

**Impact of Maternal Effects on Ranking of Animal Models in
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Impact of Maternal Effects on Ranking of Animal Models in Genetic Parameter Estimation for 18-Month Weight in Tuli Cattle of Zimbabwe

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Abstract

Direct and 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 for 18-months weight records of Tuli cattle of Zimbabwe. All 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 effects of the dam were 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 response to selection if individual performance of animals is used in selection for post weaning growth in Tuli cattle.

Key words: Direct, maternal, 18-months, Tuli, Zimbabwe.

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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. The search for a suitable statistical model is an important step in the development of genetic improvement schemes (Hagger, 1998). Animal models used to analyze post weaning growth traits in beef cattle typically may not include maternal effects. However, maternal effects on post weaning growth traits of beef cattle have been found in some cattle breeds (Meyer, 1992). Animal's models in beef cattle may be complicated than in dairy cattle because of correlated direct and maternal effects (Nobre, et al., 2003).

There has been increased interest in accuracy of prediction of breeding values and ranking of animal models to determine their suitability in genetic evaluation. Models used to conduct genetic evaluation need best describe the data and ultimate usefulness of predicted breeding values. Appropriate ranking of animals will be determined by the choice of a suitable model animal. Meyer, (1997) reported that in literature 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. 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). Estimates of genetic parameters using different animal models and ranking them for post weaning growth in beef cattle in Zimbabwe has never been studied. Hence, 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 Tuli cattle of Zimbabwe.

Materials and Methods

Location

Matopos Research Station is situated in southwest Zimbabwe, an area primarily suited to semi-extensive forms of land utilization (Vincent and Thomas, 1961). The production environment is

characterized by a dry tropical climate with two distinct seasons: a long dry season from October to June and a short rainy season from November to April. The climate is characterized by wide fluctuations in the quantity and distribution of rainfall within and across season. Annual biomass production is closely related to the amount of rainfall the area receives each year. Mean recorded rainfall is 609mm with a range of 257 to 1376mm. Very high summer temperatures, maximum and minimum mean temperatures of hottest months are 21.6 °C and 11.4 °C, respectively with possibility of severe droughts (Hagreveas et al., 2004). Day et al (2003) and Gambiza and Nyama (2000) give a detailed description of the climate and vegetation type, respectively.

Herd history

In 1946, a Tuli herd was established at Tuli sub-station as part of a national programme to conserve the indigenous cattle resources of the country (Ward, 1978). With closure of the substations in 1978, the Tuli conservation herd was subsequently transferred to Matopos Research Station. Approximately 180 breeding females of the breed was maintained in single sired mating groups. The development and management of the herds were described by Brownlee (1977).

Herd management and selection procedure

With the exception of the foundation animals and purchased replacement heifers, experimental animals were progeny of selected sires and dams. Prior to 1965 calves with pre-weaning daily gains below 0.6 kg were culled together with their dams. This was subsequently raised to 0.7kg. In addition, only those calves that exceeded the mean growth rate for that year's calf crop were retained for breeding, provided they had no physical defects. Male calves failing to meet these criteria were castrated. Final selection of bulls was made prior to their first mating at three years of age and their subsequent retention was dependent on progeny performance. Heifers which failed to calve following first mating were culled while cows were allowed one conception failure. A cow remained in the breeding herd for as long as she was productive (Tawonezwi et al., 1986).

After 1992 the proportion of animals retained depended on the rate of offtake (death, emergency slaughters and sales) and replacement. These factors also determined selection cut-off points. There was more intense selection of replacement sires than there was of replacement heifers. Particularly bad years as 1992 with reduced calf crops were associated with low intensities.

All animals were grazed on free range without provision of protein rich concentrate during the dry season. Routine veterinary practices were followed. Cows were naturally bred and the breeding season was limited to 90 day period from 1st January each year. Single sire herds comprised of one bull to 30 females were introduced to the breeding herd for mating. Bulls were used for breeding when they had attained two years of age. Calves were born between late September and early January. They were identified by means of ear tags. Calves were weighed and recorded within 18 hours of birth. At the same time both the identity of dam and that of the each calf crop was weaned at an average age of 210 days of age.

Statistical Analysis

Records for 18-MO weight were obtained from experimental herd of Tuli cattle kept at Matopos Research Station between 1983 to 1997. The data included a total of 1500 progeny records of 27 sires and 228 cows of Tuli. Fixed factors for model were determined through preliminary analyses using procedure GLM of SAS (1996) (SAS Inst. Inc., Cary, NC). The analytical model included fixed effects of age of dam, sex of calf and year of birth. Genetic parameters were estimated using the Average Information Restricted Maximum Likelihood (AIREML) methodology (Gilmour, 1995) using different Animal Model. Different models were compared by using the Maximum Likelihood Ratio Test (Kendall and Stuart, 1973). 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:

- (1) $y = Xb + Z_a a + e$
- (2) $y = Xb + Z_a a + Z_m m + e$
- (3) $y = Xb + Z_a a + Z_c c + e$
- (4) $y = Xb + Z_a a + Z_m m + Z_c c + e, \quad \text{Cov}(a, m) = 0$
- (5) $y = Xb + Z_a a + Z_m m + Z_c c + e, \quad \text{Cov}(a, m) = A\sigma_{am}^2$

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: $V(a) = A\sigma_{am}^2$, $V(m) = A\sigma_m^2$, $V(c) = \sigma_c^2 I$, $V(e) = \sigma_e^2 I$ and $\text{Cov}(a, m) = A\sigma_{am}$, where σ_{am} is the covariance between direct and maternal genetic effects, σ_a^2 , the direct additive genetic variance, σ_m^2 , the maternal additive genetic variance, σ_c^2 , the variance of the permanent environmental effect of the dam, and σ_e^2 , the variance of the residuals. A is the numerator additive genetic relationship matrix between animals, I the identity matrix, Heritability of total additive genetic contribution to a maternally influenced trait was calculated according to the following equation (Willham, 1972).

The Likelihood Ratio Test

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 $100 \times (1-\alpha)$ 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. 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 than 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 (Diop, 1997 (0.13); Lee et al., (0.11) (0.11)). Literature estimates on 18-mo are scarce although Denise (1988)

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 (Koch, et al 1973; Alenda et al., 1980). Reasonably high maternal effects than direct effects were observed in model 2 which resulted in a high maternal heritability. 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, (1992b) 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 (Gerstmayr, 1992; Meyer, 1992a; Willham, 1980) which was also confirmed by Albuquerque, (2001) using regression models.

The correlations between direct and maternal genetic effects obtained in the present study were strong and positive, 0.86, indicating that there was no antagonism of genes for 18-months weight. Elzo et al., (1998) and Plasse et al., (2002) have reported

positive genetic correlation between direct and maternal effects for post weaning daily gain in cattle. The Zebu cattle in Sarmiento and Garcia, (2007) showed also a positive value for post weaning weight of (0.02).

The positive and negative genetic correlations between direct and maternal in cattle were in conformity with those reported in literature for post-weaning weight traits using bivariate and univariate analysis (Kaps, 2000; Meyer, 1994). 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).

Apart from inconclusive reports on real differences among populations analyzed, differences in preparation of data could play an important role in influencing the sign and magnitude of covariance between direct and maternal genetic effects for growth traits in sheep, goat and cattle. Maniatis and Pollot (2003) reported that estimation of the correlation between direct and maternal genetic effects is dependent on key pedigree relationships where a high proportion of both dams and maternal grand dams with their own records are essential. More over Pribyl et al., (2008) showed that editing the data base plays a role in estimating genetic parameters and includes a more complex pedigree as well as produces slightly different results. From the reported results in literature researchers have not agreed on the minimum number of records to effectively estimate the covariance of direct and maternal genetic effect. However, it has been mentioned that the size of maternal genetic effects and their relationship among themselves and with direct genetic effects are less clear and far from being known (Meyer, 1993).

In another study by Assan (2009) in Tuli cattle, the covariance of direct and maternal genetic effects were small and positive (0.11) in males and 0.15 in female calves for post-weaning growth. The positive covariance in males and females may have been caused by the changes in the structure in the data set which became small due to partitioning. The impact of data structure on separating maternal genetic and maternal environmental effects from

combined and direct effects was demonstrated by Maniatis and Pollot (2003). Showed that the accuracy of estimation of maternal genetic effects depends on the family structure and demonstrated that the both the number of progeny per dam and the proportion of dams having their own records in the data considerably affects the variance components estimation. Hence, the partitioning of data for genetic evaluation may be found wanting in the sense that it distorts the family structure and reduces both the number of progeny per dam and the proportion of dams having their own records. The reduction of records in preparation of data may impose light differences in the estimation of covariance between direct and maternal genetic effects for growth traits in sheep, goats and cattle.

Reliable estimation of direct and maternal genetic parameters accounting for direct and maternal covariance requires data with a sufficient amount of reliable records and good pedigree records. This can be a major limitation in artificial insemination related programs because accessibility of pedigree information on artificial insemination sires may be difficult to compile. Data collected from cattle farmers with traditional rearing system and having incomplete record of production, identification and pedigree reduced inverse matrix of genetic correlation. Generally in developing countries with traditional rearing system, artificial insemination or using bull inter-cattle herds has not been done that caused weakness of genetic correlation among herds and produced genetic variance bias (Mathur et al., 1998; Campelo et al., 2004)

Ranking of 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 $100 \times (1-0.05)$ 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 $100 \times (1-0.05)$ 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).

Table 1: Descriptive statistics of 18-mo weight data set in Tuli cattle of Zimbabwe.

Item	Value
Records	1500
Sires	27
Dams	228
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 18-mo weight fitting different animal models in Tuli cattle of Zimbabwe.

Item	Model				
	1	2	3	4	5
σ_a^2	688.40	83.34	219.50	98.82	90.52
σ_m^2		228.90		31.05	96.97
σ_{am}^2					80.91
σ_{pe}^2			0.68	0.12	0.16
σ_e^2	402.70	671.80	767.50	836.10	700.70
σ_p^2	1091.10	984.04	987.68	966.09	969.26
h_a^2	0.63	0.09	0.22	0.10	0.09
Se	0.10	0.06	0.001	0.001	0.001
h_m^2		0.23		0.03	0.10
Se		0.04		0.001	0.001
r_{am}					0.86
c^2			0.00	0.00	0.00
h_T^2	0.63	0.20	0.22	0.12	0.14

σ_a^2 = additive direct variance

σ_m^2 = additive maternal genetic variance

σ_{am}^2 = direct-maternal additive variance

σ_{pe}^2 = permanent environmental dam variance

σ_e^2 = error variance

h_a^2 = direct heritability

σ_p^2 = phenotypic variance= sum of variance and covariance components

h_m^2 = maternal heritability

h_T^2 = Total heritability (total genetic effects)

r_{am} = direct and maternal genetic correlation

Comparison between Model 3 and Model 1 gives $\chi^2 = 0.153$ which is less than the upper 100

$\times (1-0.05)$ 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 study shows that including maternal effects for 18-MO will not improve estimates of direct heritability, especially where permanent environmental effects are accounted for. The high additive variance indicates a greater genetic influence of individual animals than their dams for 18-month weight in this population. Can conclude that a simple additive model was the appropriate model due to the positive correlation of direct and maternal genetic effects in Tuli cattle. In some models maternal effects were higher than direct effects this may be the result of the insufficient data which may have not provided a good pedigree structure, as a result limiting the partitioning maternal genetic and permanent environmental maternal effects. Suggest further investigation is needed for the same trait using a larger data set.

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