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The direct-maternal genetic correlation has little impact on genetic evaluations

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ABSTRACT: Obtaining unbiased estimates of the direct-maternal genetic correlation proves far from straightforward for several reasons. Consequently, the use of such over- or underestimated correlations may introduce errors in genetic evaluation models. The objective of our study was to evaluate how the value of the direct-maternal genetic correlation affects EBV. Direct, maternal, and total breeding values were predicted for the ADG or weight at weaning for 3 different species (sheep, rabbits, and pigs) using models that differ depending on the fixed value of the direct-maternal genetic correlation (ranging from -0.9 to 0.9) as well as a model in which the correlation was estimated. The results were consistent between species. The direct-maternal genetic correlation had a greater

impact on the estimated maternal genetic effects than on direct effects. The lowest correlations between maternal breeding values obtained with different models were -0.20 , -0.01 , and -0.72 in pigs, sheep, and rabbits, respectively, whereas for the direct breeding value, the lowest correlations were 0.45 , 0.90 , and 0.95 in pigs, sheep, and rabbits, respectively. The total EBV, calculated as the unweighted sum of direct and maternal genetic effects, did not differ greatly between the models, the lowest correlations between total breeding values being 0.93 , 0.98 , and 0.97 for pigs, sheep, and rabbits, respectively. Given the uncertainty associated with estimating the direct-maternal genetic correlation, setting its value to 0 in genetic evaluation models appears to be a good compromise.

Key words: breeding values, direct-maternal genetic correlation, growth, pig, rabbit, sheep

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INTRODUCTION

Maternal effects occur when an animal's phenotype is influenced by its mother's phenotype in addition to the genes it inherits. Willham (1972) proposed to model such traits by decomposing the phenotype into the sum of unobserved direct and maternal phenotypes, which are the sum of both a genotypic and an environmental value. Generally, the variance and covariance components estimated with such models are direct and maternal genetic variances, the maternal permanent environmental variance, the residual variance, and direct-maternal genetic covariance (Dodenhoff et al., 1999). To estimate variance components, such models require

the use of both appropriate methods (Thompson, 1976) and appropriate data structure (Gerstmayr, 1992). Still, in some cases, the model produces surprising results such as a strong negative direct-maternal genetic correlation (Robinson, 1996; Koerhuis and Thompson, 1997). Various explanations for such bias have been proposed in the literature: misidentification of sires (Lee and Pollack, 1997a), lack of genetic connectedness between herds (Clement et al., 2001), omission of the random sire \times herd \times year effect (Lee and Pollack, 1997b; Hagger, 1998), or environmental covariances among dam-offspring records (Koch, 1972; Bijma, 2006). However, in practice, perfectly designed data that fits complex models is not always available when estimating the genetic parameters to use for genetic evaluation (Dodenhoff et al., 1999), so some uncertainty about the true value of the direct-maternal genetic correlation remains. Choosing the direct-maternal

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Table 1. Descriptive statistics

Statistics	Pigs	Sheep	Rabbits
No. records	15,572	22,807	62,139
No. dams (% of dams with their own record)	796 (33%)	7,149 (83%)	3,633 (87%)
No. litters	1,236	21,016	8,080
No. animals in the pedigree	19,987	37,195	63,858
Variable of interest	ADG 0–21 d, g/d	ADG 0–45 d, g/d	Weight at 31 d, g
Mean	223	258	641
SD	52	62	128
Minimum	5	31	113
Maximum	415	523	1,375

genetic correlation for a genetic evaluation model can, therefore, be challenging. This article attempts to answer the question “does the use of a wrong direct-maternal genetic correlation seriously impact breeding value (EBV) predictions?” by comparing EBV for growth obtained with different direct-maternal genetic correlations in 3 different species: pigs, sheep, and rabbits.

MATERIALS AND METHODS

The ADG or the weight at weaning was analyzed in 3 different species (pig, sheep, and rabbit). Rearing facilities are described in detail in Banville et al. (2015), David et al. (2011), and Piles et al. (2006) for pigs, sheep, and rabbits, respectively. Briefly, pig data consisted of 15,572 ADG records of Tai Zumu piglets born in 3 GENE+ (Erin, France) nucleus herds between 2009 and 2012. Piglets were weighed at birth and at 3 wk of age (20.5 ± 1.4 d) to calculate the ADG between birth and 21 d (223 ± 52 g/d). Sheep data consisted of records for 22,807 Romane lambs born between 1987 and 2009 on the experimental farm of La Sapinière (INRA; France). This experimental population is the nucleus flock of the composite sheep strain INRA401 (Ricordeau et al., 1992). All animals were bred in the same system. Lambs were weighed at birth and at 44.8 ± 3.8 d of age using a standardized method (i.e., same animal restraint method and same weight scale). Resulting weights were used to calculate the ADG between birth and 45 d (258 ± 62 g/d). Rabbit data consisted of the weaning weights of 62,139 young rabbits. This experimental rabbit population was bred at the experimental INRA farm Pôle d'Expérimentation Cunicole Toulousain (Castanet-Tolosan, France). Kittens were weighed at weaning, that is, at approximately 31 d of age (31.1 ± 1.0 d). Data are summarized in Table 1.

Let y_{ijk} be the ADG or weaning weight of animal i nursed by female j in litter k . For all species, the linear mixed models used to study y_{ijk} can all be decomposed from the following general model:

$$y_{ijk} = \mu_{ijk} + d_i + m_j + p_j + l_k + \varepsilon_{ijk}$$

in which μ_{ijk} represents the fixed effects, d_i and m_j represent the direct and maternal genetic effects, p_j represents the permanent maternal effect, l_k represents the litter random effect, and ε_{ijk} represents the residual. All random effects were distributed as centered normal distributions with variance–covariance matrices equal to

$\mathbf{A} \otimes \begin{bmatrix} \sigma_d^2 & \sigma_{dm} \\ \sigma_{dm} & \sigma_m^2 \end{bmatrix}$ for the genetic effects, in which \mathbf{A} is the relationship matrix, $\mathbf{I}_p \sigma_p^2$ is for the maternal permanent effects, $\mathbf{I}_l \sigma_l^2$ is for the litter effect, and $\mathbf{I}_\varepsilon \sigma_\varepsilon^2$ is for the residual effects, in which \mathbf{I} are identity matrices of appropriate sizes. The fixed effects included in the models were those used for genetic evaluation purposes (rabbits) or those that had been used in previous studies (pigs and sheep): litter size (20 levels), age at weighting (10 levels), sex (2 levels), and the combination herd \times year \times season (48 levels) in pigs; type of birth (3 levels) in interaction with sex of the lamb (2 levels), year \times season (36 classes) combination, age of the dam (8 levels), and litter size (2 levels) in sheep; and age at weighing (6 levels), litter size at 21 d old (10 classes), kindling rank (5 classes), and the combination year \times month of birth (105 levels) in rabbits.

The goal of the analysis was to compare EBV obtained with models that differ according to the value of the direct-maternal genetic correlation ($\rho = \sigma_{dm} / (\sigma_d^2 \sigma_m^2)^{1/2}$) and/or the value of the direct or maternal genetic variance. Twenty-two different models were fitted to the data. In the first model, all the parameters of the general model described above had to be estimated (called EST model). The second model included only a maternal genetic effect; i.e., $\sigma_d^2 = \sigma_{dm} = 0$ (called MEf model = general model with direct genetic effects excluded), and the third model excluded a maternal genetic effect; i.e., $\sigma_m^2 = \sigma_{dm} = 0$ (DEf model = general model with maternal genetic effects excluded). In the last 19 models, the genetic correlation between the direct and maternal genetic effect was fixed (i.e., $\sigma_{dm} = \rho_{fixed} \times (\sigma_m^2 \sigma_d^2)^{1/2}$) and varied from -0.9 to 0.9 with a 0.1 step. We designated these models **MOD_ρ**, in which ρ is the fixed value of the genetic correlation. All models were fitted using ASReml software (Gilmour et al., 2009). Heritabilities were computed based on the resulting estimates of variance and covariance components:

Table 2. Variance component and heritability estimates obtained with the EST model (all the parameters of the general model had to be estimated)

Component	Pigs	Sheep	Rabbits
Direct genetic effect	236	365	2,677
Maternal genetic effect	189	153	1,143
Litter	295	309	2,103
Maternal permanent environmental effect	146	279	723
Genetic correlation	-0.54 (0.18)	0.21 (0.12)	-0.36 (0.07)
Direct heritability	0.10 (0.03)	0.13 (0.02)	0.26 (0.02)
Maternal heritability	0.08 (0.03)	0.06 (0.01)	0.09 (0.01)
Total heritability	0.08 (0.02)	0.22 (0.02)	0.20 (0.02)

$\sigma_m^2 / (\sigma_m^2 + \sigma_d^2 + \sigma_{dm}^2 + \sigma_p^2 + \sigma_l^2 + \sigma_\varepsilon^2)$ for maternal heritability, $\sigma_d^2 / (\sigma_m^2 + \sigma_d^2 + \sigma_{dm}^2 + \sigma_p^2 + \sigma_l^2 + \sigma_\varepsilon^2)$ for direct heritability, and $(\sigma_d^2 + \sigma_m^2 + 2\sigma_{dm}^2) / (\sigma_m^2 + \sigma_d^2 + \sigma_{dm}^2 + \sigma_p^2 + \sigma_l^2 + \sigma_\varepsilon^2)$ for total heritability (Eaglen and Bijma, 2009). The correlations between the direct, maternal, or total EBV (\hat{d}_i , \hat{m}_i , and total $\widehat{EBV}_i = \hat{d}_i + \hat{m}_i$, respectively, for individual i) were calculated between each model to evaluate the change in EBV depending on the model.

RESULTS

The estimates for variance components and heritabilities obtained with the EST model are shown in Table 2. Maternal heritabilities were low for all species (ranging from 0.06 to 0.09). Direct heritability was low for pigs and sheep (0.10 and 0.13, respectively) and moderate for rabbits (0.26). The genetic correlation between direct and maternal effects for ADG was strongly negative in pigs (-0.54) and slightly positive in sheep (+0.21), but the accuracy of the estimates was low. The genetic correlation between direct and maternal effects obtained for the weight at weaning in rabbits was negative (-0.36). The total heritability was low for pigs (0.08) and moderate for sheep and rabbits (0.22 and 0.20, respectively). Both heritability estimates and log likelihood (**LogL**) values are presented for the different models in Fig. 1, 2, and 3 for pigs, sheep, and rabbits, respectively. In the MOD $_{\rho}$ models, the maternal genetic variance could not be estimated for several extreme values of the genetic correlation between direct and maternal effects. For $-0.9 \leq \rho \leq -0.7$ in sheep and $0.8 \leq \rho \leq 0.9$ in rabbits, the model failed to converge and maternal genetic variance was fixed at a boundary (i.e., 0) during the estimation process. The results from these models were, therefore, not used when comparing EBV. Results were consistent between species. The EST model showed the highest LogL value. Omitting the direct genetic effects (MEf model) led to a significantly lower LogL value associated with a substantial decrease of the total heritability in comparison with the EST model. The changes observed when maternal ge-

netic effects were excluded (DEf model) were less substantial. The results obtained with the MOD $_{\rho}$ models showed that direct and maternal heritabilities decreased with the value of the genetic correlation whereas total heritabilities increased.

Figures 4 to 6 illustrate the correlations between the maternal EBV obtained with the different models (DEf model excluded). To help with reading Fig. 4 to 11, all values of ρ were not used to draw the correlation matrices. Maternal EBV varied with models. For the MOD $_{\rho}$ models, the correlation between maternal EBV decreased when the absolute difference between fixed genetic correlations increased, the lowest value being -0.20, -0.01, and -0.72 for pigs, sheep, and rabbits, respectively. When direct genetic effects were excluded (MEf model), maternal EBV were close to those obtained with the MOD $_{\rho}$ models that had a moderately positive fixed genetic correlation. The correlation between the maternal EBV obtained with the EST model and the MOD $_{\rho}$ models decreased symmetrically with the absolute difference between the estimated and fixed genetic correlation ($|\Delta|$) in sheep and pigs (the lowest values being 0.11 and 0.60 in pigs and sheep, respectively). In rabbits, the decrease was greater when Δ was positive than when it was negative (the lowest correlation being -0.30). The correlations between the direct EBV obtained with the different models (except for the MEf model) are also shown in Fig. 4 to 6 for the 3 species. As for the maternal EBV, the correlation between direct EBV decreased, although to a lesser extent, when the absolute difference between the fixed genetic correlations increased in MOD $_{\rho}$ models (the lowest correlations being 0.45, 0.90, and 0.96 in pigs, sheep, and rabbits, respectively). The direct EBV generated by the EST model were highly correlated with the direct EBV obtained with the different MOD $_{\rho}$ models in sheep and rabbits (the lowest correlations being 0.96 and 0.98 in sheep and rabbits, respectively). In pigs, slightly lower values were found for the same comparison (the lowest value being 0.76). The correlations between the total EBV obtained with MOD $_{\rho}$ models were high for all species (Fig. 7 to 9), the lowest

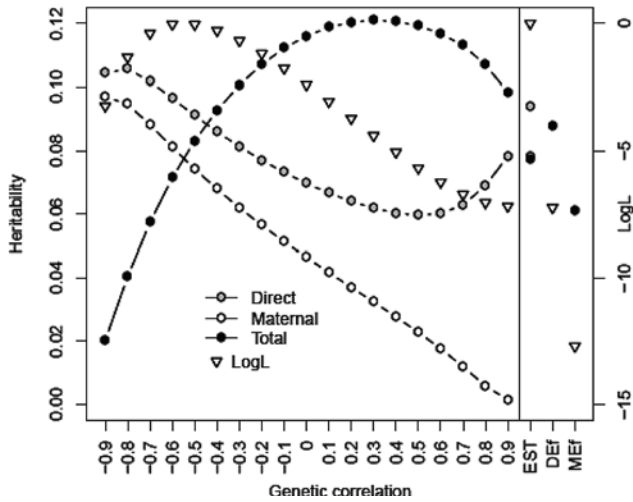


Figure 1. Direct, maternal, and total heritabilities and log likelihood (LogL) of the different models in pigs. EST model = all the parameters of the general model had to be estimated; MEF model = general model with direct genetic effects excluded; DE model = general model with maternal genetic effects excluded; MOD_ρ models = general model with fixed value for the direct maternal genetic correlation ρ (on the x-axis).

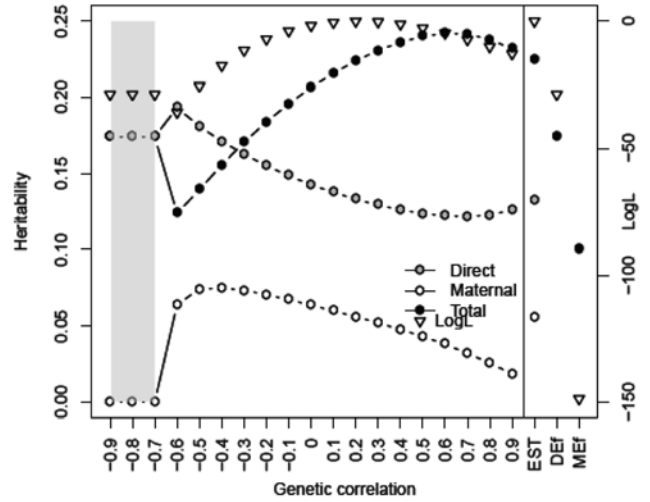


Figure 2. Direct, maternal, and total heritabilities and log likelihood (LogL) of the different models in sheep. EST model = all the parameters of the general model had to be estimated; ME model = only maternal genetic effect; DE model = only direct genetic effect; MOD_ρ models = ρ is the fixed value of the direct-maternal genetic correlation (on the x-axis). Gray box: model did not converge.

correlation being 0.93 between MOD_{0.9} and MOD_{0.9} in pigs. Omitting maternal effects from the model (Def model) did not have a significant impact on total EBV in rabbits and sheep (correlations with other models >0.96). However, more substantial changes were observed when direct effects were excluded (MEf model; correlations < 0.96 in all cases). The same pattern was observed in pigs although correlation values were found to be lower. The total EBV obtained with the EST model were strongly correlated with the total EBV

of MOD_ρ models whatever the value of ρ (>0.98 in sheep and rabbits and >0.95 in pigs).

DISCUSSION

We chose to compare the EBV obtained between and within 3 different sets of models (EST, MOD_ρ, and DEF/MEf). The EST model, in which all the parameters of the general model are estimated, was considered to be the reference model. Its variance and covariance parameters

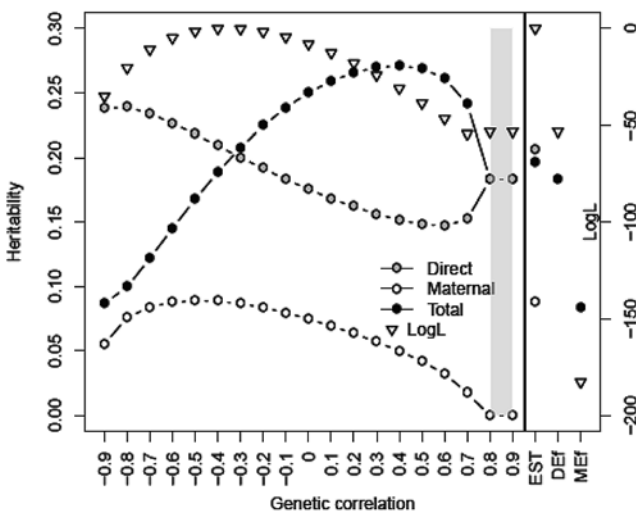


Figure 3. Direct, maternal, and total heritabilities and log likelihood (LogL) of the different models in rabbits. EST model = all the parameters of the general model had to be estimated; MEF model = general model with direct genetic effects excluded; DEF model = general model with maternal genetic effects excluded; MOD_ρ models = general model with fixed value for the direct maternal genetic correlation ρ (on the x-axis). Gray box: model did not converge.

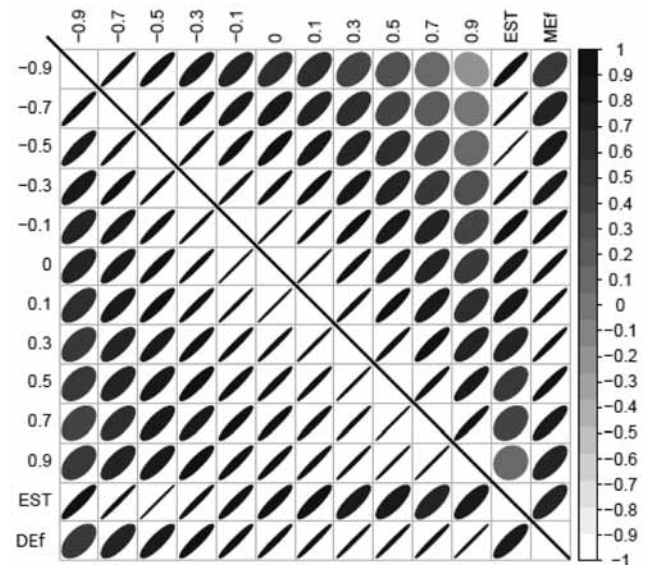


Figure 4. Correlation between maternal EBV (above the diagonal) and between direct EBV (below the diagonal) obtained with the different models in pigs. EST = all the parameters of the general model had to be estimated; MEF = general model with direct genetic effects excluded; DEF = general model with maternal genetic effects excluded. Figures correspond to the value of ρ in MOD_ρ models.

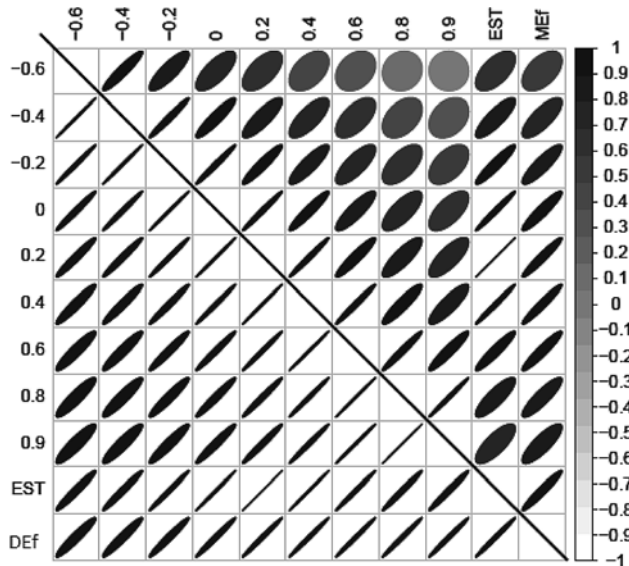


Figure 5. correlation between maternal EBV (above the diagonal) and between direct EBV (below the diagonal) obtained with the different models in sheep. EST = all the parameters of the general model had to be estimated; MEF = general model with direct genetic effects excluded; DEf = general model with maternal genetic effects excluded. Figures correspond to the value of ρ in MOD $_{\rho}$ models.

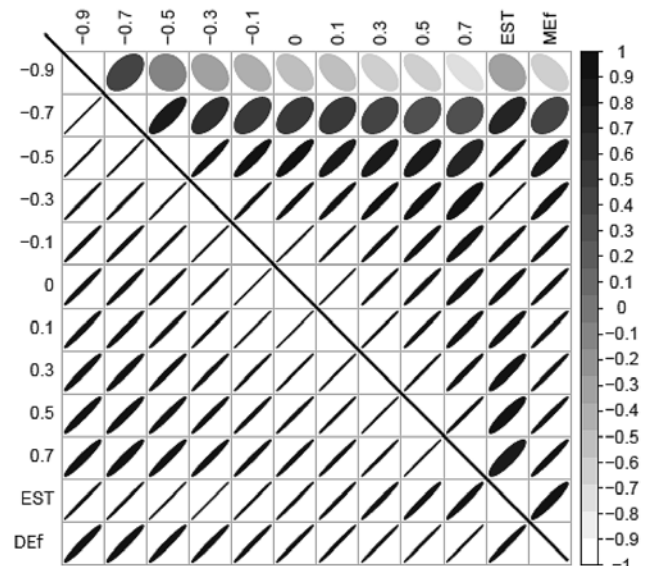


Figure 6. Correlation between maternal EBV (above the diagonal) and between direct EBV (below the diagonal) obtained with the different models in rabbits. EST = all the parameters of the general model had to be estimated; MEF = general model with direct genetic effects excluded; DEf = general model with maternal genetic effects excluded. Figures correspond to the value of ρ in MOD $_{\rho}$ models.

would have been used to predict EBV in genetic evaluation procedures. Nonetheless, given the potential sources of bias in the estimation (Gerstmayr, 1992; Lee and Pollack, 1997a,b; Clement et al., 2001; Bijma, 2006), we cannot actually ascertain that this is the model that provides the EBV closest to the true values. The EBV generated by the various MOD $_{\rho}$ models practically covered the range of values that can be obtained whatever the value of the direct-maternal genetic correlation. The DEf and

MEf models were fitted to the data to evaluate the impact of applying a “wrong” model on the EBV when the trait studied is governed by direct and maternal genetic effects.

We chose to apply the models to several different species to have a wide range of data types and be able to draw conclusions that are not data specific. Depending on the species, the structure of the data was variable with large (pigs and rabbits) or limited (sheep) litter sizes. The variance and covariance component values were also

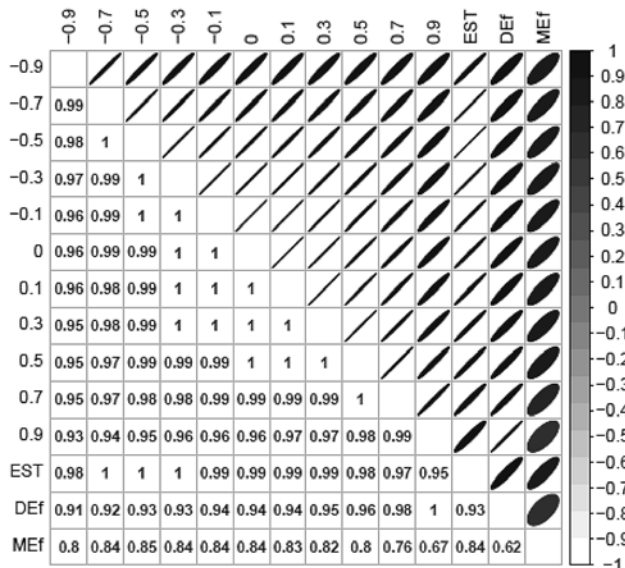


Figure 7. Correlation between total EBV = maternal EBV + direct EBV obtained with the different models in pigs. EST = all the parameters of the general model had to be estimated; MEf = general model with direct genetic effects excluded; DEf = general model with maternal genetic effects excluded. Figures correspond to the value of ρ in MOD $_{\rho}$ models.

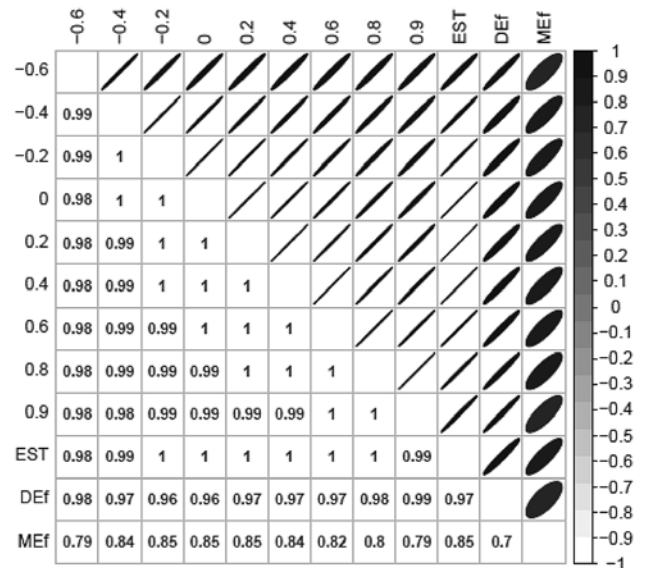


Figure 8. Correlation between total EBV = maternal EBV + direct EBV obtained with the different models in sheep. EST = all the parameters of the general model had to be estimated; MEf = general model with direct genetic effects excluded; DEf = general model with maternal genetic effects excluded. Figures correspond to the value of ρ in MOD $_{\rho}$ models.

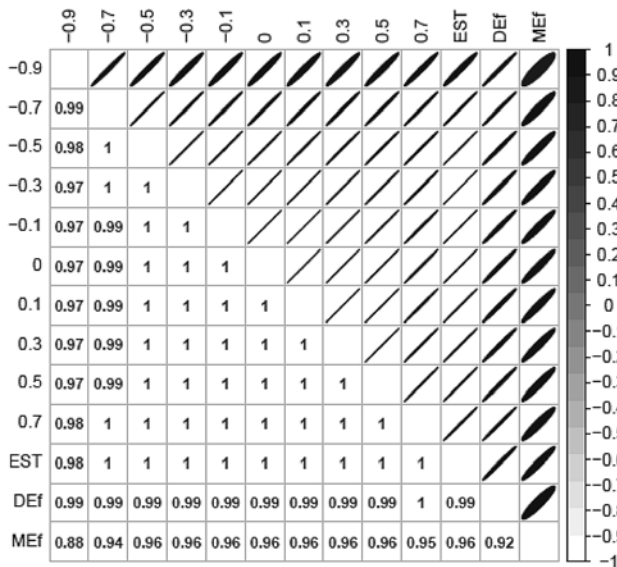


Figure 9. Correlation between total EBV = maternal EBV + direct EBV obtained with the different models in rabbits. EST = all the parameters of the general model had to be estimated; MEf = general model with direct genetic effects excluded; DEF = general model with maternal genetic effects excluded. Figures correspond to the value of ρ in MOD_ ρ models.

variable with strongly negative (pigs), moderately negative (rabbits), or slightly positive (sheep) direct-maternal genetic correlations, as were the proportions of direct genetic effect ($\hat{\sigma}_d^2 / (\hat{\sigma}_d^2 + \hat{\sigma}_m^2)$) obtained with the EST model (55% in pigs, 68% in sheep, and 74% in rabbits).

The heritabilities obtained with the EST model in pigs were in accordance with Bouwman et al. (2010), who reported low heritabilities for direct and maternal effects (0.07 and 0.06, respectively), but lower than those reported by Rosendo et al. (2007; 0.24 and 0.41, respectively), who also reported a highly negative direct-maternal genetic correlation (-0.74). There was probably an overestimation of the heritability in this last study that ignored the common environmental effect of the sow in its model. Bouwman et al. (2010) reported a higher direct-maternal genetic correlation than the one obtained in the present study (-0.21 versus -0.58), which is probably explained by the higher proportion of cross-fostering in their study (29 versus 6%) that helped in the parameter estimations. Our estimates of heritability in sheep are consistent with most of the heritabilities reported in the literature for preweaning ADG. Bromley (2000) reported heritabilities varying from 0.07 to 0.20 for direct effects and from 0.04 to 0.05 for maternal effects, depending on the breed. In a review on such studies, Safari et al. (2005) reported an average heritability of 0.15 for the direct effect and 0.05 for the maternal effect. In another study, however, Snowden and Van Vleck (2003) reported a low heritability for direct effects (0.03) and a higher heritability for maternal effects (0.28). Previous studies in sheep have reported estimates of the genetic correlation between direct and maternal effects that vary to a

great extent, with values ranging from -0.52 (Mousa et al., 1999) to 0.52 (Bromley, 2000). In rabbits, our total heritability estimate was in line with the values reported by García and Baselga (2002; 0.22) and slightly lower than the values reported by Niranjana et al. (2010; 0.25) but higher than those provided by Lukefahr et al. (1996; 0.04), Drouilhet et al. (2013; 0.06), Garreau and De Rochambeau (2003; 0.10), and Iraqi (2003; 0.10). Most of these previous studies did not include maternal genetic effects in their models. However, the comparison is still relevant because the heritabilities estimated with EST and DEF models were quite close in rabbits.

The small changes of the total heritability estimates observed when maternal genetic effects were ignored (DEF model) are consistent with previous studies (Hagger, 1998; Berweger Baschnagel et al., 1999; Clement et al., 2001). On the other hand, when direct genetic effects were ignored (MEf model), the total heritability calculated using $\sigma_m^2 / (\sigma_m^2 + \sigma_d^2 + \sigma_p^2 + \sigma_l^2 + \sigma_e^2)$ substantially decreased. In this specific case, offspring records are considered repeated measurements of their dam. Consequently, similarly to the sire-dam model, part of the dam variance has to be multiplied by 4 to obtain the genetic variance (Matos et al., 1997; Wolf et al., 2011). It can be noted that the magnitude of the decrease of heritability is proportional to the relative importance of the maternal effects obtained using the EST model. In MOD_ ρ models, the increase of the total heritability with the direct-maternal genetic correlation was attenuated by the simultaneous decrease of the direct and maternal genetic variances. However, we observed changes in the total heritability with ρ for all species. The relative SD of the heritability were 0.12, 0.17, and 0.15 for pigs, sheep, and rabbits, respectively, for ρ varying in the reasonable interval $[-0.5, 0.5]$. Consequently, the expected accuracy of selection varies with ρ .

Comparison of the EBV obtained with the different MOD_ ρ models shows that direct EBV are less sensitive to the value of ρ than maternal EBV. If the changes in direct and maternal EBV are considered to be more or less interrelated, 2 hypotheses can be postulated to explain our results. First, direct EBV were derived from the animal's own performance and maternal EBV were not. Consequently, if changes to the value of ρ affect 1 set of EBV, then it would be most likely to have an impact on maternal EBV. Second, in this study, the variance of the maternal genetic effect is generally lower than that of the direct effect. Therefore, small changes to the direct EBV lead to more substantial changes of the maternal EBV. This assumption is consistent with the decrease in the correlation between maternal EBV of the different MOD_ ρ models when the relative contribution of direct genetic variance ($\sigma_d^2 / (\sigma_d^2 + \sigma_m^2)$) estimated in the EST model) increases (pigs < sheep < rabbits). That also

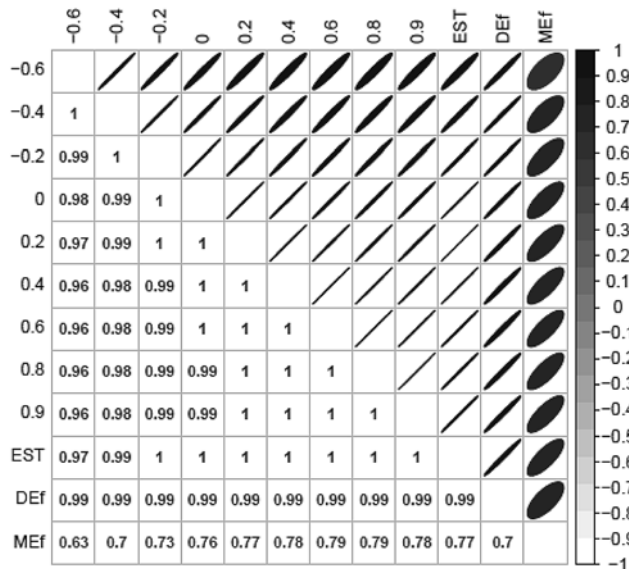


Figure 10. Correlation between total EBV = $0.5 \times$ maternal EBV + direct EBV obtained with the different models in sheep. EST = all the parameters of the general model had to be estimated; MEf = general model with direct genetic effects excluded; DEf = general model with maternal genetic effects excluded. Figures correspond to the value of ρ in MOD $_{\rho}$ models.

explains the high correlations between total EBV among several MOD $_{\rho}$ models observed in rabbits whereas the correlations between maternal EBV were highly negative. Total EBV were not significantly affected by the value of the direct-maternal genetic correlation. Given the difficulty of obtaining reliable estimations of this correlation, we therefore consider that setting the value of the direct-maternal genetic correlation to 0 in genetic evaluation models is a good compromise. Similar recommendations were issued by Phocas and Laloë (2004). In this study, for the sake of simplicity and in accordance with Eaglen and Bijma (2009) and Willham (1972), the total EBV was calculated as the sum of the direct and maternal EBV, each trait being considered to have the same weight. Nonetheless, a “classical” selection index procedure in which the traits have different weights (Vleck, 1976) could be envisaged. Weights are defined depending on the level at which the breeding objective is defined. For example, the following weights are used to calculate the total EBV in some maternal French rabbit lines used in crossbreeding systems: total $\widehat{EBV}_i = 0.25\hat{d}_i + 0.5\hat{m}_i$ (Garreau et al., 2005). On the other hand, the following is used in French meat sheep: total $\widehat{EBV}_i = \hat{d}_i + 0.5\hat{m}_i$ (Jacques Bouix, INRA-GenPhySE, personal communication). In that case, the breeding objective is focused on the growing animal and hence the dam contributes half of its genes to the growth of animals. Figures 10 and 11 show the correlation between these total EBV in the 2 species, respectively. In both cases, the correlation between total EBV calculated with the EST and all MOD $_{\rho}$ models is still high (>0.97 in sheep and 0.98 in rabbits). Therefore, a set value of 0 for the direct-maternal genetic

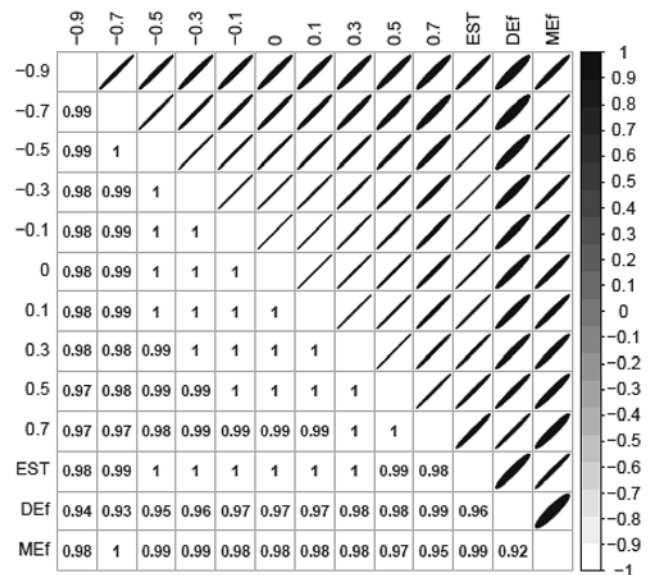


Figure 11. Correlation between total EBV = $0.5 \times$ maternal EBV + $0.25 \times$ direct EBV obtained with the different models in rabbits. EST = all the parameters of the general model had to be estimated; MEf = general model with direct genetic effects excluded; DEf = general model with maternal genetic effects excluded. Figures correspond to the value of ρ in MOD $_{\rho}$ models.

correlation remains a good compromise. It is impossible to test and assess how all the possible weight values for the direct and maternal genetic effects might affect the total EBV. Nonetheless, the weights given above (1:2 or 2:1) for the direct and maternal effects correspond, a priori, to the range of weights that might be used for the genetic evaluation of traits controlled by direct and maternal effects.

In this study, we describe how the total EBV is affected by the direct-maternal genetic correlation in the case of only single trait analysis. In the case of multiple trait analysis (Wolfová et al., 2005), different results may or may not be obtained. The extent of any potential differences will probably be related to the strength of the correlation between the different traits analyzed. In a previous study based on a social model (the maternal model being is a specific kind of social model), Canario et al. (2012) studied the changes in the genetic correlation between 2 traits (1 simple trait and a second trait controlled by direct and associative effects) with different set values of the direct-associative correlation in the social genetic model. They showed that for 3 of the 10 simple correlated traits, the genetic correlation between traits varied a little (up to 0.3) with extreme values of the direct-associative correlation. Nonetheless, their study did not provide any clear insight into the effect of the direct-associative correlation on the total EBV or on the total heritability in multiple trait analysis.

To conclude, we showed that the influence of the direct-maternal genetic correlation on the total EBV is minimal. Given that it is difficult to ascertain that the

direct-maternal genetic correlation has been estimated without bias, we suggest setting the direct-maternal genetic correlation to 0 for genetic evaluation purposes. Our results were obtained in a context of single trait analysis. Although it is highly probable that same conclusion will be obtained in the multiple trait case, further investigation will be needed to confirm the results for multiple trait analysis with other traits of interest.

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