Research Article

Estimation of genetic parameters for weaning weight of Awassi lambs by using classical and Bayesian methods

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Abstract: The aim of this study was to estimate variance components and genetic parameters with six different animal models and two approaches (Bayesian and classical) on weaning weight (WW) of Awassi lambs. For this purpose, the data were obtained from Sheep and Goat Breeders' Associations of Osmaniye in Turkey. The data of 4971 progenies (from 80 rams and 1917 ewes) born between 2012 and 2016 raised under traditional conditions were evaluated. Year/season, sex, birth type, dam age, and flock size were fixed effects. All these effects except birth type were found statistically significant (P < 0.01). The overall least squares mean of weaning weight (WW) was obtained as 17.93 ± 0.05 kg. Variance components and genetic parameters were estimated by MCMC algorithms with R (for Bayesian approach) and by REML procedure with MTDFREML (for classical approach) programs. The Akaike information criterion (AIC), the log likelihood function (-2logL), and deviance information criterion (DIC) values were taken as criteria to choose the best model. Direct heritabilities of WW ranged from 0.20 to 0.35 across the models. The genetic correlation between additive genetic effect and maternal effect ranged from 0.00 to 1.00. The results were found similar across methodologies and maternal additive genetic variance resulted in lower than direct additive genetic variance. According to this study, both approaches are suitable for estimation of genetic parameters in the case of low sample size. However, the Bayesian approach, becoming increasingly popular, may be feasible to estimate variance-covariance components and genetic parameters.

Key words: Heritability, variance components, REML, MCMC

1. Introduction
Variance sources are the basis for organization of progeny testing, calculation of genetic-environment interaction, construction of selection index, calculation of mixed model BLUP, estimation of phenotype-environment correlation, planning of improvement program with identified genetic structure in quantitative characters, estimation of variance components, and estimation of accurate breeding value [1,2]. Accuracy of estimation of variance components depends on factors that include observations, statistical model used, and method [3]. Therefore, many researchers have tried to improve different methods for estimation of variance components [4–9].

ANOVA, ML, and REML are the most used methods for estimation of genetic variance [10]. These methods have been called classical approaches (frequentist, Berkeley methods) and are based on normality assumption. However, the existence of threshold traits and the observation of binary data in animal breeding violates the rule of normality assumption [11,12]. Therefore, the Bayesian approach, another alternative method to overcome this

concern, has been developed and this approach that does not require normality can be alternatively used to estimate variance components by using posterior distribution in discrete and continuous distributed traits [13–16]. In this respect, the Bayesian approach has more advantages than the classical approach in practice [17]. At the same time, no negative variance can be estimated under the Bayesian approach [18]. In the genetic evaluation of animals, the use of the MCMC algorithm in Bayesian approach has been a good option and this approach has been reducing bias in the estimations even when the dataset is too small [19]. At the same time, the Bayesian approach is statistically more flexible for estimations of variance components than the REML procedure [15]. In addition, some researchers have suggested that the use of the MCMC algorithm in the Bayesian approach is more feasible although it is computationally more expensive [20,21]. However, with the developed computer technology, various programs such as MTGSAM [22], GIBANAL [23], MCMCglmm [24], and FlexQTLs [25,26] have increased the popularity of the Bayesian approach. Under the National Small

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Ruminant Improvement Project under Farmer Conditions carried out in Turkey, the live weights of Awassi lambs were collected. However, no important steps were taken in order to evaluate these records accurately to estimate parameters that would be the basis for ongoing selection programs. In the literature, there are many studies using the REML method to estimate genetic parameters of different breeds [27–32]. However, some researchers used different animal models under the Bayesian approach in small ruminant animals [18,19]. Therefore, in this study, we aimed to estimate genetic parameters of the weaning weight of Awassi lambs by using 6 different animal models with both the classical approach (REML algorithm) and Bayesian approach (MCMC algorithms).

2. Materials and methods

2.1. Data

The data and pedigree information of Awassi sheep raised in traditional conditions in Sheep and Goat Breeders' Associations of Osmaniye within the subproject of the General Directorate of Agricultural Research and Policies (TAGEM) were used. For this purpose, records of weaning weight (WW) were analyzed. The sheep were kept in the sheep fold during the winter and were fed cotton seed meal, peanut straw, and dry grass straw. During the spring period, animals were moved to pasture or plateau and grazed without additional feeding. Each breeder put his own rams into the flock in order to mate randomly after mid-June. The rams were joined to the flock for 2 months, then left the flock for two weeks and then rejoined the flock for mating for another two weeks. The lambing season started in early October and lasted until the end of February. The lambs were kept with their dams for up to 45 days after birth and were completely weaned after 2–2.5 months. Within the first 24 h after birth, the lambs were weighed with digital hand weighing scales (up to 10 g sensitivity). When the lambs reached an average age of 1 month they were fed with starter feeds. Weaning weights were recorded when the age of the lambs was about 60 ± 2 days.

2.2. Statistical methods

The records of weaning weight of 4971 lambs born between the years of 2012 and 2016 from 80 rams and 1917 ewes were used. Year/season, birth type, sex, age, and flock size were used as fixed effects. Since each flock usually used its own rams, when the data were classified according to the farms, the genetic variance among the sires were also dispersed within the farms. To prevent this confounding effect, the farms according to flock sizes (the number of sheep raised) were classified as n < 400 (1), 401 < n < 500 (2), or n > 501 (3). Birth weight of the lamb was included as a covariate in all models. The GLM procedure of SAS was conducted under the following model:

$$Y_{ijklmn} = \text{m} + a_i + b_j + c_k + d_l + t_m + \beta (X_{ijklmn} - \bar{X}) e_{ijklmn}$$

Here, Y_{ijklmn} is the weaning weight; μ is population mean; a_i is the effect of year/season (2012 - 2013, 2013 - 2014, 2014 - 2015, 2015 - 2016); b_j is the effect of birth (single or twin); c_k is the effect of sex of lamb (male or female); d is the effect of age of dam (1, 2, 3, …, 6 years); t_m is the effect of flock size (n < 400 (1), 401 < n < 500 (2), n > 501 (3)); β is the partial regression coefficient of weaning weight on birth weight; X_{ijklmn} is the birth weight of the nth lamb born in the ith season of jth birth type, kth sex, dth age of dam, and mth flock size; $\bar{x}$ is mean of birth weight; and e_{ijklmn} is the random residual. All interactions between fixed effects were found nonsignificant in initial analyses and hence they were ignored.

The direct additive genetic effect, additive maternal effect, maternal permanent environmental effect, and residual were fitted in all the models as random effects.

(Co)variance components and genetic parameters were estimated for weaning weight (WW) by using univariate animal models. These models were fitted for WW using the REML procedure in the classical approach and MCMC procedure in the Bayesian approach. In the matrix notations the univariate mixed linear models used were:

Model 1 $Y = Xb + Zd + e$
Model 2 $Y = Xb + Zd + Zm + e$ $Cov(a,m) = A\sigma_{dm}$
Model 3 $Y = Xb + Zd + Zm + e$ $Cov(a,m) = 0$
Model 4 $Y = Xb + Zd + W c + e$
Model 5 $Y = Xb + Zd + Zm + Wc + e$ $Cov(a,m) = A\sigma_{dm}$
Model 6 $Y = Xb + Zd + Zm + Wc + e$ $Cov(a,m) = 0$

Here, Y is the vector of WW. b is the vector of fixed effects (year/season, type of birth, sex, dam's age, and flock size). $d \sim N (0, A\sigma^2_d)$, $m \sim N (0, A\sigma^2_m)$, $c \sim N (0, I\sigma^2_c)$, and $e \sim N (0, I\sigma^2_e)$ are direct additive genetic effects (animal), maternal genetic effects, and maternal permanent environmental and error vectors, respectively. X, Z_d, Z_m, and W_c are the corresponding incidence matrices relating the effects with y. A is the numerator relationship matrix among animals, and σ_{dm} is the additive genetic covariance between the additive genetic effects and maternal genetic effects.

The following was assumed:

$Var (d) = A\sigma^2_d$; $Var (m) = A\sigma^2_m$; $Var (c) = I_d\sigma^2_c$; $Var (e) = I_n\sigma^2_e$; $Cov (d,m) = A\sigma_{dm}$

Here, σ^2_d is the direct additive genetic variance, σ^2_m is the maternal additive genetic variance, σ_{dm} is the direct-maternal additive genetic covariance, σ^2_c is the maternal permanent environmental variance, σ^2_e is the random residual variance, and I_d and I_n are the identity matrices of an order equal to the number of dams and records, respectively [32]. The total heritability (h^2_t), the ratio of the maternal permanent environmental variance on the phenotypic variance (c^2), and the ratio of covariance

between direct additive genetic effects and maternal effects on the phenotype (c_{am}) were calculated according to [33]:

$$h^2_t = [(\sigma^2_d + 0.5\sigma^2_m + 1.5\sigma_{dm})] / (\sigma^2_p)$$

$$c^2 = (\sigma^2_{pe} / \sigma^2_p); c_{dm} = (\sigma_{dm} / \sigma_p)$$

According to the REML procedure, if the value of -2Log likelihood variance in a simplex function is less than 10^{-9}, it is accepted that convergence has been reached. The most suitable model for WW was chosen based on Akaike's information criterion (AIC) [34]:

$$AIC_i = -2logL_i + 2p_i$$

Here, log L_i represents the maximized log likelihood, and p_i is the number of parameters obtained for each model. The model with the lowest AIC was accepted as the model best fitting the records of WW [9].

In the Bayesian approach, an improper flat prior uniform distribution was assigned to **b: P(b) ~ constant**, due to lack of prior knowledge about the vector of fixed effects.

In the MCMC algorithm, the inverse Wishart distribution was used as a prior distribution for variance and co(variance) components (genetic, residual, and permanent environmental effects) and REML estimations were taken as initial values in all univariate animal models [20]. To control the sampling process, three important parameters should be considered: **nitt**, the total number of iterations; **burn-in**, which is the number of iterations initially dropped; and **thinning interval**, which is the number of iterations discarded. A single chain was used and 250,000–350,000 nitt were produced. Initial discard (burn-in period) and thinning interval were set to 100,000 and 1, respectively. De Villemereuil [35] reported that greater numbers of iterations in theory cause greater effective sample size and more reliable estimates. The Heidelberg test was used to control the convergence that existed in the CODA library (Convergence Diagnosis and Output Analysis) in R software [36]. If the P value is higher than 0.05, convergence is monitored [24]. The deviance information criterion (DIC) offered in the MCMC package was used to compare models [24]. If the DIC value is the smallest and the difference among the models is higher than 7, this model fits best [37].

3. Results and discussion

The weaning weight of Awassi lambs was found to be 17.93 ± 0.05 kg. All fixed effects (year/birth season, sex, dam age, and flock size) except birth type were found to be highly significant (P < 0.01).

The (co)variance components and genetic parameter estimates obtained with single-trait animal models using the REML procedure for weaning weight (WW) in Awassi lambs are shown in Table 1.

The direct heritability of WW varied from 0.20 to 0.35 across models. Model 5, which provided the highest phenotypic variance, has the lowest estimate (0.20) of direct heritability. Phenotypic variance estimates were similar in Models 1, 3, and 4, and the direct heritability obtained under these models provided the same value of 0.35. All the models estimated null or almost null (0.01) maternal genetic variance. The highest genetic direct-maternal covariance was obtained under Model 2. On the other hand, the highest maternal genetic variance was estimated under Model 5. Maternal permanent variance was fitted in Models 4, 5, and 6, and it was always estimated close to zero. As a result, c^2 ($\sigma^2_{pe} / \sigma^2_p$), which is the ratio of the variance of the maternal permanent environmental effect over the phenotypic variance, was negligible. The highest value for the total heritability was seen in Model 1, while the lowest value was found under Model 5. In general, when the estimations of variance components and genetic parameters are examined, Models 1 and 3 are very close to each other. In these six different univariate animal models, genetic correlations between additive genetic effect and maternal genetic effect were between 0.00 and 1.00.

A significant estimate of the direct-maternal genetic covariance was found under Models 2 and 5, jointly with an increase of the residual variance. In addition, the extreme estimated direct-maternal genetic correlation of 1.00 suggests that both genetic effects were confounded. Therefore, the existence of this correlation decreased the direct heritability estimates due to confounding genetic variance with the residual variance. Model 1 was determined as the best fitting according to the AIC criterion, suggesting that the available information is insufficient to fit complex models.

The results for the six different models on the same trait of the same population under a Bayesian approach are given in Table 2.

For the weaning weight, the heritability estimates were the highest in Model 5, while similar results were obtained from the other models. It is underlined that only the values of highest posterior density (HPD) of additive genetic effect are seen in the region higher than zero in all the models. Hossein-Zadeh and Ardalan [38] supported the view that if HPD is zero, related parameters are unimportant. The confidence intervals for additive genetic variances were above zero in all the models, suggesting that additive genetic effects may be important criteria in selection. In general, when the estimation of maternal heritability of the WW was examined, the lowest estimation values were obtained in Model 2. Both the low estimates of the ratio of maternal permanent environmental effects and the low confidence intervals of these effects in all models have revealed the negligible effects on selection. Genetic correlations between additive genetic effect and maternal effect for WW were negative and lower, almost zero, in Models 2 and 5. This is an indication of antagonism between the

Table 1. Variance components and genetic parameters of weaning weights of Awassi lambs estimated by REML.

(Co)variance components and parameters	Model 1 $Y = Xb + Za + e$	Model 2 $Y = Xb + Za + Wm + e$ cov (am) ≠ 0	Model 3 $Y = Xb + Za + Wm + e$ cov (am) = 0	Model 4 $Y = Xb + Za + Wc + e$	Model 5 $Y = Xb + Za + Wm + Wc + e$ cov (am) ≠ 0	Model 6 $Y = Xb + Za + Wm + Wc + e$ cov (am) = 0
σ^2_a	1.00602	0.59482	1.00672	1.00557	0.62103	0.94941
σ^2_{am}	-	0.09565	-	-	0.02024	0.00000
σ^2_m	-	0.01538	0.00000	-	0.00066	0.03957
σ^2_{pe}	-	-	-	0.310170E-07	0.447393E-07	0.105650E-06
σ^2_e	1.86662	2.08431	1.86625	1.86679	2.45828	1.85590
σ^2_{dp}	2.87264	2.79016	2.87297	2.87237	3.10022	2.84488
$h^2_d\ (\sigma^2_a / \sigma^2_p)$	0.35 ± 0.03	0.21 ± 0.02	0.35 ± 0.03	0.35 ± 0.03	0.20 ± 0.02	0.33 ± 0.03
$m^2\ (\sigma^2_m / \sigma^2_p)$	-	0.01 ± 0.01	0.00 ± 0.00	-	0.00 ± 0.01	0.01 ± 0.02
$c^2\ (\sigma^2_{pe} / \sigma^2_p)$	-	-	-	0.11E-07 ± 0.02	0.14E-07 ± 0.03	0.37E-07 ± 0.03
$c_{am}\ (\sigma^2_{am} / \sigma^2_p)$	-	-	-	-		
r_{am}	-	1.00	-	-	1.00	0.00
$h^2_t\ ((\sigma^2_a + 0{,}5\,\sigma^2_m + 1{,}5\,\sigma^2_{am}) / \sigma^2_p)$	0.35 ± 0.03	0.28 ± 0.01	0.35 ± 0.01	0.35 ± 0.03	0.21 ± 0.02	0.33 ± 0.02
e^2	0.65 ± 0.03	0.75 ± 0.02	0.65 ± 0.03	0.65 ± 0.03	0.79 ± 0.02	0.65 ± 0.03
$-2LogL$	9886.094	9959.226	9886.094	9886.094	9957.959	9893.875
AIC	9900.094	9975.226	9902.094	9902.094	9975.959	9911.875

σ^2_a: direct additive genetic variance; σ_{am}: direct–maternal additive genetic covariance; σ^2_m: maternal additive genetic variance; σ^2_{pe}: maternal permanent environmental variance; σ^2_e: residual variance; σ^2_p: phenotypic variance; h^2_d: direct heritability; m^2: maternal heritability; c^2: ratio of maternal permanent environmental variance in phenotypic variance; c_{am}: ratio of covariance; r_{am}: genetic correlation between additive and maternal genetic effect; h_t: total heritability; e^2: ratio of environment in phenotypic variance; $-2LogL$: likelihood value; AIC: Akaike information criterion.

Table 2. Variance components and genetic parameters of weaning weights of Awassi lambs estimated by MCMC.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
	$Y = Xb + Za + e$	$Y = Xb + Za + Wm + e\ cov\ (am) \neq 0$	$Y = Xb + Za + Wm + e\ cov\ (am) = 0$	$Y = Xb + Za + Wc + e$	$Y = Xb + Za + Wm + Wc + e\ cov\ (am) \neq 0$	$Y = Xb + Za + Wm + Wc + e\ cov\ (am) = 0$
Posterior mod h^2_a	0.351	0.345	0.340	0.354	0.381	0.347
Posterior mean h^2_a	0.356	0.350	0.342	0.351	0.3850	0.346
HPD (a)	0.292–0.418	0.296–0.406	0.281–0.404	0.290–0.413	0.320–0.451	0.283–0.408
Posterior mod h^2_m	-	2.558766e-05	0.024	-	0.001	0.022
Posterior mean h^2_m	-	0.000	0.026	-	0.003	0.024
HPD (m)	-	1.254884e-15 to 0.002	0.017–0.037	-	0.000–0.006	0.015–0.034
Posterior mod h^2_{per}	-	-	-	0.025	0.001	0.022
Posterior mean h^2_{per}	-	-	-	0.027	0.003	0.024
HPD (per)	-	-	-	0.017–0.038	0.000–0.006	0.015–0.033
r_{am} mod	-	-2.352188e-06	-	-	-0.0003236939	-
r_{am} mean	-	-0.0003	-	-	-0.0003454861	-
σ_{am}	-	-7.013374e-07	-	-	-2.976417e-05	-
DIC	19,467.15	18,596.5	19,483.81	19,484.13	19,444.58	19,502.74

Posterior mod h^2_a: posterior mode of heritability of additive genetic effects; *Posterior mean h^2_a:* posterior mean of heritability of additive genetic effects; *HPD (a):* highest posterior intervals at 95 % for heritability of additive genetic effects; *Posterior mod h^2_m:* posterior mode of heritability of maternal effects; *Posterior mean h^2_m:* posterior mean of heritability of maternal effects; *HPD (m):* highest posterior intervals at 95 % for heritability of maternal effects; *Posterior mod h^2_{per}:* posterior mode of heritability of maternal permanent environment effects; *Posterior mean h^2_{per}:* posterior mean of heritability of maternal permanent environment effects; *HPD (per):* highest posterior intervals at 95 % for heritability of maternal permanent environment effects; σ_{am}: covariance between additive genetic and maternal effects; r_{am}: genetic correlation between additive genetic and maternal effects; *DIC:* Deviance information criterion.

additive genetic effect and the maternal effect. Barbosa et al. [19] reported that the antagonist relationships between additive genetic effects and maternal genetic effects may be due to natural selection. Some researchers reported that, if maternal effects were not included in the model, they increased the estimations of additive genetic effects and, as a result, increased the value of heritability and decreased the efficiency of selection [9,39–41].

According to the DIC values used as the model comparison criterion in MCMC algorithms, Model 2 was the best model and the results obtained from Model 2 were very similar to Model 1. However, in Model 2 the heritability of the maternal effect can be considered zero, and Model 1 shows similar results with fewer parameters, so Model 1 may be the most practical model.

The number of related animals in this study was 107, and therefore there was little inbreeding in the whole population, which was computed as an average of 0.00328. The low rate of inbreeding, lower rate of dams with records in the population, and low number of progeny records per dam directly affected variance-covariance components and genetic parameter estimates. With this data structure, the results obtained from both methodologies (REML and MCMC) showed that the estimated genetic variances of the maternal effects were minimal. As a result, the maternal heritability was also very low. The same case was valid for the variance of maternal permanent environmental effect. Therefore, it was concluded that maternal effects were not an important part of variance in this study or at least the data structure used was not suitable in Awassi lambs.

It has been emphasized in the literature that the impact of data structure was important in the estimation of variance-covariance components and genetic parameters in maternal models [9,42,43]. Gerstmayr [43] examined the change of maternal effects on simulated data and reported that maternal effects depend on the number of offspring per dam, the number of dams with records, and the number of generations. In this report, it was stated that if there were no dams with records, the genetic covariance could only be estimated by using the relationships between offspring, and the maternal heritability increased as the number of offspring records per dam increased. The low estimate obtained in our study could be due to the low number of dams and the low number of offspring per dam as reported by Gerstmayr [43]. Maniatis and Pollott [44] emphasized that pedigree information plays an important role in determining the maternal effects and essentially reported that the proportion of dams with records in the population should be high. Some researchers stated that the separation of maternal genetic and maternal permanent environmental variances depended on the existence of repeated yield records [43,44]. Therefore, close relationships between generations and relationships

due to dams are needed to estimate maternal effects. In the present study, low genetic relationships are consistent with the results of the Maniatis and Pollott [44]. As a result, the findings obtained from heritability estimations from both REML and Bayesian methodologies under Model 1 (simple animal model, $Y = Xb + Za + e$) were the same, and accordingly, the heritability of the weaning weight was moderate to high (0.35). Since maternal genetic and environmental variances in the models with maternal effects were negligible, the estimates of total heritability (h^2_t) were not changed and were similar to direct heritability estimations (h^2_a).

Okut et al. [45] obtained values ranging from –0.99 to 0.99 for direct-maternal genetic correlation in their study. However, Synman et al. [46] in Merino lambs and Assan et al. [47] in Sabi lambs found a direct-maternal genetic correlation of 1.00, which was similar to our study (Models 2 and 5).

In this study, the value of direct heritability of WW was 0.35, which is higher than the values of Aguirre et al. [48] in the Santa Ines (0.20), Hammoud and Salem [49] in the Barki (0.012) and in Rahmani (0.139), Kumar et al. [50] in Nellore (0.03), Mallick et al. [51] in Bharat Merino lamb (0.16), Jawasreh et al. [27] in Awassi (0.19), and Tariq et al. [28] in Mengali sheep (0.125); it is similar to the results of Kariuki et al. [52] in Dorper (0.28), Aksoy et al. [29] in Karayaka (0.27), Hassen et al. [30] in Awassi sheep in Ethiopia (0.33), Gamasaee et al. [53] in Mehraban (0.30), El-Wakil and Gad [31] in Barki (0.30), and Hassen et al. [30] in Nation (0.31); and it is lower than the values of El-Awady et al. [54] in Rahmani (0.42) via Reml. In addition, the direct heritability of WW was estimated by Nassiri et al. [55] in Zandi lambs (0.169), Barbosa et al. [19] in Santa Ines (0.09), and Gowane et al. [18] in Malpura (0.40) using Bayesian methodology.

4. Conclusion
Maternal heritabilities and maternal permanent environmental effects close to zero as well as genetic correlations between direct and maternal effects also close to zero or 1.00, estimated with various statistical models, probably point to an inappropriate data structure. On the other hand, the simple models (Model 1 in both methods) provide relatively reliable estimates [29,30,52].

In the present study, when comparing Bayesian and REML approaches, both of the applied approaches performed identically for estimation of genetic parameters. Both methods indicated a high to moderate level of direct heritability of WW of Awassi lambs. It can be concluded that both approaches are suitable for estimation of genetic parameters in the case of low sample size.

On the other hand, Bayesian analysis was much slower than REML analysis concerning computation time in this

research, like in other studies [56,57]. In this study, when comparing Bayesian and REML approaches in terms of models, for direct heritability using Model 1 and Model 4, both approaches estimated similar values. However, in Model 2, the estimates of direct heritability from the Bayesian approach were higher than those from REML. In addition, the estimates of maternal heritability from the Bayesian approach were lower than estimates of maternal heritability from REML. As for Model 3, there was little difference between the two approaches for the estimates of direct heritability. In Model 5 and Model 6, the estimates of direct heritability from the Bayesian approach were higher than those from REML like in Model 2.

Besides, in the presence of a wide range of biological problems, the Bayesian approaches provide flexibility through posterior condition distribution, even when data do not fit normal distribution. Considering these advantages of the Bayesian approach, it can be preferred. The results obtained from the models with the Bayesian approach were compatible with the results of the models with the classical (Berkeley, frequentist) approach. In this respect, it may be feasible to estimate variance-covariance components and genetic parameters with the Bayesian approach, which is increasingly popular.

As a result, we can speculate that if estimation of genetic parameters were to be carried out on records obtained from different farms, more than about 250–300 dams should be kept in these farms. Repeated records of farms that include high numbers of animals can increase the reliability of the estimated parameters. Increasing the number of generations in flock, variance components, and genetic parameter estimations can provide more meaningful results. A pedigree based on several generations would also provide the genetic connection of the farms, which prevents the confounding of genetic and farm effects.

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