Estimation of additive and dominance variance for litter size components in rabbits

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ABSTRACT: Additive, dominance, and permanent environmental variance components were estimated for the number of kits born alive, number of kits born dead, and total number of kits born of a synthetic rabbit line (called Pannon Ka). The data file consisted of 11 582 kindling records of 2620 does collected between the years 1996–2013. The total number of animals in the pedigree files was 4012. The examined traits were evaluated using single-trait and two-trait (number of kits born alive-dead) animal models containing all or part of the following effects: additive genetic effects, permanent environmental effects, dominance effects. Heritability estimates calculated using the basic single-trait and two-trait models were 0.094 ± 0.018 and 0.090 ± 0.016 for number of kits born alive, 0.037 ± 0.010 and 0.041 ± 0.012 for number of kits born dead, and 0.117 ± 0.018 for total number of kits born, respectively. The relative significance of permanent environmental effects was 0.069 ± 0.014 and 0.069 ± 0.012 for number of kits born alive, 0.025 ± 0.011 and 0.023 ± 0.010 for number of kits born dead, and 0.060 ± 0.013 for total number of kits born, respectively. Using the extended single-trait and two-trait models, the ratios of the dominance components compared to the phenotypic variances were 0.048 ± 0.008 and 0.046 ± 0.007 for number of kits born alive, 0.068 ± 0.006 and 0.065 ± 0.006 for number of kits born dead, and 0.005 ± 0.0073 for total number of kits born, respectively. Genetic correlation coefficients between number of kits born alive and number of kits born dead were 0.401 ± 0.171 and 0.521 ± 0.182, respectively. Spearman's rank correlations between the breeding values of the different single-trait models were close to unity in all traits (0.992–0.990). Much lower breeding value stability was found for two-trait models (0.384–0.898), especially for number of kits born dead. Results showed that the dominance components for number of kits born alive and number of kits born dead were not zero and affected the ranking of the animals (based on the breeding values).

Keywords: REML analysis; dominance effects; family class effect; genetic parameters

In animal science, in most genetic evaluations (prediction of genetic merit) conducted in the course of breeding programmes, simplified models are applied. Thus, in most cases, from the genetic effects only the additive genetic components are included. A possible reason is that the response to selection (which is the central interest of animal breeders) is proportional to the additive genetic variance. Nonadditive effects are generally considered a nuisance and ignored whenever possible, though it has been long recognized that it is the nonadditive effects that underlie inbreeding depression (Roff and Emerson, 2006). However, as noted by Toro and Varona (2010), estimation of nonadditive genetic effects in animal breeding is important because ignoring these effects produces less accurate estimates of breeding values and affects ranking breeding values. Toro and Varona (2010) also mentioned the greater computational complexity of these models and the inaccuracy in the estimation of variance components. Dominance variance can be given as an example which is gener-

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ally confounded with other effects such as random litter effects. The reason for ignoring dominance effects can also be the available database unsuitability for estimating non-additive effects (Misztal, 2001). Estimation of the dominance component requires a large number of full-sibs which is available for multipara species such as fish, poultry, and pig. In these species the results of several studies are available predicting the nonadditive variance components and comparing the results of genetic evaluations with and without nonadditive (and/or other) effects (Winkelman and Peterson, 1994; Lutaaya et al., 2001; Mielenz et al., 2006). Yet according to our best understanding so far only one study has been conducted for rabbits (Nagy et al., 2013). Our hypotheses to be tested were that extending the models used for genetic evaluation with the dominance effects has an effect on the predicted breeding values and on the ranking of the evaluated animals. Consequently, the first objective of our study was to estimate genetic parameters for reproductive traits of a rabbit line using different animal models with and without dominance effects. The second objective was to evaluate the effects of application of these models on the stability of the predicted breeding values.

MATERIAL AND METHODS

Population management and recorded traits. The development of the maternal line (Pannon Ka) at the rabbit farm of the Kaposvár University started in 1995 with sperm of some prolific Hungarian and foreign breeds. The sperm was used for inseminating Pannon White (another rabbit breed selected as a closed population at Kaposvár since 1992) does. Beside the sperm, in 1999 some newborn female and male kits of rabbit breeds showing high reproductive performance were bought. These imported rabbits mated among themselves (and with Pannon White rabbits of high prolificacy) forming the base of the maternal line (called Pannon Ka). Since then the breed is selected as a closed population for number of kits born alive. Pannon Ka was officially recognized as a new synthetic rabbit breed by the Hungarian National Institute of Agricultural Quality Control in 2003. Matings of close relatives are avoided using a mating system where at the initiation of each line, rabbits were divided into four groups. The purpose of dividing the breed into groups is to control its inbreeding rate. The matings among the groups are carried out in the following way: 1♀ × 4♂; 2♀ × 1♂; 3♀ × 2♂; 4♀ × 3♂. After the parturition the progeny born receives the group number of the sire. Thus descendents of any buck are placed back to its own group only after four generations.

The analysis of this study was conducted using 11 582 kindling records of 2620 Pannon Ka rabbit does. Kindling records were collected at the Experimental Rabbit Farm of the Kaposvár University between the years 1996–2013. The total number of Pannon Ka rabbits in the pedigree was 4012. The analyzed traits were number of kits born alive (NBA), number of kits born dead (NBD), and total number of kits born (TNB). For NBA only those records were considered where at least one kit was born alive (n = 11 110). Due to the large number and unbalanced structure of parities they were combined into 4 groups (1, 2, 3–10, 11+). For all the pairs of individuals additive and dominance relationship coefficients were computed following Cockerham (1954), i.e. inbreeding was not accounted for in the computation of dominance relationship coefficients. Descriptive statistics are presented in Table 1.

Statistical models. NBA, NBD, and TNB were evaluated with the REML and BLUP procedures in order to estimate genetic parameters and breeding values. For the study a super-computer (1536 processor cores, 6 TB of memory, and computing capacity over 18 teraFLOPS) developed by Silicon Graphics International was used. From the available resources one processor with 16–20 GB RAM enabling serial processing depending on the characteristics of the applied models was used.

PEST software (Version 3.1, 1990) and VCE software (Version 6.0, 2008) were applied. Altogether eight animal models were performed. Six single

Table 1. Descriptive statistics for the analyzed traits

Trait	n	Mean	SD	Minimum–maximum
NBA	11 110	8.90	2.99	1–20
NBD	11 582	0.65	1.74	0–16
TNB	11 582	9.19	3.11	1–21

NBA = number of kits born alive, NBD = number of kits born dead, TNB = total number of kits born, SD = standard deviation trait models were used to evaluate NBA, NBD, and TNB. For each trait two single trait models were used. These models differed only in the inclusion of the dominance effect (for each trait the first model did not include the dominance effects). Besides, NBA and NBD were also evaluated together using two two-trait models and similarly to the single trait models these models differed only in the inclusion of the dominance effect.

Thus the most complete models had the following structure:

$$y = \mathbf{X}b + \mathbf{Z}pe + \mathbf{W}a + \mathbf{U}c + e$$

where:
y = vector of phenotypic observations
b = vector of fixed effects
pe = vector of individual permanent environmental effects
a = vector of individual additive genetic effects
c = vector of family class effects
e = vector of residuals
X, **Z**, **W**, **U** = incidence matrices linking phenotypic records to fixed, random, permanent environmental, and family effects, respectively

Fixed effects (b) in the model were parity and year-month of kindling. Dominance was included in the model via the family class effect following the work of Hoeschele and VanRaden (1991), which provides a way to efficiently set up a sparse inverse of dominance covariance matrix between family classes. Model assumptions for the most complete model were as follows:

where:
A, **C** = covariance (relationship) matrices for the additive genetic and family class effects, respectively
I = identity matrix
E = expected value
Var = variance
sym. = symmetric
V_{Pe}, V_A, V_C, V_E = variance components
V_P = phenotypic variance
(for other explanations see the preceding model)

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 (pe^2) variance to total phenotypic variance $V_P = V_{Pe} + V_A + 1/4V_D + V_E$ were also calculated. Correction for $3/4V_D$ in the calculation of phenotypic variance was necessary due to the use of V_D instead of V_C. The structures of the used models are given in Table 2.

RESULTS AND DISCUSSION

Variance components and variance ratios. The estimated variance components and their ratios compared to the phenotypic variance are presented in Table 3. Using the single-trait and two-trait models without dominance components it was found that heritability estimates and relative importance of permanent environmental effects were low for all traits (NBA, NBD, and TNB) (Table 3). Using the Pannon Ka rabbit line the estimated heritabilities and permanent environmental effects were com-

$$E\begin{bmatrix}\mathbf{y}\\ \mathbf{pe}\\ \mathbf{a}\\ \mathbf{c}\\ \mathbf{e}\end{bmatrix}=\begin{bmatrix}\mathbf{Xb}\\ 0\\ 0\\ 0\\ 0\end{bmatrix},\quad Var\begin{bmatrix}\mathbf{y}\\ \mathbf{pe}\\ \mathbf{a}\\ \mathbf{c}\\ \mathbf{e}\end{bmatrix}=\begin{bmatrix}V_P & \mathbf{Z}V_{Pe} & \mathbf{WA}V_A & \mathbf{UC}V_C & \mathbf{I}V_E\\ & \mathbf{I}V_{Pe} & 0 & 0 & 0\\ & & \mathbf{A}V_A & 0 & 0\\ & & & \mathbf{C}V_C & 0\\ sym. & & & & \mathbf{I}V_E\end{bmatrix}$$

Table 2. Structure of the applied models

	Effect		Model	
	level	type	APe	ADPe
Parity	4	F	x	x
Year-month	157	F	x	x
Permanent	2 620	R	x	x
Additive	4 012	A	x	x
Family	160 497	D	–	x

F = fixed effects, A = additive genetic effects, R = random effects, D = dominance effects, APe = model with permanent environmental and additive effects, ADPe = model with permanent environmental, additive, and dominance effects

Table 3. Estimated variance components and variance ratios of the analyzed traits

Trait	Model	Type	V_A	h^2	V_{Pe}	p^2	V_D	d^2	COV_A	r_g
NBA	APe	single-trait	0.779 ± 0.158	0.094 ± 0.018	0.572 ± 0.113	0.069 ± 0.014	–	–	–	–
	ADPe		0.716 ± 0.153	0.087 ± 0.017	0.498 ± 0.124	0.060 ± 0.015	0.399 ± 0.276	0.048 ± 0.008		
NBD	APe		0.111 ± 0.032	0.037 ± 0.010	0.075 ± 0.033	0.025 ± 0.011	–	–		
	ADPe		0.073 ± 0.034	0.025 ± 0.011	0.039 ± 0.032	0.013 ± 0.011	0.205 ± 0.075	0.068 ± 0.006	–	–
TNB	APe		1.075 ± 0.184	0.117 ± 0.018	0.555 ± 0.119	0.060 ± 0.013	–	–	–	–
	ADPe		1.068 ± 0.199	0.116 ± 0.020	0.548 ± 0.097	0.060 ± 0.011	0.043 ± 0.270	0.005 ± 0.007	–	–
NBA	APe	two-trait	0.781 ± 0.149	0.090 ± 0.016	0.595 ± 0.105	0.069 ± 0.012	–	–	0.123 ± 0.051	0.401 ± 0.171
	ADPe		0.727 ± 0.133	0.085 ± 0.015	0.514 ± 0.096	0.060 ± 0.011	0.402 ± 0.233	0.046 ± 0.007	0.132 ± 0.040	0.521 ± 0.182
NBD	APe		0.122 ± 0.036	0.041 ± 0.012	0.069 ± 0.032	0.023 ± 0.010	–	–	0.123 ± 0.051	0.401 ± 0.171
	ADPe		0.088 ± 0.032	0.029 ± 0.011	0.033 ± 0.030	0.011 ± 0.010	0.194 ± 0.068	0.065 ± 0.006	0.132 ± 0.040	0.521 ± 0.182

NBA = number of kits born alive, NBD = number of kits born dead, TNB = total number of kits born, APe = model with permanent environmental and additive effects, ADPe = model with permanent environmental, additive, and dominance effects, V_A = additive variance, V_D = dominance variance, V_{Pe} = permanent environmental variance, $h^2 = V_A/V_P$, $d^2 = V_D/V_P$, $p^2 = V_{Pe}/V_P$, COV_A = additive genetic covariance between NBA and NBD, r_g = genetic correlation coefficient between NBA and NBD

parable to the results of Nagy et al. (2011). It has to be noted that contrary to results of the present study, Nagy et al. (2011) found higher heritabilities than p^2 estimates for NBA and TNB. However, Nagy et al. (2011) evaluated the records of the first four parities only over a shorter period thus the size of the evaluated dataset was substantially smaller (3413 kindling records) than in the present study. In the Pannon White rabbit population Nagy et al. (2013) used numerous models. When the models contained the same effects as the basic model of this study, slightly lower h^2 and p^2 estimates were obtained for NBA (0.057 and 0.066), NBD (0.022 and 0.015), and TNB (0.064 and 0.069) compared to the findings of this study. Using slightly different models for different Spanish lines, Piles et al. (2006) and Ragab and Baselga (2011) estimated h^2 values for NBA (0.08–0.12) and TNB (0.10–0.14) similar to our estimates. The estimated ratios of the permanent environmental variance to the phenotypic variance were also in the same range for NBA (0.07–0.10) and for TNB (0.07–0.10) in the Spanish lines compared to the p^2 estimates of the Pannon Ka line (Table 3). When NBA and NBD were evaluated by two-trait models, then the alterations of the estimated additive genetic and permanent environmental components were negligible. There was a moderate and positive genetic correlation between NBA and NBD (Table 3). Nagy et al. (2011) reported a genetic correlation between TNB and NBA close to unity for Pannon White (0.97) and for Pannon Ka (0.96) in agreement with Mantovani et al. (2008) who reported a similar value (0.97) for these traits evaluating an Italian synthetic rabbit line. These results suggest that NBA increasing will also be reflected in TNB increase, thus indirectly supporting our positive genetic correlation estimate between NBA and NBD.

Extending the models with the dominance effects, the estimated dominance variance components of NBA and NBD showed lower and higher magnitudes, respectively compared to those of the additive genetic variances (Table 3). On the contrary, the dominance component was practically zero for TNB (Table 3).). Similarly to this last finding, Fernández et al. (2010) observed the lack of dominance for litter size at weaning in a maternal line of rabbits (d^2 = 0.017). According to the results of a recent study Nagy et al. (2013)

reported similar importance of the dominance components for the results of the study for NBA (0.050) and NBD (0.052) but for TNB these authors observed a value (0.080) which was higher than that of the estimated heritability of that trait (0.062). To the best of our knowledge, no other studies were conducted with rabbits estimating dominance components for NBA, NBD, and TNB. In different pig populations Culbertson et al. (1997; 1998) reported that the dominance variances were only 18–68% of the magnitude of the additive genetic variance for NBA and their proportion to the total phenotypic variance was small (0.016–0.057). Also in pigs somewhat higher dominance variances (44–66% of those of the additive genetic variances) and d^2 estimates (0.037 and 0.068) were found by Norris et al. (2006; 2010) for the same trait.

When the extended models were used, the inclusion of the dominance components resulted in the decrease of the other variance components for NBA and NBD. On the contrary, as the dominance components were negligible for TNB, the genetic parameters were the same with the basic and extended models. The heritabilites decreased by 7.4% (NBA) and by 32% (NBD), respectively and the ratios of permanent environmental effects compared to the phenotypic variances were decreased by 13% (NBA) and 48% (NBD) respectively, applying the single-trait models. Using two-trait models, similar tendencies were received and the magnitudes of the decreases for h^2 and p^2 values of NBA and NBD were 5.5 and 29% and 13 and 52%, respectively and the same remark can be made as for the single-trait models. When the inclusion of dominance effect decreases the other components than the residual effect, this phenomenon is called confounding which is often reported in connection with dominance effects. Confounding between dominance and the additive genetic variance components was also detected in the study of Wei and van der Werf (1993). These authors analyzed several egg production traits of laying hens mainly connected to egg number and egg weight. Like in our study the basic model contained only the additive genetic effects while the extended models also contained the dominance effect. Wei and van der Werf (1993) received consistently lower h^2 estimates under the dominance model than under the additive model. Depending on the specific trait the decrease of the h^2 estimates ranged 3–53%. Under the dominance models the residual variances also decreased thus the total phenotypic variances remained almost unchanged. Serenius et al. (2006) observed similar tendencies for pig longevity traits. Common litter variance components were twice as high using models that did not contain dominance effects compared to a more complete model containing dominance and

Table 4. Spearman's rank (above the diagonal) and Pearson's (below the diagonal) correlations between the estimated breeding values across different models for the number of kits born alive, number of kits born dead, and total number of kits born

Trait	Model	U_APe	U_ADPe	B_APe	B_ADPe
NBA	U_APe	–	0.999	0.984	0.915
	U_ADPe	0.999	–	0.984	0.913
	B_APe	0.989	0.988	–	0.898
	B_ADPe	0.946	0.946	0.933	–
NBD	U_APe	–	0.992	0.684	0.787
	U_ADPe	0.993	–	0.681	0.793
	B_APe	0.754	0.745	–	0.384
	B_ADPe	0.768	0.772	0.454	–
TNB	U_APe	–	0.999		
	U_ADPe	0.999			
	B_APe				
	B_ADPe				

NBA = number of kits born alive, NBD = number of kits born dead, TNB = total number of kits born, U_Ape = single-trait model with permanent environmental and additive effects, U_ADPe = single-trait model with permanent environmental, additive, and dominance effects, B_Ape = two-trait model with permanent environmental and additive effects, B_ADPe = two-trait model with permanent environmental, additive, and dominance effects common litter effects simultaneously. Contrary to these results Rye and Mao (1998) observed no substantial confounding between dominance and common environmental effects for body weight of salmons. Rye and Mao (1998) found that inclusion of common environmental effects decreased the residual component but had only marginal effect on the other (additive genetic and dominance) components. However, by including nonadditive genetic effects in the model, the estimates of additive genetic variance were reduced dramatically (by 50–79%).

Breeding values. Based on the different single-trait models, the estimated breeding values showed very high Spearman's rank correlations for NBA, NBD, and TNB (Table 4). On the contrary, the two-trait models exhibited lower rank correlation of breeding values for NBA and it was low for NBD (Table 4). When Spearman's rank correlations between the breeding values were estimated with single-trait and two-trait models, the observed values were high for NBA and moderate for NBD (Table 4). Pearson's correlations showed the same tendencies as observed for the rank correlations but slightly higher values were found (Table 4). In the Pannon White rabbit population Nagy et al. (2013) reported Spearman's rank correlations between breeding values estimated with the different single-trait models close to unity for NBA, NBD, and TNB. Similarly, Gallardo et al. (2010) observed that the estimated breeding values of harvest body weight in Coho salmon showed correlation close to unity when the applied single-trait models differed only in the inclusion of the dominance effects. Similar tendency was reported for the trait of stature in cattle (Varona et al., 1998). Beside the overall stability, the breeding value stability of the top 100 and 1000 rabbits showed (Table 5) that the common proportion of the highest ranked rabbits based on the different models was high based on the single-trait models of all examined traits. The breeding value stability of the top ranked animals was assessed in a slightly different way by Mielenz et al. (2003) evaluating several traits connected to the egg production of laying hens. In their study the top ranked animals (50 or 100 per generation) were selected based on the breeding values estimated with animal models containing dominance effects. Using the same animals, their breeding values were estimated with models without the dominance effects. The rank correlations between the breeding value-pairs of these animals varied between 0.899 and 0.996 depending on the trait and evaluated line. However, in our study based on the other model combinations (single-trait vs. two-trait models; including or excluding the

Table 5. Stability of breeding values expressed as a number of concordant top 100 rabbits (above diagonal) and 1000 rabbits (below diagonal) across different models for the number of kits born alive, number of kits born dead, and total number of kits born

Trait	Model	U_APe	U_ADPe	B_APe	B_ADPe
NBA	U_APe	–	94	84	65
	U_ADPe	991	–	82	67
	B_APe	963	960	–	63
	B_ADPe	928	928	913	–
NBD	U_APe	–	93	60	39
	U_ADPe	953	–	56	41
	B_APe	536	525	–	30
	B_ADPe	690	700	344	–
TNB	U_APe	–	99		
	U_ADPe	999	–		
	B_APe				
	B_ADPe				

NBA = number of kits born alive, NBD = number of kits born dead, TNB = total number of kits born, U_Ape = single-trait model with permanent environmental and additive effects, U_ADPe = single-trait model with permanent environmental, additive, and dominance effects, B_Ape = bivariate model with permanent environmental and additive effects, B_ADPe = bivariate model with permanent environmental, additive, and dominance effects dominance effects) the re-ranking among the top ranked rabbits was substantial especially for NBD (Table 5). In connection with breeding value stability, Wolf et al. (2001) noted that the accuracy of the estimated variance components depends on the data structure. Accurate estimates might be obtained even on a small dataset. However, to achieve a given accuracy, estimation of genetic correlation requires more data than estimation of heritabilities (Wolf et al., 2001). It also has to be mentioned that inclusion of dominance effect resulted in longer CPU times and compared to the extended single-trait models, the two-trait animal model containing the dominance effect required more than 10 times longer CPU time (141 h).

CONCLUSION

Including the dominance variance in the models of the litter size components of the Pannon Ka rabbits was justified. Ignoring the dominance resulted in a slight overestimation of permanent environmental effects and these two effects showed partial confounding. For single-trait models the general correlations between breeding values were near the unity but some re-ranking occurred among the top ranked rabbits with the introduction of the most complete models for NBA and NBD. On the contrary, the breeding value stability was much lower with two-trait models, which may be also the consequence of the relatively small data set. Using larger datasets and multi-trait models, computing capacity and long CPU times might be a limiting factor preventing the application of extended animal models.

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