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Research article

IMPACT OF MATERNAL EFFECTS ON RANKING OF ANIMAL MODELS IN GENETIC PARAMETER ESTIMATION FOR 18-MONTHS WEIGHT IN INDIGENOUS TULI CATTLE OF ZIMBABWE

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ABSTRACT: Maternal effects have been reported using different animal models for post weaning growth traits in some cattle breeds. Variance components for additive direct, additive maternal, permanent environmental maternal effects, the covariance between additive direct and maternal effects were estimated by restricted maximum likelihood, fitting five animal models from 2978 of 18 months (18MW) weight pedigree records of indigenous Tuli cattle of Zimbabwe. All investigated models included a random direct genetic effect, but different combinations of random maternal genetic and permanent environmental effects as well as for direct-maternal genetic covariance. The direct heritability (h^2_a) was constant (0.10) when the maternal genetic effects were included in the model, while (h^2_a) estimates were higher (0.22) and (0.63) when maternal effects were excluded. The maternal heritability (h^2_m) was (0.23) and higher than the direct heritability (0.10) when only maternal genetic effects were included in the model and did not change even when the permanent environmental effects of the dam was added. The permanent environmental effect of the dam was negligible and a strong positive correlation between direct and maternal genetic effects (σ^2_{am}) was observed. The strong positive genetic correlation between direct and maternal genetic effects would not limit the effective utilization of both direct and maternal effects in selection for 18MW growth in indigenous Tuli cattle. A simple animal model with additive direct genetic effects as the only random effect would be appropriate for genetic evaluation of 18MW in indigenous Tuli cattle.

Key words: Direct, Maternal, Animal Model, 18 Month Weight, Tuli Cattle

INTRODUCTION

In order to make fair animal model ranking for identification of genetic merit of individual animals need to develop an operational model closer to the biological one taking into account computational feasibility. Estimates of genetic parameters using different animal models and ranking them for 18MW in beef cattle breeds in Zimbabwe have never been studied. Animal models utilize all relationships available in a given data set. The search for a suitable statistical model is an important step in the development of genetic improvement schemes. Genetic models, including maternal effects and the covariance of direct and maternal genetic effects, fit data better than the simple additive model. Animal models used to analyze post weaning growth traits in beef cattle typically may not assume maternal effects. However, maternal effects on post weaning growth traits of beef cattle have been found in some cattle breeds [10, 2, 15]. Animal models in beef cattle may be complicated than in dairy cattle because of correlated direct and maternal effects [19].

There has been increased interest in accuracy of prediction of breeding values and ranking of animal models to determine their suitability in genetic evaluation [6]. Models used to conduct genetic evaluation need best describe the data and ultimate usefulness of predicted breeding values will be determined by the choice of a suitable model after ranking. [14, 16] reported that in literature the majority of estimates derived using animal models were from analyses of small data files or were from larger data sets with restricted amount of pedigree information. No studies have investigated the use of different animal models on genetic parameter estimates and ranking them for 18MW in indigenous cattle of Zimbabwe. Random regression models have been used in beef genetic evaluation [16] and have been complicated and extensively optimized in dairy [9]. Multiple trait models have also been used in genetic evaluation with growth traits defined at certain ages of animals (e.g. at birth, 205 d, and 305 d). The aim of this study was to investigate the effects of fitting different models including genetic, maternal and permanent environmental effects and choosing the appropriate model for post weaning growth in indigenous Tuli cattle of Zimbabwe.

Table 1 Summary statistics of 18MW data set in indigenous Tuli cattle of Zimbabwe

Item	Value
Records	2978
Base parents	1373
Animals	4351
Sires	125
Dams	1247
Mean(kg)	241.14
Standard Deviation (kg)	35.38
Coefficient of Variation (%)	12.99
Coefficient of Determination (%)	46

Table 2. Estimates of covariance components and genetic parameters for 18MW fitting different animal models in indigenous Tuli cattle of Zimbabwe

	Model				
Item	1	2	3	4	5
σ^2_a	688.40	83.34	219.50	98.82	90.52
σ^2_m		228.90		31.05	96.97
σ^2_{am}					80.91
σ^2_{pe}			0.68	0.12	0.16
σ^2_e	402.70	671.80	767.50	836.10	700.70
σ^2_p	1091.10	984.04	987.68	966.09	969.26
h^2_a	0.63	0.09	0.22	0.10	0.09
se	0.10	0.06	0.001	0.001	0.001
h^2_m		0.23		0.03	0.10
se		0.04		0.001	0.001
r_{am}					0.86
h^2_T	0.63	0.20	0.22	0.12	0.14

σ^2_a= additive direct variance, σ^2_m= additive maternal genetic variance, σ^2_{am}= direct-maternal additive variance, σ^2_{pe}= permanent environmental dam variance, σ^2_e= error variance, h^2_a= direct heritability, σ^2_p= phenotypic variance= sum of variance and covariance components, h^2_m= maternal heritability, h^2_T= Total heritability (total genetic effects), r_{am}= direct and maternal genetic correlation

MATERIALS AND METHODS

Study location

Matopos Research Station (20^0 23' S, 31^0 30' E) situated 30 km South West of Bulawayo in Zimbabwe. Altitude is low (800m) and the area experiences low erratic rainfall of less than 450 per annum.

Very high summer temperatures, maximum and minimum mean temperatures of hottest months are 21.6 ^{0} C and 11.4 ^{0} C, respectively with possibility of severe droughts. The most common type of vegetation is sweet veldt with comparatively high nutritional value of browse and annual grass species [25]. Managed well the rangelands should be able to meet the nutritional requirements of goats and other livestock. However, significant proportion of the rangeland are now degraded, resulting in low biomass and thus limited feed resource of poor quality particularly during the dry season give a detailed description of the climate and vegetation type, respectively. Herd history and management of the herd were described by [28].

Herd management

Animals were grazing on free range without provision of protein rich concentrate during the dry season. Routine cattle veterinary practices were followed. Cows were naturally bred and breeding season was limited to 90 days period from 1 January each year. Single sire herds comprised of one bull to 30 females were introduced to the breeding herd for mating when they had attained two years of age and bulls were seldom used for service until they were three years old. Calves were born between late September and early January. They were numbered by means of ear tag and were weighed and recorded within 18 hours of birth. At the same time both the calf number and that of the sire were recorded there after all calves weighed and weaned at an average age of 210 days.

Animal Models

The models vary in these components as well as in the assumptions that that are made about them. Genetic parameters were estimated using the Average Information Restricted Maximum Likelihood (AIREML) methodology [8] fitting different animal models. The analytical models included fixed effects of age of dam, sex of calf and year of birth. The five models fitted Model 1 was a simple animal model with additive direct genetic effects as the only random effect. Model 2 fitted in addition, the maternal effects as an uncorrelated random effect. Model 3 ignored maternal genetic effects and included permanent environmental effects as the second random effect. Model 4 considered both maternal and permanent environmental maternal effects as uncorrelated to the additive direct genetic effect. Model 5 considered maternal effects as the second random effect but allowed for covariance between the direct and maternal effects. The following models were used:

$$y=Xb + Z_a a + e \qquad (1)$$

$$y=Xb + Z_a a + Z_m m + e \qquad (2)$$

$$y=Xb + Z_a a + Z_c c + e \qquad (3)$$

$$y=Xb + Z_a a + Z_m m + Z_c c + e, \quad Cov(a, m)=0 \qquad (4)$$

$$y=Xb + Z_a a + Z_m m + Z_c c + e, \quad Cov(a, m)= A\sigma^2_{am} \qquad (5)$$

where: y is the vector of observations while b, a, m, c and e are the vectors of fixed effects, direct additive genetic effects (animal), maternal genetic effects, permanent environmental effects of dam and the residual, respectively. X, Z_a, Z_m and Z_c are incidence matrices of fixed effects, direct additive genetic effects, maternal additive genetic effects and permanent environmental effects of the dam. (Co)variances can be described as: $V(a)= A\sigma^2_{am}$, $V(m)= A\sigma^2_m$, $V(c)= \sigma^2_c I$, $V(e)= \sigma^2_e I$ and $Cov(a, m)= A\sigma_{am}$, where σ_{am} is the covariance between direct and maternal genetic effects, σ^2_a, the direct additive genetic variance, σ^2_m, the maternal additive genetic variance, σ^2_c, the variance of the permanent environmental effect of the dam, and σ^2_e, the variance of the residuals. A is the numerator additive genetic relationship matrix between animals, I the indentity matrix. Heritability of total additive genetic contribution to a maternally influenced trait was calculated according to the following equation below suggested by [26].

$$h_T^2 = \frac{\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am}^2}{\sigma_p^2}$$

The Likelihood Ratio Test

Different models were compared by using the Maximum Likelihood Ratio Test as follows. Let L_1 be the likelihood of the data with all the parameters unrestricted and maximum likelihood estimates substituted for these parameters, and L_0 be the maximum value of the likelihood when the parameters are restricted (and reduced in number) based on the assumption. Assume *k* parameters were lost (i.e., L_0 has *k* less parameters than L_1). Form the ratio $\lambda = \frac{L_0}{L_1}$. This ratio is always between 0 and 1 and the less likely the assumption is, the smaller λ will be. This can be quantified at a given confidence level as follows:

1. Calculate $\chi^2 = -2\ln\lambda$. The smaller λ is, the larger χ^2 will be.
2. We can tell when χ^2 is significantly large by comparing it to the upper 100 × (1-α) percentile point of a Chi Square distribution with *k* degrees of freedom. χ^2 has an approximate Chi-Square distribution with *k* degrees of freedom and the approximation is usually good, even for small sample sizes.
3. The likelihood ratio test computes χ^2 and rejects the assumption if χ^2 is larger than a Chi-Square percentile with *k* degrees of freedom, where the percentile corresponds to the confidence level chosen by the analyst.

RESULTS AND DISCUSSION

Means, standard deviation and characteristics of the data structure and covariance components are summarized in Table 1 and 2. It is evident that the relative values of direct heritability were influenced by the model used in the analysis (Table 2), which may emphasize the need of ranking of models for appropriateness in genetic evaluation of 18-mo weight. Estimates of direct heritability range from 0.09 to 0.63, in comparison model 1 where maternal effects were ignored direct heritability was biased upwards, while inclusion of maternal genetic effects in model 2 reduced direct heritability by 85%. Although in model 1 as compared with models 4 and 5 in which total variance attributed to maternal genetic effects were 3% and 8%, respectively, direct heritability dropped by almost 80%. In model 4 and 5 in which both genetic and environmental maternal effects were taken into account, the direct heritability were of the same magnitude with model 2 where permanent environmental maternal effects of the dam was assumed to be zero.

The estimates of direct heritability for 18-mo in the present study were high to low considering the different models studied. Lower estimates of direct heritability of (0.04) for 18-mo in Korean native cattle was reported by Lee et al. (1991). However, our estimates of direct heritability of 0.13 within the range reported elsewhere [4, 11, 13]. Literature estimates on 18-mo are scarce although [3] reported direct heritability of 0.29 for Hereford for 20-mo which is within the range of 0.09 to 0.63 found in the present study.

Maternal effects on post-weaning growth traits of beef cattle have been found in some cattle breeds [10, 2]. Reasonably high maternal effects than direct effects were observed in model 2 which resulted in a high maternal heritability. We can conclude that fitting maternal genetic component for 18-mo genetic evaluation would maximize genetic response in this herd. When total maternal effects, genetic and/or environment were fitted in model 2 the direct additive variance was drastically reduced. An indication that there was substantial maternal contribution of which when partitioned it constitute more of genetic than maternal environmental component. It could be reasonably to suggest that maternal effects is more of maternal genetic than maternal environmental effects resulting in a moderate maternal heritability (0.23), which was twice than the direct heritability (0.09) in model 2. The increase in maternal additive variance three times from 31.05 to 96.97 also increased the corresponding maternal heritability values from 0.03 to 0.10. This may suggest that permanent environmental maternal effects of the dam was negligible hence fitting a covariance between direct and maternal effects would not improve permanent environmental effects and this indicates that by including only one of the maternal components (additive maternal and environment maternal) may be sufficient for genetic evaluation for 18-mo in Tuli cattle. This may be in agreement with observation made by Meyer, [18] that inclusion of one of the maternal components in models result in most maternal variation being accounted for. Elsewhere an observation was made that partitioning maternal effects mainly from field data presents some difficulties even for simple univariate analyses [27, 7, 18] which was also confirmed by Alburquerque, [1] using regression models

The correlation between direct and maternal genetic effects obtained in the present study were strong and positive, 0.86, however estimates for genetic correlation between direct and maternal genetic effects for 18-mo were scarce in literature and those few reported gave negative values for correlation between direct and maternal genetic effects. [4] reported negative genetic correlation between direct and maternal effects for 18-mo of Gobra in cattle to be -0.28. It seems that negativity or positivity of covariance could vary with the models differing in accounting for sources of variation [22]. Other authors suggested that the negativity of covariance between direct and maternal genetic effects may be influenced by the nature of the fixed effects fitted in a model [12, 5]. It is difficult to explain conflictive results in the literature because estimates from different genetic backgrounds, different measurement conditions and different genetic model of analysis (animal or sire models).

A quantity of interest when maternal genetic effects are present as in the Tuli cattle population under study is the 'total genetic variance' defined as $\sigma^2_G = \sigma^2_A + 0.5\sigma^2_M + 1.5\sigma^2_{AM}$. This is the covariance between an animal's phenotypic and sum of its genetic effects i.e. the 'total heritability', determining selection response is
$h_T = \sigma^2_G / \sigma^2_P$ [26]. Our estimates of maternal heritability for Tuli cattle where on the upper side of the range of 0.05 to 0.36 reported by Meyer in Zebu crosses. Postweaning growth unlike preweaning growth rate is dependent on the animal's genetic potential for growth suggesting that subsequent weights are only minimally influenced by either maternal genetic or permanent environmental effects except for carry over effects. In a different note [4] reported maternal effects accounted for a significant proportion of total variance for 19-mo weight in Gobra beef cattle of Senegal. In future studies there is need to ascertain the magnitude of maternal carry over effects in different breeds in different environment with different management system. The magnitude of maternal effects in the present study supports the notion that maternal genetic effects generally are important for measurement of weight trait at younger ages and diminishes with increasing age [21].

Ranking the Models

Assumption was that model 5 is the appropriate model because none of the parameters of interest in the model were restricted. The likelihood ratio test showed that restricting some of the parameters will result in a better model than the one with unrestricted parameters. As a result, the first restriction subjected to model 5 was assuming Cov(a, m)= 0 instead of Cov(a, m)= $A\sigma_{am,}$ i.e. a likelihood ratio comparison test was made between model 5 and model 4. In this test k =0 because no parameter was lost so we compare the likelihood values. Comparison of model 5 and model 4 showed that model 5 had a better logarithmic maximum likelihood value; as a result model 5 was a better model than model 4.

Comparison of model 5 and Model 3 $\chi^2 = 0.153$ which is less than the upper 100 × (1-0.05) percentile point of a Chi-square distribution with k(=1) degrees of freedom. That is, χ^2 is not significantly large which means that model 3 was better than model 5. Using the same comparison model 3 had a higher logarithmic maximum likelihood value than model 2, which makes a better model. Comparison of model 2 against model 5 taking into account that model 3 was better than both model 5 and model 2.The likelihood test where $\chi^2 = 0.0009$ which is less than the upper 100 × (1-0.05) percentile point of a Chi Square distribution with k (=1) degrees of freedom showed that model 2 was better than model 5 and comes after model 3 (Table 3).

Comparison between model 3 and model 1 gives $\chi^2 = 0.153$ which is less than the upper 100 × (1-0.05) percentile point of a Chi-square distribution with *k*(=1) degrees of freedom. As a result, model 1 was the better than model 3 and therefore, appropriate model amongst the five models. The above model comparison analysis using the likelihood ratio test can be summarized in Table 3 below.

Table 3. Log likelihood ratio test ranking of animal models

Model	Log L	Ranking
1	-4006	1
3	-4009	2
2	-4325	3
5	-4327	4
4	-4336	5

CONCLUSION

The estimates of direct heritability depended on the model used. A simple animal model with additive direct genetic effects as the only random effects seems to be the best model as compared to other models. However, the influence of maternal effects could not be ruled out in this population and its contribution may be taken care of by the fact that genetic correlation between direct and maternal effects is strong and positive which can result in correlated response.

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