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Bayesian Inference of Variance Components for Litter Size in Rasa Aragonesa Sheep¹

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ABSTRACT: Variance components were estimated for litter size in Rasa Aragonesa sheep, a meat breed from northern Spain, to determine whether selective breeding for litter size is a reasonable strategy to improve reproductive performance. We assumed an animal mixed effect threshold model with a binary response variable. Marginal estimates of the genetic parameters were obtained in the underlying scale using Bayesian inference, implemented via the Gibbs sampling procedure and a data augmentation ap-

proach. Posterior marginal means of heritability and repeatability were .077 and .141, respectively. Moreover, the 95% highest marginal posterior density region of heritability ranged from .051 to .101. Therefore, we conclude that litter size is a trait that could be selected for in breeding programs. The effect of the loss of pedigree information, a common feature of sheep production, on the estimation of the genetic parameters was also studied using simulation. The results indicate that the lack of pedigree information has little effect on our estimates of heritability.

Key Words: Sheep, Litter Size, Threshold Models, Bayesian Theory, Genetic Parameters

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Introduction

Rasa Aragonesa is the most important meat sheep breed in the Aragón region of northeastern Spain, but its reproductive performance is poor (Valls, 1983). Successful breeding strategies are hindered by low sexual precocity and prolificacy and seasonal anestrus (Gabiña, 1989a). The major limitation seems to be litter size (**LS**, the number of lambs born per lambing). Gabiña (1989b) combined reproductive traits in a selection index and found that LS contributed 74 to 96% of the economic value of genetic progress. Thus, LS is an important component of selection programs.

Efficient selection programs rely on estimated genetic parameters of the traits involved (Fogarty et al., 1985). Statistical analysis of LS is complicated, because of its categorical nature, and methods based on approximations have produced biased estimates of variance components (Gianola, 1982; Gilmour et al., 1985; Hoeschele et al., 1987; Moreno, 1993; and Hoeschele and Tier, 1995). This drawback coupled

with the low heritability of LS (Lasley, 1987; Van Vleck et al., 1987) has resulted in a wide range of published parameter estimates, including negative values, and some workers have questioned the feasibility of improving litter size by selection (María, 1995). In addition, in mating systems in which ewes are mated to several males, valuable information from male pedigrees is lost. Males are usually unidentified, and AI techniques are inefficient. The lack of knowledge of genetic relationships can also lead to biased variance component estimates (Jackson, 1983; Dong et al., 1988).

Our objective was to estimate genetic variance for LS to decide whether a selective breeding strategy could improve reproductive performance in Rasa Aragonesa. We also used simulation methods to study the effect of the lack of pedigree information on estimates of variance components.

Material and Methods

Data Description

The data set (for descriptive statistics see Table 1) consisted of 58,493 parities of the Rasa Aragonesa ewes in 26 flocks from 1982 to 1995. These flocks have been monitored since 1978 and represent the semiextensive production of Rasa Aragonesa sheep in Aragón

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Table 1. Description of the Rasa Aragonesa data set

No. of records	58,493	
No. of sires	46	
No. of ewes	16,519	
No. of ewes with records	13,147	
No. of ewes with known sire	117	
No. of ewes with known dam	10,791	
Mean records per ewe	4.45	
Mean ewes per flock	506	
Mean records per flock	2,250	
Mean records per year-season	1,539	
Mean lambs born per litter	1.35	
Phenotypic standard deviation for no. of lambs born	.48	
Distribution of no. of lambs born live or dead, per ewe lambing, %		
One lamb	65.21	
Two lambs	33.81	
Three lambs	.98	
	No. of records	Lambs per litter
Age at parity		
< 3 yr	16,965	1.19
3 to 5 yr	19,712	1.39
5 to 7 yr	12,783	1.45
> 7 yr	9,033	1.41
Estrus synchronization		
With	7,295	1.60
Without	51,198	1.31

(ANGRA). Farms varied in habitat, semiarid to rich pastures (for complete description see Sierra, 1987), and in mating system. The most common mating system was three lambings every 2 yr (Gabiña, 1989a). In this system rams are kept with the ewes during three periods of the year (January–February, May–June, and September–October). Lambings were concentrated approximately 5 mo after each mating period. In some flocks, gonadotropin (PMSG) was provided and estrus was synchronized using intravaginal pessaries. Although this practice was rare, it is being used more frequently.

With respect to pedigree information, all female ancestors, but few males (.9%), were known. Therefore, as seen in Table 1, the pedigree file consisted of 13,147 ewes with records, 3,373 known female ancestors, and 46 rams with 117 daughters.

Reliable parameter estimates are not available for this breed, and no selection program has been applied in Aragón. In fact, genetic parameters for LS have only been estimated in a few experimental flocks of Rasa Aragonesa (Gabiña et al., 1983; and Gabiña, 1989b).

Model and Statistical Analysis

We assumed that our data set fit a probit threshold model with two categories (single vs multiple birth), which were analyzed with a Bayesian approach. The threshold model used (Wright, 1934) related the response observed in the categorical scale with an

underlying continuous normal variable. The relationship between the two scales is established by the thresholds. We defined only one threshold and obtained a response in the first category when the value of the underlying normal variable was lower than the threshold. The underlying variable was assumed to follow a normal distribution:

$$\mathbf{U}|\theta \sim N(\mathbf{W}\theta, \mathbf{I}\sigma_e^2)$$

where \mathbf{U} is the underlying variable vector of order r ; $\theta' = (\mathbf{T}', \mathbf{S}', \mathbf{H}', \mathbf{P}', \mathbf{a}', \mathbf{p}')$ is the parameter vector of order s with \mathbf{T} , \mathbf{S} , \mathbf{H} and \mathbf{P} defined, under a frequentist point of view, as fixed effects, and \mathbf{a} and \mathbf{p} as random effects; \mathbf{W} is a known incidence matrix of order r by s ; \mathbf{I} is an identity matrix of order r by r ; and σ_e^2 is the residual variance. More specifically, the following model is for the underlying variable:

$$U_{ijklmn} = T_i + S_j + H_k + P_l + a_m + p_m + e_{ijklmn}$$

where U_{ijklmn} is the value of the underlying variable for the n^{th} parity of the m^{th} ewe with l^{th} age at parity (P_l), which belongs to the k^{th} flock (H_k), obtained in the j^{th} year-season (S_j), with the i^{th} hormonal treatment (T_i).

Some justification of the model is required. The hormonal treatment factor (T_i) had two levels: estrus with and without treatment. It has been included due to the important influence hormones have on LS (see Table 1). In addition, the application of hormones in hormone-treated flocks was not always consistent; therefore, its effect cannot be explained by the flock factor. The year-season factor (S_j) had 38 levels, and its definition is determined by the mating system (described above). Thus, each year was divided into three periods (January–April, May–August, and September–December), which include the lambing time corresponding to the three mating periods. In this way, the S_j factor explains the joint variation due to season and year and their interaction. The flock factor (H_k) had 26 levels and was included to explain the great differences that exist among farms. The age at parity (P_l) had four levels (less than 3 yr, 3 to 5 yr, 5 to 7 yr, and more than 7 yr) and was included following the results of Marín et al. (1983). Its effect on LS is shown in Table 1. Finally, a_m and p_m are the breeding and the permanent environmental values of the m^{th} animal, and e_{ijklm} is the residual term.

From a Bayesian perspective, we assumed that prior distributions for the breeding and permanent environmental effects and the residuals followed multivariate normal distributions:

$$\begin{aligned} p(\mathbf{a}|\sigma_a^2) &\sim N(\mathbf{0}, \mathbf{A}\sigma_a^2) \\ p(\mathbf{p}|\sigma_p^2) &\sim N(\mathbf{0}, \mathbf{I}\sigma_p^2) \\ p(\mathbf{e}|\sigma_e^2) &\sim N(\mathbf{0}, \mathbf{I}\sigma_e^2) \end{aligned}$$

where \mathbf{A} is the numerator relationship matrix and σ_a^2 and σ_p^2 are the additive genetic and the permanent environmental variances, respectively. Because σ_e^2 is not estimable (Gianola and Foulley, 1983), an arbitrary value must be assigned. In this case, the residual variance was set at 80 square units. Proper uniform priors were defined for the fixed effects ($\mathbf{b}' = (\mathbf{T}', \mathbf{S}', \mathbf{H}', \mathbf{P}')$) and for σ_a^2 and σ_p^2 :

$$\begin{aligned} p(\mathbf{b}) &= U(-4\sigma_e, 4\sigma_e) \\ p(\sigma_a^2) &= U(0, 50) \\ p(\sigma_p^2) &= U(0, 50) \end{aligned}$$

After the parameters of the model have been defined, the linkage between both scales (categorical and continuous) can be established unequivocally. The contribution to the likelihood of one observation falling in the first category is proportional to

$$\begin{aligned} P(Y_v = 0 | t, \theta) \\ &= P(U_v < t | t, \theta) \\ &= \Phi((t - \mathbf{w}'_v \theta) / \sigma_e), \end{aligned}$$

where Y_v is the response variable for the v^{th} observation, taking values 0 or 1 if the observation belongs to the first or second category, respectively; t is the value of the threshold which, because it is not estimable, is set to an arbitrary value; U_v is the value of the underlying variable for the mentioned observation; $\Phi(\cdot)$ is the cumulative distribution function of a standardized normal variate; and \mathbf{w}'_v is a row incidence vector linking θ to the v^{th} observation. Because observations are conditionally independent given θ , likelihood is defined by the product of the contributions from each record.

According to Bayesian inference, the product of the prior distribution and the likelihood is proportional to the posterior distribution of θ , σ_a^2 , and σ_p^2 . Marginal posterior distributions of these parameters were here obtained using the Gibbs sampler (Geman and Geman, 1984; Gelfand and Smith, 1990). This method was chosen because it is not based on analytic approximations. To apply the Gibbs sampler, the conditional posterior distribution of each parameter of the model is required. In this case, in which a threshold model is assumed, some of these conditional distributions are not defined in closed form. This fact complicates the application of the procedure. Nevertheless, this inconvenience can be overcome if the continuous underlying variable (\mathbf{U}) is included as an unknown parameter in the model (Sorensen et al., 1995). This approach is known as data augmentation

(Tanner and Wong, 1987; Albert and Chib, 1993) and leads to the definition of simple conditional posterior distributions for all the parameters of the model. A detailed analysis and implementation of this method was performed by Sorensen et al. (1995).

In the present work, the Gibbs sampler ran via a data augmentation approach with a single chain of 350,000 points and the first 5,000 were discarded. This procedure allows for an accuracy of .1 with a significance level of 5% for additive genetic and permanent environmental components of variance, and .001 accuracy for heritability and the coefficient of permanent environmental variance (Raftery and Lewis, 1992).

Effect of the Loss of Pedigree Information on Variance Component Estimates

There is general agreement that the exclusion of pedigree information can lead to biased estimates of genetic variances, but there is still some controversy with respect to the type of bias (over- or underestimation). Jackson (1983), who studied the effect of ignoring full-sib relationships in estimates of heritability based on sire models (via an analysis of variance), clearly specified the conditions in which heritability overestimation is obtained. Dong et al. (1988), however, concluded that by ignoring genetic relationships, estimates of genetic variances based on restricted maximum likelihood (from an animal model) were biased downward. With the exception of simple designs (Jackson, 1983), it is unclear how to determine the magnitude and sign of the bias in estimates of parameters of genetic variance when a loss of pedigree information is detected. For this reason, we carried out a simulation study to ascertain whether our estimates were affected by this bias.

In this study, frequentist properties of estimators of genetic variance were studied in two cases. The first one (case I) mimics the mating policy and family structure of the Rasa Aragonesa breed. For the second case (case II), there was a large proportion of full-sib families. In both cases, estimates of the genetic parameters are obtained in two situations: using all the genealogical information (all the sires and ewes were identified), and under a situation in which the male pedigree information is assumed to be unknown. Case I provides the basis for drawing conclusions about the effect of the loss of genetic relationships on the estimation of the genetic parameters in the analyzed Rasa Aragonesa data set. In case II, wherein individuals are more related than in case I, we attempted to clarify the effect of the loss of genealogical information.

It is important to highlight that in both cases we simulated a population consisting of 3,090 animals (three non-overlapping generations with 1,000 ewes and 30 rams each generation) with four records per ewe. In the first case, animals were mated and

replacement occurred at random (like the mating system followed in the Rasa Aragonesa). These conditions produced a low degree of genetic relationship. In the second case, the second and third generations of the population were composed of 200 full-sib families of five ewes. In both cases, the records were randomly assigned to a fixed effect, which can be understood as a flock-year-season joint factor. Therefore, the simulation model was

$$U_{ijk} = F_i + a_j + p_j + e_{ijk}$$

where U_{ijk} is the k^{th} record of the j^{th} animal obtained in the i^{th} fixed level (a factor with 10 levels equally spaced in its prior domain), a_j and p_j are the breeding and the permanent environmental values of the j^{th} animal, respectively, and e_{ijk} is the residual effect. Proper prior distributions for the defined factors were exactly the same as those described in the previous section. Hence:

$$\begin{aligned} p(\mathbf{F}) &= U(-4\sigma_e, 4\sigma_e) \\ p(\sigma_a^2) &= U(0, 50) \\ p(\sigma_p^2) &= U(0, 50) \end{aligned}$$

The response observed in the categorical scale was a binary variable with an incidence of 35% (proportion of observations in the second category; i.e., parities with more than one lamb). Following a Bayesian perspective, marginal estimates of the parameters of the described model were obtained with a Gibbs sampler using a data augmentation approach. In this sense, to obtain the same accuracy as with the Rasa Aragonesa data set, a single chain of 11,000 points was generated, with the first 1,000 points discarded.

Parameter estimates for each situation (full vs incomplete pedigree information) in each case (case I and case II) were obtained from data generated

assuming different values of heritability and repeatability. Results of the simulation were all based on 20 replicates and the difference between situations contrasted with a two-tailed t -paired test (Steel and Torrie, 1985).

Results and Discussion

Effect of the Loss of Pedigree Information on Variance Component Estimates

Estimates of the mean of the marginal posterior distribution of heritability and repeatability obtained in several settings are shown in Tables 2 and 3. Table 2 corresponds to the results from the case that mimics the mating policy of the Rasa Aragonesa breed (case I). No statistically significant differences were found between the parameter estimates obtained with full or incomplete pedigree information. Furthermore, the posterior standard deviation of the estimates (**PSD**) is of the same order of magnitude. From these results, it seems reasonable to conclude that the loss of pedigree information has a negligible effect on inferences about genetic variances in the Rasa Aragonesa data set.

Results of case II, in which a population with stronger genetic relationship was generated, are shown in Table 3. We found significant differences between the heritability estimates of full vs incomplete pedigree information. No significant differences were found between the repeatability estimates. Results from this case show that heritability is overestimated when the pedigree is incomplete. Furthermore, the magnitude of PSD of all the parameter estimates was similar.

These results are clearly in agreement with the conclusions reached by Jackson (1983), who quantified the heritability overestimation obtained in a

Table 2. Results of estimation with full and incomplete pedigree information in simulated populations with random mating (case I). Means and standard deviations (PSD) of marginal posterior distribution of heritabilities (h^2) and repeatabilities (r) are shown (average of 20 replications)

Simulated			Estimates				P^a
			Full		Incomplete		
h^2	r		Mean	PSD	Mean	PSD	
.05	.10	h^2 :	.054	.016	.056	.011	.5423
		r :	.108	.015	.108	.015	.6181
	.15	h^2 :	.057	.018	.057	.018	.9418
		r :	.152	.019	.152	.017	.9030
.10	.15	h^2 :	.101	.023	.098	.025	.6150
		r :	.159	.018	.157	.018	.1215
	.20	h^2 :	.098	.017	.099	.020	.8313
		r :	.207	.012	.207	.013	.5294

^aProbability of two tailed t -paired test.

Table 3. Results of estimation with full and incomplete information in simulated populations with full-sib groups (case II). Means and standard deviations (PSD) of marginal posterior distribution of heritabilities (h^2) and repeatabilities (r) are shown (average of 20 replications)

Simulated		Estimates					
		Full		Incomplete		P^a	
h^2	r	Mean	PSD	Mean	PSD		
.05	.10	h^2 :	.053	.014	.063	.014	.0043
		r :	.101	.016	.101	.017	.7025
	.15	h^2 :	.052	.012	.067	.015	.0003
		r :	.147	.017	.147	.017	.4693
.10	.15	h^2 :	.094	.025	.107	.026	.0001
		r :	.157	.018	.157	.020	.7808
	.20	h^2 :	.104	.030	.120	.032	.0001
		r :	.203	.015	.202	.016	.2177

^aProbability of two tailed t -paired test.

progeny test case wherein dams were ignored. Heritability was estimated from the sire family variance component using an analysis of variance. Jackson showed that overestimation increased with the increment of the mean and the variance of the dam family size and the reduction of the sire family size. Moreover, he also stated that, in this situation, the variance of the estimated heritability can be equal or even smaller than that obtained by including dams in the model. Hence, it is expected that treating full-sib families as if they were half-sib families will generate a positive bias of heritability. This is precisely what was obtained in the analysis of this second simulated case when male pedigree information was assumed unknown.

Our results contradict the conclusions of Dong et al. (1988). These authors analyzed the effect of relationships on the estimation of variance components with an animal model using restricted maximum likelihood. They estimated the heritability of milk, fat, and protein yields from data sets of Holstein cows and concluded that a reduction in the amount of assumed relationships produces estimates of heritability that are biased downward. The contradictory conclusions of Jackson (1983) and Dong et al. (1988) may, however,

be due to the different structures of the populations analyzed. It would seem that more research is necessary to clarify the effect of the exclusion of pedigree information on the estimation of genetic parameters.

Estimation of Variance Components From the Rasa Aragonesa Data Set

Marginal posterior distributions of the additive genetic and permanent environmental variances, heritability, coefficient of permanent environmental variance, and repeatability are summarized in Table 4, in which the mean, mode, median, standard deviation, and the 95% highest posterior density region (**HPD95**) are shown. Means for heritability and repeatability were .077 and .141, respectively. It is important to note that the HPD95 of the heritability is defined between .051 and .101. Hence, the probability of obtaining a zero estimate for this parameter was almost null (the probability of obtaining a value lower than .04 is .0007). Consequently, the implementation of a selection breeding strategy using LS is a reasonable strategy to improve reproductive performance of the Rasa Aragonesa breed.

Table 4. Variance component estimates for litter size in Spanish Rasa Aragonesa sheep ($\sigma_e^2 = 80$)

Item	Mean \pm SD	Mode	Median	HPD95 ^a
σ_a^2	7.14 \pm 1.19	7.30	7.16	4.78 to 9.44
σ_p^2	5.94 \pm 1.24	5.60	5.88	3.64 to 8.49
h^2	.077 \pm .017	.079	.077	.051 to .101
c^2	.064 \pm .013	.061	.063	.039 to .091
r	.141 \pm .006	.140	.140	.128 to .153

^aHighest posterior density at 95%.

As mentioned in the Introduction, difficulties with the statistical analysis of a categorical trait such as LS have led to the implementation of approximate methods that have yielded a wide range of estimates (González, 1982, cited by Waldron and Thomas, 1992), reported values ranging from $-.15$ to $.35$). The full Bayesian approach used in conjunction with the Gibbs sampler, the method applied in our work, avoids the use of analytic approximations. This procedure produces a Monte Carlo estimate of the marginal posterior distribution of heritability, which provides for a rich inferential framework.

Implications

The results obtained in this work confirm that it is feasible to improve the reproductive performance of the Rasa Aragonesa breed of sheep from a selection breeding strategy on litter size. Loss of pedigree information, which is a common feature of the production of this meat breed, does not affect estimates of genetic parameters in the present data set. The proposed Gibbs sampling procedure is a useful technique for the study of litter size because it avoids the use of analytical approximations that can lead to distorted inferences.

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