46
5	-0.0018 ^d ±0.00066	4.53	5.38E-6	0.49
6	-0.0018 ^d ±0.00066	4.53	5.38E-6	0.49
7	0.0049 ^c ±0.0009	4.67	0.00001	0.48
8	-0.0017 ^d ±0.00045	4.40	2.70E-6	0.51
9	-0.0017 ^d ±0.0004	4.40	2.70E-6	0.51
10	0.0055 ^c ±0.00101	4.78	-4.54E-6	0.46
11	-0.0023 ^d ±0.00064	4.48	-0.00002	0.49
12	-0.0021 ^d ±0.00069	4.48	-0.00002	0.49

^{cd}Estimated genetic trends with different letters (superscripts) were significantly different for NBD. MSE – mean squared error. R – correlation between observed and predicted performances.

Table 8. Estimated genetic trends and parameters evaluating the goodness of fit for models for the total number of born kits

Model	Genetic trend	MSE	BIAS	r
1	0.061 ^e ±0.003	8.59	-0.0006	0.56
2	0.024 ^f ±0.004	6.93	-0.0003	0.66
3	0.024 ^f ±0.004	6.93	-0.0003	0.66
4	0.059 ^e ±0.003	8.65	-0.0006	0.55
5	0.027 ^f ±0.004	6.96	-0.0004	0.65
6	0.027 ^f ±0.004	6.96	-0.0004	0.65
7	0.049 ^e ±0.002	8.30	-0.0005	0.57
8	0.016 ^f ±0.003	6.71	-0.0003	0.67
9	0.016 ^f ±0.003	6.71	-0.0003	0.67
10	0.064 ^e ±0.003	8.50	-0.0006	0.56
11	0.023 ^f ±0.003	6.87	-0.0003	0.66
12	0.023 ^f ±0.003	6.87	-0.0003	0.66

^{ef}Estimated genetic trends with different letters (superscripts) were significantly different for TNB. MSE – mean squared error. R – correlation between observed and predicted performances.

selected for litter size composite traits. The obtained average genetic trend for NBA was higher than the reported value (0.03) for the Botucatu rabbit, which is a multi-purpose line [Moura *et al.* 2001]. Nevertheless, the genetic trends reported in the present study were lower than those obtained by other researchers [Garreau *et al.* 2005], García and Baselga 2002a, García and Baselga 2002b, Lenoir and Garreau 2009]. These authors estimated an annual genetic trend of 0.11-0.21 kits per year for TNB and 0.11-0.23 kits per year for NBA using reproductive performance records of Spanish and French

maternal rabbit lines (selected for reproductive traits). However, the direct response to selection may also be determined using embryo cryopreservation [García and Baselga 2002a; García and Baselga 2002b]. At thawing of embryos the selection response was obtained for the Spanis V line (selected for litter size at weaning) between the 15th and 21st and between the 17th and 26th generations. The annual genetic trends were also estimated using the BLUP methodology. García and Baselga [2002a] observed a very good agreement between the results based on the two methods (when converted to the annual trend they were 0.14 vs 0.15 for TNB and 0.13 vs 0.15 for NBA). In contrast, values reported by García and Baselga [2002b] were much less consistent (0.11 vs 0.21 for TNB and 0.11 vs 0.23 for NBA). As it was noted by the authors, a possible explanation for this difference may be provided by the fact that the applied BLUP model contained no dominance effects, thus heritability of these traits could be overestimated.

The goodness of fit values for the used models developed for the studied traits are presented in Tables 6-8. It may be seen that the BIAS was practically zero for all traits and models. Based on the MSE values and on the correlation coefficients between the observed and predicted NBA, NBD and TNB, the models containing age or age square showed a better goodness of fit when compared to the other models (Tab. 6-8).

When comparing squared differences between the observed and predicted values based on the 12 models, we see that they were highly significant for NBA and TNB ($p < 0.0001$), respectively, but they were non-significant for NBD ($p = 0.7$). Based on the parameters evaluating the goodness of fit for different models, model 8 was selected for NBA and TNB as the “best” model. For the sake of simplicity, model 8 was also chosen for NBD (where the fit of the models was not different). Unfortunately, no similar analysis was available in the literature. Using the performance records of the Pannon White and Pannon Ka rabbits, Nagy *et al.* [2011] applied MSE and correlation coefficients between the observed and predicted NBA and TNB when comparing repeatability and multivariate models. The repeatability model of Nagy *et al.* [2011] had the same structure as model 8 of the present study. When comparing model 8 of the present study and the repeatability models of Nagy *et al.* [2011] it may be concluded that both studies showed MSE and correlations for NBA and TNB.

Dominance effects

After determining the best fitted models for every trait they were extended with dominance effects. The variance component estimates and their relative contributions to the total phenotypic variance for NBA, NBD and TNB are presented in Table 9. When comparing the estimated variance components of NBA, NBD and TNB in Table 9 and those of model 8 in Tables 3-5 it may be seen that the estimated additive genetic variances decreased for NBA and for TNB, while the permanent environmental variance substantially decreased for all examined traits for the extended models (containing dominance effects). This phenomenon is called confounding and because the litter effect is highly confounded with family [Vitezica *et al.* 2013] it

is often observed to be connected to dominance models in prolific species such as chickens and pigs. Confounding between dominance and common litter effects in swine and poultry was observed in several studies summarized by Nagy *et al.* [2013]. However, as it was mentioned by Nagy *et al.* [2013], it is generally assumed that common litter effects are negligible for litter size composite traits. Consequently, according to the relevant literature this effect is not used when genetic parameters are estimated. In similar studies confounding between the additive genetic dominance and permanent environmental effects was reported by Nagy *et al.* [2013 and 2014] for the Pannon White and Pannon Ka rabbit breeds; however, the magnitude of the phenomenon was much smaller than in the present study. In contrast to a study by Nagy *et al.* [2013 and 2014], where the magnitudes of the additive genetic and the dominance variances were similar, in the present study the ratio of dominance variance to phenotypic substantially exceeded the heritability estimates for all examined traits. This finding may be a consequence of the relatively small dataset. As it was mentioned by Toro and Varona [2010], one of the reasons that dominance effects are often neglected is that due to the computational complexity this variance component requires larger datasets when compared to conventional animal models. Due to the decreased additive genetic variances of the extended models the annual genetic trends (0.03, -0.003 and 0.01) of NBA, NBD and TNB were also decreased when compared to the estimates of model 8 (Tab. 6-8). The possibility of overestimating the additive genetic variance with models that ignore dominance effect was demonstrated by Norris et al. [2002] in a simulation study, where the overestimation of the additive genetic variance with reduced models (not containing the dominance effects) was proportional with the increasing proportion of full-sibs and also with the increasing magnitude of dominance effects. The direct consequence of ignoring dominance effects from the animal models may probably be best evaluated by comparing the estimated breeding values predicted with the best fitted model (model 8) and with the same model extended with dominance effects. Estimated breeding values (with and without dominance effects) of NBA, NBD and TNB showed high rank correlation coefficients (0.98, 0.96 and 0.97), respectively.

Table 9. Estimated variance components and variance ratios based on extended models for the 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	0.52±0.26	0.06±0.0283	0.87±0.29	0.090±0.0310	2.52±0.85	0.27±0.0236	5.29±0.17	0.58±0.0162
NBD	0.09±0.07	0.02±0.0125	0.25±0.12	0.05±0.0237	0.24±0.25	0.047±0.0133	4.74±0.10	0.89±0.0163
TNB	0.19±0.22	0.02±0.0202	0.69±0.29	0.07±0.0277	3.84±0.87	0.38±0.0251	5.35±0.17	0.53±0.0152

V_A , V_{Pe} , V_D , and V_E are additive, dominance, 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). 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).

When the best 100 does were selected according to the different model types, the number of animals included jointly in the models was 80, 86 and 80. According to Nagy *et al.* [2013, 2014], single trait models showed high breeding value stability, but even in this case some re-ranking may occur among the top ranked animals. In contrast, Nagy *et al.* [2014] observed a much lower concordance among breeding values when NBA and NBD were evaluated based on bivariate models.

In the analyzed rabbit population the dominance components exceeded the additive genetic variance components for NBA, NBD and TNB, thus inclusion of dominance effects in the model was justified. In this study neglecting dominance effects resulted in an overestimation of additive genetic variances and genetic trends and due to the re-ranking certain differences were found among rabbits selected as top ranked animals. However, it has to be kept in mind that precise estimation of dominance effects requires a relatively large dataset and a high proportion of full-sibs.

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