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Effectiveness of genetic grouping with different strategies for estimation of genetic parameters in growth traits in Merino lambs

Serdar Duru [a], Şeniz Öziş Altınçekiç [a,*], Hülya Hanoğlu Oral [b]

[a] Department of Animal Science, Faculty of Agriculture, Bursa Uludag University, TR-16059 Bursa, Turkey
[b] Department of Animal Production and Technologies, Faculty of Applied Science, Mus Alparslan University TR-49250 Muş, Turkey

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ABSTRACT

The effectiveness of genetic grouping in genetic evaluations for growth traits in Merino sheep was researched in this study. In the study, 17,537 lambs born to 48 rams and 7118 ewes in 30 flocks were evaluated in animal models using REML. A model without a genetic group (GG0) was used in the analysis, as well as a model with three different genetic groups (GG). Maternal genetic and common environmental effects are included in all models. However, the models with and without covariance between direct and maternal effect were used for each trait. The Akaike Information Criterion (AIC) was used to compare models, taking into account the accuracy and Pearson and Spearman correlations between 48 rams for breeding values. Direct heritability (h_d^2), maternal heritability (m^2) and maternal common environmental effects (c_m^2) were generally found to be less than 0.10. The most important source of variation was found to be flock-year-season (FYS). It is worth bearing in mind that c_{FYS}^2 has a very high share of phenotypic variance in all models, ranging from 0.07 ± 0.01–0.43 ± 0.03. The fact that there is such a wide environmental difference between enterprises in the same region is a major issue for the improvement programme. It is necessary to intensify studies on the one hand for the expansion of small businesses and on the other hand for more modern animal husbandry to achieve this. AIC found that models based on GGs were better suited for all traits. Unlike AIC, the GG0 model had the highest accuracy for rams. The accuracy of the model (GG3), in which the mothers of animals whose father was unknown were also deleted and genetically grouped for both, was found to be lower for ADG and higher for WW. Furthermore, while the average accuracy for BW decreased to 0.60 in the other genetic group (GG1: lambs born in the same year in a flock and GG2: lambs born in a flock) models, it was found to be around 0.80 for ADG and above 0.80 for WW. According to research findings, it is possible to perform a genetic evaluation without losing data, especially in pedigrees with unknown fathers.

1. Introduction

Developing optimum genetic evaluation and breeding programmes for growth traits in sheep production requires knowledge of genetic parameters (Safari et al., 2005). Growth traits are affected by both direct additive genetic effects and maternal effects (Albuquerque and Meyer, 2001). In mammals, maternal effects particularly affect growth characteristics prior to weaning. Maternal effects are more important than the cattle's, especially since the lambs grow with milk to a significant extent before weaning.

Despite the contribution of the uterine environment and extra genes, maternal effects primarily reflect the mother's milk production and maternity ability. There are three reasons for maternal effects (Falconer, 1989); 1) Those due to the mother's genotype (maternal additive effects) for milking and maternity ability; 2) Those that are permanent among all lambs of a mother but not of additive genetic origin (permanent environmental effects); and 3) Those that belong to the lambs individually (temporary environmental effects). A mother's genotype thus influences the phenotype of her offspring via a sample of half of the direct additive genes and maternal effects that affect growth.

The maternal genetic effect is transmitted to the offspring via mitochondrial DNA (mDNA), and it affects the offspring and can be passed down through generations. When maternal effects are significant and are not taken into account, genetic parameters are biased and overestimated, resulting in a decrease in selection efficiency (Dodenhoff et al., 1999; Maniatis and Pollott, 2002). This is especially important if

* Corresponding author.
E-mail address: sduru@uludag.edu.tr (Ş.Ö. Altınçekiç).

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there is an antagonistic relationship between direct and maternal effects (Meyer, 1992). The estimation of (co)variance components resulting from maternal effects is simplified by REML algorithms that can be used for suitable animal models (Meyer, 1997). Furthermore, thanks to linear animal models, direct and maternal effects can be included in genetic evaluation models (Mrode, 2014). However, for meaningful separation of direct and maternal effects, an adequate data and pedigree structure is still required.

Animal models facilitate the estimation of additive genetic variance by distinguishing between individuals' phenotypic similarity resulting from direct additive genetic effects, maternal genetic effects, environmental similarities (maternal permanent, maternal common), inbreeding, and non-additive genetic effects (Kennedy et al., 1988). Traditionally, sufficient pedigree is required to measure relatedness between individuals in such analyses. The phenotypic similarity of relatives can also be used to predict additive genetic variance.

An incomplete pedigree, in which one or both of an individual's parents are unknown, is known to significantly bias genetic parameter estimates. It may cause bias in animal improvement by underestimating inadequate pedigree depth, relatedness, and inbreeding effects, thus hindering the prediction of ancestor genetic and environmental effects (Dong et al., 1988; Cassell et al., 2003). However, if there are animals in the pedigree with unknown parents, bias in the estimation of breeding values and components of variance is expected (Peškovičová et al., 2004; Petrini et al., 2015). Prediction of breeding values forms an integral part of many breeding programmes based on phenotypic data and pedigree information. Unknown parents also reduce the accuracy or reliability of predicted breeding values. When all parameters are equal, individuals with many close relatives with observed phenotypes have the maximum accuracy (Postma, 2006; Mrode, 2014).

Although the BLUP methodology allows for the simultaneous estimation of fixed and random effects, gaps in the relationship matrix may compromise BLUP's unbiasedness due to the inability to accurately predict genetic and environmental components (Postma, 2006; Gómez et al., 2016; Wolak and Reid, 2017). Indeed, inadequate pedigree information can lead to an inaccurate estimation of the animal's genetic potential, over-or under-estimation of the animal's breeding value, hindered selection-based decisions, and ultimately economic losses (Raoul et al., 2016; Carneiro et al., 2017; Abdel-Shafy et al., 2020). Random mating, which is still common in sheep flocks and complicates parental determination, is one of the reasons for inadequate pedigree information. Random mating, which is still common in sheep flocks and complicates parental determination, is one of the causes of inadequate pedigree information. Even though it is a routine analysis, farmers find it nearly impossible to bear the total cost of parental verification and genotyping of the entire flock. Although a similar problem is experienced in cattle improvement, the rate of incomplete pedigree is expected to be lower than in sheep due to artificial insemination. One of the major obstacles to sheep improvement research is incomplete pedigree.

A suggested solution to the incomplete pedigree problem is to use the "genetic groups" approach. The genetic group method has a long history in the animal improvement and was originally developed to control selection in sire models (Henderson, 1973). It has also been demonstrated in the animal model how to calculate inadequate pedigree information by assigning unknown parents to different genetic groups (Quaas, 1988; Westell et al., 1988).

The estimation of variance components and breeding value in dairy cattle using genetic groups is a well-accepted and validated method (Peškovičová et al., 2004; Petrini et al., 2015; Wolak and Reid, 2017). Genetic group methods developed in animal improvement can minimise the bias in quantitative genetic parameter estimations resulting from genetic heterogeneity among individuals whose parents are unknown (Wolak and Reid, 2017). The inclusion of genetic groups in the mixed model equation has been reported to have an effect on the variance component estimates (Gómez et al., 2021). Furthermore, not using the genetic groups can result in biased estimates of the selection response (Theron et al., 2002).

Robinson (1986) redefined group effects in the context of all individual relationships to reflect differences in breeding values of unknown parents. This enabled the animal model to account for any selection that resulted in differences in breeding values between unknown parents (Westell et al., 1988). Finally, Misztal et al., (2013) demonstrated how to calculate genetic group effects in an animal model using a combined relatedness matrix derived from genomics and pedigrees.

This study aims to determine the efficiency of various genetic group approaches in estimating variance components for growth traits and breeding values in sheep reared on 30 different farms in the National Merino Sheep Breeding Project.

2. Materials and methods

2.1. Data

This research was carried out in Kocaeli, Türkiye, in the Marmara region. Data were collected from 17,745 lambs born from 118 rams and 7208 ewes in 30 flocks over a 6-year period as part of the National Sheep and Goat Breeding Project. However, 198 data from 69 rams with fewer than ten progenies were deleted, and data from 17,537 lambs born from 48 rams and 7118 ewes were used (Table 1). The sheep are kept in the flock until they are 6–7 years old, while the rams are kept in the flock until they are 4 years old. Lambs are weaned when they are 90 days old. Typically, the flock is raised under semi-intensive feeding conditions. After all of the animals have grazed during the day, they are fed supplementary feed in the barn at night. They are mostly grown entirely in barns during the winter. Birth weight (BW), weaning weight at the 90th day (WW), and daily weight gain (ADG) from birth to weaning were evaluated in these lambs.

2.2. Determination of genetic groups

During data editing, phenotypic data were available for 17,745 animals, but only 3163 of these animals had both parents known. But even though the dam of 14,582 animals is known, the sire is unknown. Since the father of roughly 82 per cent of the animals with phenotypic data is unknown, it was decided to make a genetic group in the research. Whether or not direct maternal genetic covariance was considered, eight different models were used for each trait. A model without a genetic group (GG0: model 1, model 2) was used in the analysis, as well as a model with three different fixed genetic groups (GG). Genetic groups were formed according to different criteria. Therefore, the following GG are named; GG1 (model 3, model 4): Lambs born in the same year in a flock were assumed to have the same genetic background, resulting in the formation of 132 genetic groups. GG2 (model 5, model 6): A genetic group was formed from those born in each flock, and 29 genetic groups were formed. GG3 (model 7, model 8): In GG2, the mothers (6079 dam) of the animals whose father is unknown were deleted, and 29 mother groups were created in addition to the 29 father groups, for a total of 58 genetic groups.

Table 1
The characteristics of the pedigree and data structure for growth traits.[a]

Item	BW	WW	ADG
Mean, kg	3.8	30.6	297.9
Standard deviation	0.81	4.91	61.9
Number of lamb	17,537	16,780	16,780
Individual in pedigree file	22,925		
Individual with unknown sire	14,582		
Number of sire	48		
Number of dam	7114		

[a] BW: Birth weight, kg; WW: Weaning weight, kg; ADG: Average daily weight gain from birth to weaning, g.

2.3. Statistical analysis

(Co)variance components were estimated with REML and breeding values with BLUP. In order to determine fixed effect factors that would be included in the model, the data were analysed using the GLM procedure and analysis of variance (ANOVA) (Minitab, 19). Birth type and sex were considered as fixed effects. In addition, the weaning period and BW for WW and BW for ADG were considered as covariates.

Because each enterprise uses its own rams, when the data is classified using the flock-year-season (FYS), the genetic variance among the rams is also distributed within the FYS. To avoid this confusion, flocks are classified according to their size as $n < 400$ (1), $401 < n < 700$ (2), and $n > 701$. ANOVA revealed that all effects were significant ($p < 0.01$). Convergence is regarded to be attained if the value of the –2Log likelihood variance in the simplex function is less than 10^{-9}.

FYS was first considered as both fixed and random, and it was seen that it was more appropriate to accept random compared to AIC. Components of (co)variance and breeding values were performed with MTDFREML in univariate animal models (Boldman et al., 1995). Maternal genetic and common environmental effects are included in all models.

The following is the matrix notation for models with and without genetic groups:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wm} + \mathbf{Sc} + \mathbf{Tfys} + \mathbf{e} \quad (1)$$

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wm} + \mathbf{Sc} + \mathbf{Tfys} + \mathbf{e} \quad (2)$$

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{ZQg} + \mathbf{Wm} + \mathbf{Sc} + \mathbf{Tfys} + \mathbf{e} \quad (3)$$

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{ZQg} + \mathbf{Wm} + \mathbf{Sc} + \mathbf{Tfys} + \mathbf{e} \quad (4)$$

In these models, **y** is a vector of observation values for each trait, **b** is a vector of fixed effects (birth type (single, twins), sex (male, female)), **g** is a fixed effects vector for genetic groups (the number of **g** levels for GG1 =132, GG2 =29 and GG3 =58), **a** is a random effect for direct additive genetic effects (animal), **m** is a random effect for maternal additive genetic effects, **c** is a random effect for common environment effect for litters, **fys** is a random effect for FYS effect, and **e** is a random effect for residual effect. **X** and **Z** are incidence matrices relating observations to elements of **b** and **a**, respectively. **W** is design matrix of random maternal additive genetic effects. **Q** is included that matrix of genetic groups, **S** is design matrix of random common environment effect for litters, **T** is design matrix of random **fys** effects. **A** is numerator relationship matrix. The following assumptions were used in the analysis:

$$V(a) = \boldsymbol{A}\sigma_a^2,\ V(m) - \boldsymbol{A}\sigma_m^2,\ V_c(c) = \boldsymbol{I_c}\sigma_c^2,\ V_{FYS}(c) = \boldsymbol{I_{FYS}}\sigma_{FYS}^2,$$
$$Cov(a, m) = \boldsymbol{A}\sigma_{am},\ V(e) = \boldsymbol{I_n}\sigma_e^2$$

where; $\boldsymbol{I_c}$, $\boldsymbol{I_{FYS}}$ and $\boldsymbol{I_n}$ are identity matrices with orders equal to number of litter groups, FYS and animals, σ_a^2, σ_m^2, σ_c^2, σ_{FYS}^2, σ_{am}, r_{am} and σ_e^2 direct additive genetic variance, maternal additive genetic variance, common environment variance, FYS variance, covariance between additive direct and maternal effects, direct-maternal genetic correlation and environmental variance, respectively. By dividing these variance components by phenotypic variance, direct heritability (h_d^2), maternal heritability (m^2), common environmental effects (c_m^2), and FYS effects (c_{FYS}^2) were calculated. In flocks where multiple births are common, it is useful to separate the permanent environmental effects of the mother over the years into maternal effects and litter effects. In this study, the litter effect was regarded as a common environmental source.

2.4. Comparison of analyses

The Akaike Information Criterion (AIC) was used to determine the best model for each trait (Akaike, 1974).

$$AIC = -2\ \mathrm{Log}\ L + 2p$$

Hereby Log L is the maximum Log-likelihood, p is the expected mean of the population for each model and the number of random parameters including error. The model with the lowest AIC value was accepted as the most suitable model. Furthermore, the Chi-square test was used to perform the Likelihood Ratio Test (LRT) between the model with the smallest AIC value and the values closest to it.

In addition, Pearson correlations, Spearman rank correlations, and accuracy between predicted breeding values (PBV) from 8 different models for 48 rams were also calculated.

3. Results

The number of lambs on the enterprises ranges from 40 to 3095, with an average of 584. The average number of lambs produced by each mother and father is 2.5 and 365, respectively. All traits were found to be significantly affected by birth type and gender ($p < 0.01$).

Table 2 shows the AIC values calculated in each model for each trait. According to the AIC, the most suitable models for all traits are those with genetic groups (models 5–8). While GG3 (M7, M8) was more suitable for BW, GG2 (M5, M6) was found to be more suitable for WW and ADG. The differences between the AIC values of most models with and without Cov (a, m) are high (except M3-M4, M7-M8 for BW). In addition to AIC, LRT and accuracy should be considered to select a model. While the differences between a few models are insignificant compared to the LRT, the differences between most models are significant. The critical khi-square value (for 0.05 and 1 degree of freedom) for LRT is 3.84. The difference between the –2LogL values of the most models with and without Cov (a, m) is greater than this khi-square value and is significant.

The predicted (co)variance components and genetic parameters in all models for each trait are given in separate tables (Tables 3–5). The direct heritabilities found in this study are significantly lower than the values reported in the literature, except for 0.16, which is estimated by GG0 (M1, M2) for WW. An animal's birth weight, and especially its growth rate until weaning, is determined not only by its genetic potential but also by the maternal environment. According to the findings of this study, while maternal heritability for BW in lambs ranged from 0.01 to 0.15, it was found to be zero in all models for WW. However, it can be said that the effects of maternal genetic effects on growth characteristics are generally limited.

According to this study, c_m^2 does not change much with age, as it is generally found to be 0.04–0.05 for BW and WW.

FYS was the most important source of variation for all traits in the study and c_{FYS}^2 ranged from 0.07 to 0.43. The proportion of these effects increased with the age of the lambs and was found to be over 0.20 for WW and 0.30 for ADG in models with GG. These findings are an indication that environmental factors have a significant impact on the growth traits of lambs and therefore the milk yield of the mothers in this region. It should be noted that this factor accounts for a significant portion of the phenotypic variance.

Table 2
AIC values for the growth traits.

			Traits[a]		
Genetic Group	Model	Equation	BW	WW	ADG
GG0	M1	1	7884	66,146	149,201
GG0	M2	2	7871	66,148	149,192
GG1	M3	3	7792	66,147	149,588
GG1	M4	4	7793	66,274	149,563
GG2	M5	3	5984	**64,083**	**146,099**
GG2	M6	4	5986	**64,078**	**146,095**
GG3	M7	3	**5953**	64,222	146,397
GG3	M8	4	**5952**	64,203	146,393

[a] BW: Birth weight; WW: Weaning weight; ADG: Average daily weight gain.

Table 3
Estimates of variance components and genetic parameters for BW in Merino sheep.

Models	σ_a^2	σ_{am}	σ_m^2	σ_c^2	σ_{FYS}^2	σ_e^2	σ_P^2	$h_d^2 \pm SE$	$m^2 \pm SE$	c_m^2	c_{FYS}^2	$r_{am} \pm SE$	CVA
1	0.017		0.063	0.007	0.043	0.487	0.617	0.03 ± 0.02	0.10 ± 0.02	0.01 ± 0.01	0.07 ± 0.01		3.43
2	0.021	-0.023	0.092	0.000	0.044	0.484	0.617	0.03 ± 0.02	0.15 ± 0.03	0.00 ± 0.01	0.07 ± 0.01	-0.53 ± 0.27	3.81
3	0.004		0.012	0.027	0.055	0.471	0.569	0.01 ± 0.01	0.02 ± 0.02	0.05 ± 0.01	0.10 ± 0.01		1.56
4	0.005	-0.013	0.030	0.021	0.055	0.470	0.569	0.01 ± 0.01	0.05 ± 0.04	0.04 ± 0.01	0.10 ± 0.01	-1.00 ± 0.03	1.93
5	0.003		0.008	0.031	0.067	0.489	0.599	0.01 ± 0.01	0.01 ± 0.02	0.05 ± 0.01	0.11 ± 0.02		1.44
6	0.006	-0.012	0.026	0.024	0.067	0.487	0.598	0.01 ± 0.01	0.04 ± 0.02	0.04 ± 0.01	0.11 ± 0.02	-1.0 ± 0.02	1.97
7	**0.000**		**0.063**	**0.029**	**0.069**	**0.492**	**0.654**	**0.00 ± 0.01**	**0.10 ± 0.01**	**0.04 ± 0.01**	**0.11 ± 0.02**		0.08
8	**0.004**	**-0.017**	**0.080**	**0.029**	**0.070**	**0.489**	**0.655**	**0.01 ± 0.01**	**0.12 ± 0.02**	**0.04 ± 0.01**	**0.11 ± 0.02**	**-0.99 ± 0.03**	1.60

[a]Direct additive genetic variance (σ_a^2), covariances between direct and maternal additive genetic effects (σ_{am}), maternal additive genetic variance (σ_m^2), maternal permanent environmental (common) variance (σ_c^2), FYS variance (σ_{FYS}^2), residual variance (σ_e^2), phenotypic variance (σ_P^2), direct heritabilities (h_d^2), standard error (SE), maternal heritabilities (m^2), the ratio of maternal permanent environmental variance to phenotypic variance (c_m^2), the proportion of FYS variance to phenotypic variance (c_{FYS}^2), correlation between direct and maternal additive genetic effects (r_{am}), additive genetic variation coefficiant (CVA).

Table 4
Estimates of variance components and genetic parameters for WW in Merino sheep.

Models	σ_a^2	σ_{am}	σ_m^2	σ_c^2	σ_{FYS}^2	σ_e^2	σ_P^2	$h_d^2 \pm SE$	$m^2 \pm SE$	c_m^2	c_{FYS}^2	$r_{am} \pm SE$	CVA
1	3.63		0.000	0.781	3.854	14.2	22.5	0.16 ± 0.03	0.00 ± 0.02	0.04 ± 0.01	0.17 ± 0.02		6.23
2	3.52	0.014	0.001	0.824	3.756	14.3	22.4	0.16 ± 0.04	0.00 ± 0.04	0.04 ± 0.01	0.17 ± 0.02	0.31 ± 0.03	6.13
3	0.86		0.008	1.020	5.020	14.9	21.8	0.04 ± 0.02	0.00 ± 0.02	0.05 ± 0.01	0.23 ± 0.02		3.03
4	0.89	-0.017	0.000	1.039	4.870	14.8	21.6	0.04 ± 0.02	0.00 ± 0.02	0.05 ± 0.01	0.23 ± 0.02	-0.89 ± 0.20	3.08
5	**1.09**		**0.001**	**0.900**	**4.419**	**15.8**	**22.3**	**0.05 ± 0.02**	**0.00 ± 0.02**	**0.04 ± 0.01**	**0.20 ± 0.01**		3.41
6	**1.35**	**-0.010**	**0.009**	**0.940**	**4.410**	**15.6**	**22.2**	**0.06 ± 0.03**	**0.00 ± 0.02**	**0.04 ± 0.01**	**0.20 ± 0.01**	**-0.99 ± 0.30**	3.79
7	2.00		0.000	1.200	4.500	14.7	22.4	0.09 ± 0.02	0.00 ± 0.02	0.05 ± 0.01	0.20 ± 0.01		4.62
8	1.98	-0.044	0.001	1.060	4.860	14.9	22.8	0.09 ± 0.02	0.06 ± 0.01	0.00 ± 0.01	0.21 ± 0.01	-1.00 ± 0.20	4.60

[a]Direct additive genetic variance (σ_a^2), covariances between direct and maternal additive genetic effects (σ_{am}), maternal additive genetic variance (σ_m^2), maternal permanent environmental (common) variance (σ_c^2), FYS variance (σ_{FYS}^2), residual variance (σ_e^2), phenotypic variance (σ_P^2), direct heritabilities (h_d^2), standard error (SE), maternal heritabilities (m^2), the ratio of maternal permanent environmental variance to phenotypic variance (c_m^2), the proportion of FYS variance to phenotypic variance (c_{FYS}^2), correlation between direct and maternal additive genetic effects (r_{am}), additive genetic variation coefficiant (CVA).

Table 5
Estimates of variance components and genetic parameters for ADG in Merino sheep.

Models	σ_a^2	σ_{am}	σ_m^2	σ_c^2	σ_{FYS}^2	σ_e^2	σ_P^2	$h_d^2 \pm SE$	$m^2 \pm SE$	c_m^2	c_{FYS}^2	$r_{am} \pm SE$	CVA
1	87		258.0	104	1184	2632	4267	0.02 ± 0.01	0.06 ± 0.02	0.02 ± 0.01	0.28 ± 0.02		4.47
2	177	-142	418	63	1186	2567	4270	0.04 ± 0.02	0.10 ± 0.02	0.02 ± 0.01	0.28 ± 0.02	-0.52 ± 0.20	3.02
3	81		0.2	241	1970	2291	4585	0.02 ± 0.01	0.00 ± 0.01	0.05 ± 0.02	0.43 ± 0.03		3.46
4	106	-69	82	223	1975	2272	4589	0.02 ± 0.01	0.02 ± 0.02	0.05 ± 0.02	0.43 ± 0.03	-0.74 ± 0.04	2.77
5	**68**		**0.05**	**211**	**1564**	**2613**	**4456**	**0.02 ± 0.01**	**0.00 ± 0.01**	**0.05 ± 0.02**	**0.35 ± 0.01**		3.17
6	**89**	**-51**	**58**	**198**	**1566**	**2597**	**4459**	**0.02 ± 0.01**	**0.01 ± 0.02**	**0.05 ± 0.02**	**0.35 ± 0.01**	**-0.71 ± 0.05**	3.09
7	85		151	218	1615	2589	4660	0.02 ± 0.01	0.03 ± 0.01	0.05 ± 0.02	0.35 ± 0.01		3.36
8	100	-77	229	217	1614	2575	4660	0.02 ± 0.01	0.05 ± 0.03	0.05 ± 0.02	0.35 ± 0.01	-0.51 ± 0.06	4.47

[a]Direct additive genetic variance (σ_a^2), covariances between direct and maternal additive genetic effects (σ_{am}), maternal additive genetic variance (σ_m^2), maternal permanent environmental (common) variance (σ_c^2), FYS variance (σ_{FYS}^2), residual variance (σ_e^2), phenotypic variance (σ_P^2), direct heritabilities (h_d^2), standard error (SE), maternal heritabilities (m^2), the ratio of maternal permanent environmental variance to phenotypic variance (c_m^2), the proportion of FYS variance to phenotypic variance (c_{FYS}^2), correlation between direct and maternal additive genetic effects (r_{am}), additive genetic variation coefficiant (CVA).

Direct maternal genetic correlation (r_{am}) was predicted negative and high in almost all models for all traits.

The mean of estimated genetic parameters in GG0 and GG models were calculated (Table 6). As it can be seen, while creating a genetic group caused a decrease in h_d^2 and m^2, it did not have the same effect on c_m^2 and c_{FYS}^2 and increased them. The mean of direct heritability for WW was 0.16 in the model GG0, while it was 0.06 in the GG models, and is generally less than 0.05 in all models for other traits. Maternal heritability BW was found to be 0.13 and 0.06 for models GG0 and GG, respectively, and 0.00 for WW. For all three features, the portion of c_m^2 in the phenotypic variance is less than 0.05. Despite all this, it is clear that, except for model GG0, c_{FYS}^2 is the most important source of variation, with or without creating genetic groups.

Spearman rank and Pearson correlations were calculated for the PBVs of 48 Merino rams for growth traits in different models (no tables are provided here). Both Pearson and rank correlations were high for BW and WW. Both correlation coefficients for WW were greater than 0.98, indicating that the models were highly compatible. Despite the fact that the lowest Pearson correlation for BW was 0.80, rank correlations were as low as 0.72. The M8 with its main information removed had the lowest correlation in both cases. ADG, on the other hand, was in a completely different situation. Surprisingly, all of the correlation coefficients between GG3 (M7 and M8), in which mothers were removed, and the other models (the highest being –0.12) were negative. The value between M7 and M8 was 0.96 and 0.97. These findings indicate that PBVs for ADG predicted by GG3 of 48 rams differ significantly from

Table 6
Means of genetic parameters in models without (GG0) and with (GG) genetic groups.

Traits	Model	h_d^2	m^2	c_m^2	c_{FYS}^2
BW	GG0	0.03	0.13	0.01	0.07
	GG	0.01	0.06	0.04	0.10
WW	GG0	0.16	0.00	0.04	0.17
	GG	0.06	0.00	0.05	0.21
ADG	GG0	0.03	0.08	0.02	0.28
	GG	0.02	0.02	0.05	0.38

[a]BW, birth weight, WW, weaning weight, ADG, average daily gain, h_d^2, direct heritabilities, m^2, maternal heritabilities, c_m^2, the ratio of maternal permanent environmental variance to phenotypic variance, c_{FYS}^2, the proportion of FYS variance to phenotypic variance.

other models. It is obvious that this outcome will have an impact on selection decisions.

All rams are sorted and numbered based on the PBV results from M1. Fig. 1 depicts the first 10 rams based on PBV and accuracy to better illustrate this situation. The highest PBV was obtained in all models from M1 and M2 without genetic grouping, as shown in the Fig. 1 by the black solid and dashed lines. The most remarkable results for PBV and accuracy are those found for ADG, as indicated in the correlations. As can be seen, the results obtained with the GG3 (M7 and M8) differ significantly from the results obtained with other models. While there is close parallelism across other models in terms of accuracy, it is quite different and low in the GG3 model. In the case of WW, on the contrary, higher accuracy was obtained in the GG3 model than GG1 and GG2. Accuracy for BW and ADG is higher in models with cov (a, m) (M2, M4, M6, M8) (Fig. 1). However, it can be said that the difference is not very significant for WW (except for M5-M6). If the selection rate is recognised at 10%, it can be said that the situation becomes even more important for the five rams to be chosen.

The mean of accuracy calculated in models without genetic grouping and genetic grouping with different scenarios in the research are shown in Fig. 2. Similar to the results in Fig. 1, average accuracy is better for models with cov (a, m). As can be clearly seen in Fig. 2, the accuracy for BW and ADG is M2 >M1, M4 >M3, M6 >M5. The accuracy for PBV estimates depends on the heritability and the structure of the data. As increasing heritability also increases accuracy, this could partially explain the result. As mentioned before, the highest accuracy for all three traits was calculated in GG0 (M1, M2). While it was higher than 0.80 in all models for WW, it decreased below 0.60 in GG3 (M7, M8) for ADG. However, while BW had the lowest accuracy, it is thought-provoking that the calculated accuracy for all rams in M7 was zero. The analysis was repeated several times after checking, but the result remained the same. The results obtained with the GG3 differ from those obtained with other models because the relatedness in the pedigree are intentionally impaired. The total number of inbred animals in the flock was 5, 59, 3685, and 5 for GG0, GG1, GG2, and GG3, respectively. Given that the number of father and mother groups for GG3 is equal, these findings can be interpreted as creating a genetic group is more effective, particularly for unknown fathers. However, according to the AIC values, finding the GG2 model for WW and ADG and the GG3 model for BW more suitable is noteworthy.

The lowest AIC values for WW and ADG were obtained from M5 and M6. Similarly, the accuracy of PBVs for these traits is above 0.70 in M5 and M6. Therefore, it can be said that M5 and M6 are more suitable for WW and ADG. On the other hand, the lowest AIC value for BW was obtained from M7 and M8. However, among the models containing GG (M3-M8), the highest accuracy was obtained from M4, M6 and M8 (0.60). These results can be interpreted as compromising accuracy to include GGs in the model used for BW.

4. Discussion

Very low genetic variation was found for most of the traits in this study. Non-genetic effects accounted for a significant portion of the phenotypic variance for all traits. FYS is the primary source of variation in growth characteristics. From birth to weaning, the proportion of these effects increased. Therefore, disregarding non-genetic factors may result in bias in genetic parameter estimation. The predicted direct additive-maternal genetic covariance was negative and very high. This has a significant negative impact on predicting the overall genetic improvement that selection will achieve. These flock differences must first be reduced in order to increase genetic variation in this population.

The mother contributes to the performance of the offspring in two ways. The first is in the form of direct genetic effects, and the second is the ability to provide a good environment. The ability of a mother to provide a suitable environment for her offspring is a result of both genetic and environmental factors. The environmental part is divided into permanent and temporary environments. The maternal additive genetic element is passed on to her offspring, but this is only visible when the daughter has progeny of her own. Maternal genetic effects are known to decrease with age in mammals and to be more important in young animals. The explanation of genetic parameters for traits affected by maternal effects in animal models depends on the model used in the analysis.

Because sheep and lambs are kept together in most sheep breeding systems, the interaction between the mother and the newborn may be one of the most important factors influencing lamb production. This interaction is more noticeable in sheep than in other farm animals such as pigs and cattle. This effect partially reflects direct-maternal genetic correlation (Abbasi et al., 2012). There are studies in which this value is estimated positive, as well as studies in which it is estimated negative. It is possible to say that selection can be made in the same direction for positive traits.

Negative r_{am} has been reported to be common in animal improvement and maybe a statistical issue rather than a biological one (Meyer, 1997; Eler et al., 2000). Negative r_{am} values may also indicate antagonism between the effects of genes associated with growth and maternal ability. Antagonism between these effects may also be caused by antagonism between an individual's growth genes and maternal contribution, or by moderate natural selection (Tosh and Kemp, 1994). According to Roff (2002), antagonistic pleiotropy has long been thought to be a possible mechanism for the appearance of genetic variation. Therefore, selection for direct additive genetic effects may reduce maternal ability and make co-selection for preweaning traits difficult (Gowane et al., 2015). According to Robinson (1996), one of the reasons for the high r_{am} was the less number of data, and the other was the inclusion of some fixed effects in the model. Another reason is the higher variety between fathers and mothers, or surprisingly, environmental influences (Vergara et al., 2009). It has been reported that it is practically impossible to distinguish between m^2 and c^2, resulting in high and negative r_{am} (Maniatis and Pollott, 2002; Mandal et al., 2006; Heydarpour et al., 2008). Lack of genetic linkage for years, random entry into flocks, and unplanned culling can also explain the difficulty in separating m^2 and c^2. Furthermore, the ability to distinguish between m^2 and c^2 is dependent on whether or not mothers have a family structure and the number of fathers formed from these mothers (Zishiri et al., 2014).

Maternal common environmental effects generally diminish with age. In other words, maternal common environmental effects have a greater impact on early life characteristics. Maternal common environmental effects influence birth weight, particularly at the end of pregnancy, through feeding level and uterine capacity. Additionally, sheep milk yield influences weaning weight.

The issue of incomplete pedigrees has existed for many years and remains one of the most significant issues in genetic evaluations. This

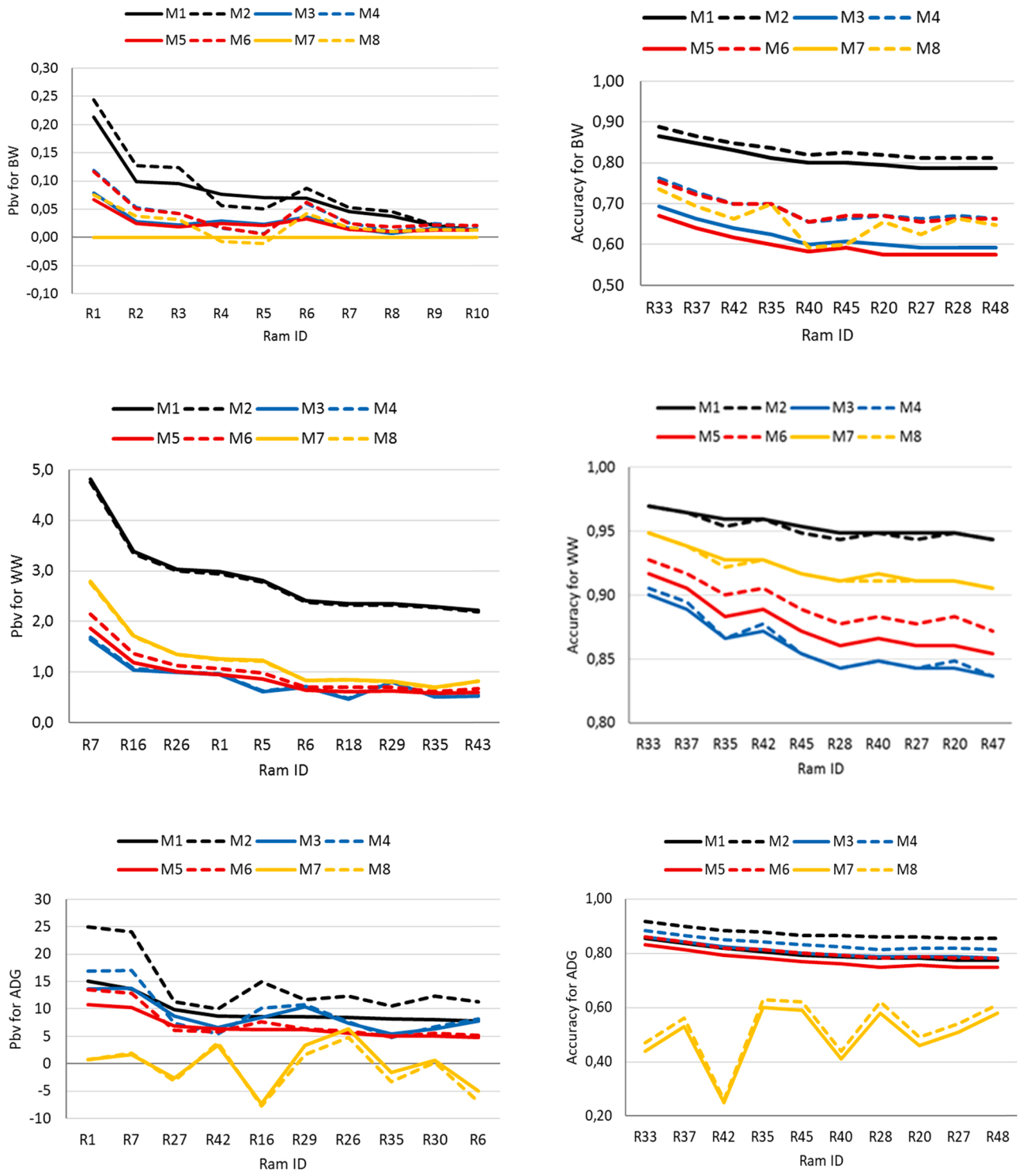


Fig. 1. PBV and accuracy changes in all three traits for the first 10 rams.

National Merino Project is confronted with a situation in which phenotypic data for many animals are available, but pedigree data for some animals is missing. Records from individuals with no pedigree information were assumed to have an unknown father, rather than being excluded from genetic analysis. New technologies, such as high-throughput single-nucleotide polymorphism (SNP) genotyping, will undoubtedly solve many of the problems associated with imprecise paternity, but only for individuals who are still alive or have biological specimens available.

Inadequate pedigree information is more noticeable in flocks managed by small farmers with limited financial resources. The scientific community has long been interested in resolving the non-paternity problem, and various methodologies have been developed over the years to manage the problems caused by gaps in a relationship matrix. There are various tools available today to improve pedigree information, such as DNA-based methods, but they can still be expensive for breeders in some countries. Similarly, this issue may arise in species that have recently undergone genetic evaluation and have historical phenotypic data for which biological sampling is nearly impossible due to the lack of a DNA bank. However, different genetic markers are used to investigate



Fig. 2. Average accuracy of Merino rams PBVs for the growth traits obtained in the different genetic group models.

the relationship between relatives and to assist selection programmes. Microsatellites and genome-wide distributed molecular markers, such as Single Nucleotide Polymorphisms (SNPs) have been widely used in parental assignment. Furthermore, the cost of genotyping with microsatellites has been estimated to be two to three times cheaper compared to SNPs when they are used for parental assignments (Vallecillos et al., 2022).

Genetic groups are typically formed according to different criteria, such as an individual's origin, sex, flock, or year of birth. Creating genetic groups is not an easy task, and sometimes complications can occur. Because groups with a small number of animals may distort the estimate of genetic group effect, genetic groups must be balanced (Rodriguez et al., 1996; Peškovičová et al., 2004; Petrini et al., 2015). At the same time, very large groups fail to capture the true differences between individuals. Some studies have emphasised the significance of genetic group structure, particularly in terms of number and size (Santana et al., 2013; Shiotsuki et al., 2013; Petrini et al., 2015).

Despite its potential benefits, the genetic grouping has its limitations. One of them is the assumption that additive genetic variance between groups is homogeneous. This assumption allows the covariance among relatives to be modelled with a single additive genetic variance for the entire population. However, the assumption of homogeneous variance may be violated by evolutionary dynamics, causing the variance in true additive genetic values within genetic groups to differ between groups (Alfonso and Estany, 1999). Another common assumption in traditional genetic group strategies is that phantom parents are unrelated within and between groups and that there is no drift or inbreeding within the base population (Legarra et al., 2015). However, some phantom parents will be widely related, particularly if undersampling is the cause of unknown parentage (Misztal et al., 2013).

Genetic group methods are not a panacea, so they cannot be expected to fully salvage incomplete pedigree-based analyses or solve all emerging problems. Even when genetic groups are modelled, inadequate pedigree information can bias genetic parameter estimates. Unknown parents reduce pedigree relatedness, which may result in phenotypic variation being attributed to environmental rather than genetic influences. Similarly, incomplete parental information may influence estimates of inbreeding and, as a result, inbreeding depression (Pemberton, 2008). Such aberrations can be minimised by using "non-pedigree" animal models that estimate realised inbreeding directly from high-density genetic marker data rather than expected inbreeding derived from a pedigree (Garant and Kruuk, 2005; Pemberton, 2008; Speed and Balding, 2015).

Models containing genetic groups yielded lower additive genetic variance estimates (Pieramati and Van Vleck, 1993). However, in another study, it was discovered that the estimated VCE and EBVs by the genetic group were quite close to the estimates obtained using full pedigree (Gómez et al., 2021). According to the researchers, these findings support the effectiveness of the GG methodology for estimating real parameters. As a result, it can be assumed that existing pedigree information and the use of the GG strategy will reduce the loss in VCE and PBV accuracy caused by inadequate pedigree information. Sullivan (1995) suggested that including genetic groups in estimating PBV is important and that data should not be discarded due to non-paternity. Of course, genomic selection could potentially solve the non-paternity problem (Abdel-Shafy et al., 2020; Macedo et al., 2020; Misztal et al., 2020), but, genotyping all animals in a flock may still be expensive for some countries. In the case of the Merino population, using GG is a practical and cost-free solution for incorporating all available information into the genetic evaluation process without jeopardising the accuracy of the results too much. However, in the end, the more suitable model than the AIC does not have a higher accuracy. This makes it difficult to make a decision in model selection.

5. Conclusions

Pedigree integrity is a fundamental requirement of any genetic evaluation. The existence of animals in species other than dairy cattle with phenotypic records but incomplete pedigrees is a significant issue. Sheep breeding is an example of such a situation. More widespread use of DNA testing is expected, which will eventually increase the use of genomic selection in sheep. However, missing pedigree information will still be present, and genomic selection will face the same issue. When inadequate pedigree information is present, incorporating genetic groups into mixed model equations used to predict both VCE and PBV in a selected population is a valuable and simple way to improve accuracy. The findings of the study confirmed the possibility of developing a genetic assessment in populations of unknown fathers without the need to delete data or use only one group selected from the current population.

Conflicts of interest

None of the authors have any conflict of interest to declare.

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References

Abbasi, M.A., Abdollahi-Arpanahi, R., Maghsoudi, A., Vaez Torshizic, R., Nejati-Javaremib, A., 2012. Evaluation of models for estimation ofgenetic parameters and maternal effects for early growth traits of Iranian Baluchi sheep. Small Rumin. Res. 104, 62–69.

Abdel-Shafy, H, Awad, M.A.A., El-Regalaty, H., Ismael, A., El-Assal, S.E.-D., Abou-Bakr, S., 2020. A single-step genomic evaluation for milk production in Egyptian buffalo. Livest. Sci. 234, 103977.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control 19, 716–723.

Albuquerque, L.G., Meyer, K., 2001. Estimates of direct and maternal genetic effects for weights from birth to 600 days of age in Nelore cattle. J. Anim. Breed. Genet 118, 83–92.

Alfonso, L., Estany, J., 1999. An expression of mixed animal model equations to account for different means and variances in the base population. Genet. Sel. Evol. 31, 105–113.

Boldman, K.G., Kriese, L.A., Van Vleck, L.D., Van Tassel, C.P., Kachman, S.D., 1995. A Manual for Use of MTDFREML. A Set of Programs to Obtain Estimates of Variances

and Covariances [DRAFT]. U.S. Department of Agriculture, Agricultural Research Service, p. 114.
Carneiro, F.F.D., Lôbo, A.M.B.O., Silva, L.P.D., Silva, K.D.M., Landim, A.V., Lôbo, R.N.B., 2017. Genetic evaluation is possible on community pastoral small ruminant flocks in the presence of multiple sires and uncertain of paternity. Small Ruminant Res. 151, 72–81.
Cassell, B.G., Adamec, V., Pearson, R.E., 2003. Effect of incomplete pedigrees on estimates of inbreeding and inbreeding depression for days to first service and summit milk yield in Holsteins and Jerseys. J. Dairy Sci. 86, 2967–2976.
Dodenhoff, J., Van Vleck, L.D., Gregory, K.E., 1999. Estimation of direct, maternal, and grand maternal genetic effects for weaning weight in several breeds of beef cattle. J. Anim. Sci. 77, 840–845.
Dong, M.C., Van Vleck, L.D., Wiggans, G.R., 1988. Effect of relationships on estimation of variance components with an animal model and restricted maximum likelihood. J. Dairy Sci. 71, 3047–3052.
Eler, J.P., Ferraz, J.B.S., Golden, B.L., Pereira, E., 2000. Influence of Sire×Herd interaction on the estimation of correlation between direct and maternal genetic effects in Nellore cattle. Braz. J. Anim. Sci. 29, 1642–1648.
Falconer, D.S., 1989. Introduction to Quantitative Genetics, third ed. Longman Scientific and Technical, UK, p. 438.
Garant, D., Kruuk, L.E.B., 2005. How to use molecular marker data to measure evolutionary parameters in wild populations. Mol. Ecol. 14, 1843–1859.
Gómez, M., Gama, L.T., León, J.M., Fernández, J., Attalla, S.A., Delgado, J.V., 2016. Genetic parameters for harmony and gaits in hispano-arabe horses estimated by bayesian methods and RestrictedMaximum Likelihood. Livest. Sci. 188, 159–165.
Gómez, M., Rossi, D., Cimmino, R., Zullo, G., Gombia, Y., Altieri, D., Di Palo, R., Biffani, S., 2021. Accounting for genetic differences among unknown parents in Bubalus bubalis: a case study from the Italian Mediterranean Buffalo. Front. Genet. 12, 625335.
Gowane, G.R., Prince, L.L.L., Lopes, F.B., Paswan, C., Sharma, R.C., 2015. Genetic and phenotypic parameter estimates of liveweight and daily gain traits in Malpura sheep using Bayesian approach. Small Rumin. Res. 128, 10–18.
Henderson, C.R., 1973. Sire evaluation and genetic trends. J. Anim. Sci. 1973, 10–41.
Heydarpour, M., Schaeffer, L.R., Yazdi, M.H., 2008. Influence of population structure on estimates of direct and maternal parameters. J. Anim. Breed. Genet. 125, 89–99.
Kennedy, B.W., Schaeffer, L.R., Sorensen, D.A., 1988. Genetic properties of animal models. J. Dairy Sci. 71, 17–26.
Legarra, A., Christensen, O.F., Vitezica, Z.G., Aguilar, I., Misztal, I., 2015. Ancestral relationships using metafounders: finite ancestral populations and across population relationships. Genetics 200, 455–468.
Macedo, F.L., Christensen, O.F., Astruc, J.-M., Aguilar, I., Masuda, Y., Legarra, A., 2020. Bias and accuracy of dairy sheep evaluations using BLUP and SSGBLUP with metafounders and unknown parent groups. Genet. Sel. Evol. 52, 47.
Mandal, A., Neser, F.W.C., Rout, P.K., Roy, R., Notter, D.R., 2006. Estimation of direct and maternal (co)variance components for pre-weaning growth traits in Muzaffarnagri sheep. Livest. Prod. Sci. 99, 79–89.
Maniatis, N., Pollott, G.E., 2002. Maternal effects on weight and ultrasonically measured traits of lambs in a small closed Suffolk flock. Small Rumin. Res. 45, 235–246.
Meyer, K., 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. Livest. Prod. Sci. 31, 179–204.
Meyer, K., 1997. Estimates of genetic parameters for weaning weight of beef cattle accounting for direct–maternal environmental covariances. Livest. Prod. Sci. 52, 187–199.
Misztal, I., Lourenco, D., Legarra, A., 2020. Current status of genomic evaluation. J. Anim. Sci. 98, skaa101.
Misztal, I., Vitezica, Z.G., Legarra, A., Aguilar, I., Swan, A.A., 2013. Unknown-parent groups in single-step genomic evaluation. J. Anim. Breed. Genet. 130, 252–258.
Mrode, R.A., 2014. Linear Models for the Prediction of Animal Breeding Values, third edition. CAB International Wallingford Oxfordshire OX10 8DE UK, ISBN-13: 978-1845939816.
Pemberton, J.M., 2008. Wild pedigrees: the way forward. Proc. R. Soc. B 275, 613–621.
Peškovičová, D., Groeneveld, E., Wolf, J., 2004. Effect of genetic groups on the efficiency of selection in pigs. Livest. Prod. Sci. 88, 213–222.
Petrini, J., Pertile, S.F.N., Eler, J.P., Ferraz, J.B.S., Mattos, E.C., Figueiredo, L.G.G., Mourão, G.B., 2015. Genetic grouping strategies in selection efficiency of composite beef cattle (Bos taurus x Bos indicus). J. Anim. Sci. 93, 541–552.
Pieramati, C, Van Vleck, L.D., 1993. Effect of genetic groups on estimates of additive genetic variance. J. Anim. Sci 71, 66–70.
Postma, E., 2006. Implications of the difference between true and predicted breeding values for the study of natural selection and micro-evolution. J. Evol. Biol. 19, 309–320.
Quaas, R.L., 1988. Additive genetic model with groups and relationships. J. Dairy Sci. 71, 1338–1345.
Robinson, D.L., 1996. Models which might explain correlations between direct and maternal genetic effects. Livest. Prod. Sci. 45, 111–122.
Raoul, J, Palhière, I., Astruc, J.M., Elsen, J.M., 2016. Genetic and economic effects of the increase in female paternal filiations by parentage assignment in sheep and goat breeding programs. J. Anim. Sci. 94, 3663–3683.
Robinson, G.K., 1986. Group effects and computing strategies for models for estimating breeding values. J. Dairy Sci. 69, 3106–3111.
Rodriguez, M.C., Toro, M., Silió, L., 1996. Selection on lean growth in a nucleus of Landrace pigs: an analysis using Gibbs sampling. Anim. Sci. 63, 243–253.
Roff, D.A., 2002. Life History Evolution. Sinauer Associates, Sunderland, MA, USA.
Safari, E., Fogarty, N.M., Gilmour, A.R., 2005. A review of genetic parameter estimates for wool, growth, meat and reproduction traits in sheep. Live. Prod. Sci. 92, 271–289.
Santana, M.L., Eler, J.P., Ferraz, J.B.S., 2013. Alternative contemporary group structure to maximize the use of field records: application to growth traits of composite beef cattle. Livest. Sci. 157, 20–27.
Shiotsuki, L., Cardoso, F.F., Silva, J.A., Albuquerque, L.G., 2013. Comparison of a genetic group and unknown paternity models for growth traits in Nellore cattle. J. Anim. Sci. 91, 5135–5143.
Speed, D., Balding, D.J., 2015. Relatedness in the post-genomic era: is it still useful? Nat. Rev. Genet. 16, 33–44.
Sullivan, P.G., 1995. Alternatives for genetic evaluation with uncertain parentage. Can. J. Anim. Sci. 75, 31–36.
Theron, H., Kanfer, F., Rautenbach, L., 2002. The effect of phantom parent groups on genetic trend estimation. S. Afr. J. Anim. Sci. 32, 130–135.
Tosh, J.J., Kemp, R.A., 1994. Estimation of variance components for lamb weights in three sheep populations. J. Anim. Sci. 72, 1184–1190.
Vallecillos, A., María-Dolores, E., Villa, J., Rueda, F.M., Carrillo, J., Ramis, G., Soula, M., Afonso, J.M., Armero, E., 2022. Development of the first microsatellite multiplex PCR Panel for Meagre (*Argyrosomus regius*), a commercial aquaculture species. Fishes 7, 117.
Vergara, O.D., Ceron-Muñoz, M.F., Arboleda, E.M., Orozco, Y., Ossa, G.A., 2009. Direct genetic, maternal genetic, and heterozygosity effects on weaning weight in a Colombian multibreed beef cattle population. J. Anim. Sci. 87, 516–521.
Westell, R.A., Quaas, R.L., Van Vleck, L.D., 1988. Genetic groups in an animal model. J. Dairy Sci. 71, 1310–1318.
Wolak, M.E., Reid, J.M., 2017. Accounting for genetic differences among unknown parents in microevolutionary studies: how to include genetic groups in quantitative genetic animal models. J. Anim. Ecol. 86, 7–20.
Zishiri, O.T., Cloete, S.W.P., Olivier, J.J., Dzama, K., 2014. Genetic parameters for live weight traits in South African terminal sire sheep breeds. Small Rumin. Res. 116, 118–125.