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**Original article**

## Genetic parameters for weaning weight of Zimbabwean Nguni cattle accounting for direct-maternal genetic covariances

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### ABSTRACT

Five models were fitted to weaning weight data of indigenous Nguni cattle to investigate their suitability for evaluation of breeding values. The animal models were ranked using a simple Mallows statistic. 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 1278 weaning weight records of indigenous Nguni cattle collected over a period of 10 years (1989- 1999). All investigated models included a random direct effect, but different combinations of random maternal genetic and permanent environmental effects as well as for direct-maternal genetic covariance. The direct heritability ( $h^2_a$ ) ranged from 0.0 to 0.25 when the maternal genetic effects were included in the model, while  $h^2_a$  estimates were 0.21 and 0.68 when maternal effects were excluded. The maternal heritability ( $h^2_m$ ) was lower (0.04) than  $h^2_a$  (0.09) when only maternal genetic effects were included in the model, and were 0.13 and 0.17 when the permanent environmental effects of the dam was fitted. The permanent environmental effects of the dam were not important. A large and negative covariance

( $\sigma_{am}^2$ ) between direct and maternal genetic effects was observed. Using Mallows statistic test Model 5 could be the best for genetic evaluation of weaning weight and this could maximize genetic response.

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## 1. Introduction

Nguni cattle of Zimbabwe forms part of the Sanga group of cattle which includes most of the type indigenous to East, Central and Southern Africa (Faulkner and Epstein, 1957). In Zimbabwe there are three indigenous breeds of cattle (Nguni, Tuli and Mashona). Nguni are medium sized pure African Sanga breed with color pattern which varies widely. The frequent pattern involves white hair with pigmented skin: black, brown red, dun, yellow are common, either as solid colors or in various combinations (black and tan or bridle). The breed has been popular for meat production and well known by their high fertility, hardiness, adaptability; ease calving and good mothering ability.

Different models and methods have been used in estimating direct and maternal genetic parameters for weaning weight data in cattle (Assan, 2012; Abera et al., 2011; Dezfuli and Mashayeki, 2009; Wasike et al., 2006; Skrypzeck et al 2000; Schoeman, 2000) and previously the ranking of models was mostly done by log likelihood ratio test (Dobson, 1990). Global, there is a paucity of reported genetic parameters estimates for purebred indigenous tropical breeds cattle and their crosses (Lobo et al., 2000). Genetic parameters are unique to the population in which they were estimated and they may change over time due to selection and management (Koots et al 1994a). Estimation of genetic parameters for growth traits is always considered problematic mainly due to confounding of direct and maternal effects (Baker, 1980). Genetic parameter estimates for indigenous African beef breeds have been estimated considering mainly direct genetic effects and to some extent maternal effects. However, in most studies where maternal effects were considered the covariance between direct and maternal effects was ignored (Wasike et al., 2006). Highly negative direct and maternal genetic co-variances were reported (Haile-Mariam and Kass-Mersha, 1995; Khombe, 1995; Maiwashe et al., 2002; Demeke et al., 2003; Nephawe, 2004; Norris et al., 2004). The negative direct and maternal genetic correlation indicated that there is an antagonism between direct and maternal genetic effects for weaning weight analysis (Ferraz et al 2000). Therefore, considering this correlation in selection program can be significant. The objective of this study was to investigate the importance of maternal effects on weaning in indigenous Nguni cattle, fitting and ranking different animal models including direct genetic, maternal and permanent environmental effects.

## 2. Materials and methods

### 2.1. Study location

Matopos Research Station (20° 23' S, 31° 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 (Homann et al., 2007). 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). The most common type of vegetation is sweet veldt with comparatively high nutritional value of browse and annual grass species (Ward et al 1979). Managed well the rangelands should be able to meet the nutritional requirements of goats and other livestock (Van Rooyen et al., 2008). 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 (Hlatshwayo, 2007). Day et al (2003) and Gambiza and Nyama (2000) give a detailed description of the climate and vegetation type, respectively. Herd history and management of the herd were described by Assan (2006).

### 2.2. 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

d 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 thereafter all calves weighed at an average age of 210 d.

### 2.3. Data analysis

Genetic parameters were estimated using the Average Information Restricted Maximum Likelihood (AIREML) methodology (Gilmour, 1995) 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:

$$y=Xb + Z_a a + e \tag{1}$$

$$y=Xb + Z_a a + Z_m m + e \tag{2}$$

$$y=Xb + Z_a a + Z_c c + e \tag{3}$$

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

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

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

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

Maternal across-year repeatability for dam performance,  $t_m = (1/4)h^2_a + h^2_m + c^2$

### 2.4. Model selection using mallows $C_p$ statistic

Siniksaran (2008) suggested the Mallows'  $C_p$  statistic that is of the form,

$$C_p = \frac{RSS_p}{s^2 - (n - 2p)} \tag{1}$$

where  $RSS_p$  is the residual sum of squares from an animal model containing  $p$  parameters,  $p$  is the number of parameters in the model including  $\beta_0$ ,  $s^2$  is the residual mean square from the largest postulated containing all the effects and  $n$  is the total number of records (Mallows 1973).  $s^2$  is presumed to be a reliable unbiased estimate of the error of variance  $\sigma_e^2$ , i.e.

$$E(s^2) = \sigma_e^2 \tag{2}$$

If we assume that an equation with  $p$  parameters does not suffer from lack of fit then

$$E(RSS_p) = (n - p)\sigma_e^2 \tag{3}$$

Substituting equations (2) and (3) into equation (1), the Mallows  $C_p$  statistic becomes

$$C_p = \frac{(n - p)\sigma_e^2}{\sigma_e^2 - (n - 2p)} \tag{4}$$

Taking the expectation of equation (4) gives  $E(C_p) = p$ , which follows that a plot of  $C_p$  versus  $p$  will show up the “adequate models” as points fairly close to the  $C_p=p$  line. Points representing well-fitting models likewise are expected to be closer to the  $C_p=p$  line because of the effects of inclusion or exclusion of respective random variables

### **3. Results and discussion**

Variance component ratios for weaning weight are shown in Table 2. All models included a random additive effect. Estimates of the direct additive heritability depended very much on the model used, with a range of 0.00 to 0.25. This partly confirms literature results that growth traits measured early in life were moderately to highly heritable, the estimates were within the range of published estimates summarized by Baker (1980). In model 1 where maternal effects were ignored, heritability was biased upwards, while inclusion of maternal genetic effects in model 2 reduced direct additive heritability to zero. Although this is unlikely to happen in a normal situation the zero heritability indicates a possible exhaustion of genetic variation after long term selection. There is a tendency for response to reach a limit or a plateau when variation has been exhausted in herd therefore when this happens there is need to introduce new sires in the herd. Another plausible explanation for zero heritability is possibly what is left of genetic variation for weaning weight in the herd was due to maternal influence than direct additive genetic variation. This also confirmed when the maternal genetic effects and / or permanent environmental were included in the model the direct additive genetic variance behaved the same ranging from 0.00 to 0.25. In model 2, it has been shown that the maternal effects were partitioned into its genetic and environmental components. However it may be reasonable to assume that maternal additive effects were equally important considering the high maternal heritability in model 4 which is even higher than the direct heritability. In model 5 in which both genetic and environmental maternal effects were taken into account, and covariance between direct and maternal effects included resulted in increased direct heritability by more than half compared with model 1. This is an indication of the strong relationship between direct and maternal effects for studied trait. This may imply that inclusion of both the direct and maternal effects and accounting for their correlation may improve the modeling of this variable in this population. Model 4 and model 5 had 13 % and 17 % of total variation attributable to maternal genetic effects, respectively, which is within the range reported in literature (Meyer, 1992). Permanent environmental variance contributed less than 5% to total variance in models 4 and 5. Considering the production system in semi arid tropics which is mostly range feeding expect not much contribution from the permanent environmental effects and also most of the indigenous cattle breeds through natural selection have tolerated the environmental stressors in the tropics.

It is evident that the relative values of direct and maternal heritability were influenced the model used in the analysis. It was noted that the maternal effects was reasonably higher than direct additive variance in model 4 which resulted in a higher maternal heritability (0.13). Permanent environmental of the dam were within the same magnitude in all models were it was included. In model 5 were permanent environmental effects of the dam were small; the total variance was attributed to maternal genetic variance, resulting in an increase in maternal heritability as compared to model 2. The covariance and correlation between direct and maternal genetic effects were strong and negative and this confirms the observations in similar studies (Meyer, 1992).

Estimates of maternal heritability in the present study were within the range reported by several authors. A comparable maternal heritability estimate ranges of 0.08- 0.12, 0.15- 0.21 and 0.13- 0.25 were reported by Dodenhoff, et al., (1999), Kriese et al., (1991) and Mercadante et al., (1997). Koch et al., (1994), Waldron et al., (1993) and Lee et al.,(1997) reported maternal heritability estimate of 0.17, 0.14 and 0.15, respectively, in beef cattle which are not also far from what has been reported from our study. However the present estimates on maternal heritability coincide with others reported in literature (Berweger Baschmagel et al., (1999)(0.04) and Lee et al., (1997)(0.09).

The proportion of variance due to direct permanent environmental effects showed that it was not important with an estimate of less than 5% and were the smallest compared to other variance components. Permanent environmental effects were small in models 4 and 5 were both maternal genetic effects and permanent environmental effects were accounted for. The inclusion of covariance of direct and maternal effects in model 5 caused a little shift upwards in the magnitude of permanent environmental effects from model 4. Higher estimates of permanent environmental effects have been associated with permanent environmental effects of the uterus

(Synman et al., 1995) and their effect on multiple birth in small ruminants, however multiple birth are rare in cattle.

**Table 1**

Structure and descriptive statistics of data set of weaning weight in indigenous Nguni cattle of Zimbabwe.

Item	
Records	4889
Sires	117
Dams	1245
Animals	8154
Base Parents	581
Mean (kg)	177.18
Standard Deviation (kg)	28.01
Coefficient of Variation (%)	13.30
R- Square	0.50

**Table 2**

Estimates of covariance components and genetic parameters for weaning weight using different animal models in indigenous Nguni cattle of Zimbabwe.

Parameter	1	2	3	4	5
$\sigma_a^2$	93.56	63.57	61.78	0.15	219.00
$\sigma_m^2$		25.08		90.97	149.20
$\sigma_{am}^2$					-154.30
$\sigma_{pe}^2$			30.14	22.29	28.24
$\sigma_e^2$	630.90	634.90	630.30	610.60	627.30
$\sigma_p^2$	724.46	723.55	722.22	724.01	869.44
$h_a^2$	0.13	0.09	0.09	0.00	0.25
$h_m^2$		0.04	0.04	0.13	0.17
$r_{am}$					-0.85
$C^2$			0.00	0.03	0.03
$h_T^2$	0.13	0.11	0.09	0.06	0.07

**Table 3**

The computed Mallows  $C_p$  statistic used to rank animal models for weaning weight in indigenous Nguni cattle of Zimbabwe.

Model	$C_p$	Ranking
5	11.80	1
4	12.44	2
3	12.52	3
1	12.52	4
2	12.70	5

Maternal heritability (0.17 vs 0.25) was lower than direct heritability in model 5 which agrees very well with findings by other workers (Kaps et al., 1999). In model 4 maternal heritability was higher than direct heritability a similar trend had been previously observed in cattle by Cantet et al., (1993). In general its understood that genetic parameter estimates before 1984 direct heritability were smaller than maternal heritability, while genetic correlation between direct and maternal effects were highly negative (-0.40), whereas more recent reports suggest that direct heritability is larger than maternal heritability with the correlations between direct and maternal effects being negative but greater than -0.35 which confirms the negative trend observed in the present study. In general the  $h_a^2$  range estimates of 0.00 to 0.25, and  $h_m^2$  range estimates of 0.04 to 0.17) are notably within the range reported in literature for cattle. (Dodenhoff et al., 1999; Kriese et al., 1991; Mercadante et al., 1997; Koch et al.,

1994; Waldron et al., 1993; Lee et al., 1997) and agrees with recent estimates in that  $h^2_a$  was larger than  $h^2_m$  (Kaps et al., 1999). The difference between direct and maternal heritability for weaning weight were obvious indicating that it may be worthwhile to utilize aggregate breeding values (direct plus maternal) for accurate ranking of animals for weaning weight because both genotype of the calf and genotype of the dam showed had an influence on weaning weight in model 2 and 4.

A negative genetic correlation between the direct and maternal genetic effects which was obtained in present study of -0.84 was stronger than the weighted mean of -0.31 from 24 studies (Cantet et al 1993) this may be explained by possible relative smaller set and structure. It was likely to get negative correlation because the data used in this study was from an experimental herd. Cundiff (1972) suggested that negative covariance between direct and maternal effects could be explained from an evolutionary point of view, prevent animal species from becoming increasingly larger. Other workers mentioned that a possible existence of a negative environmental covariance between dam and offspring in growth traits could result in a biased estimation of genetic correlation between direct and maternal genetic effects (Meyer, 1992). In this population the environmental covariance although negative it seemed to be important as shown by the improvement of the expression of genetic parameters in model 5. In previous studies in which the magnitude of covariance between dam and offspring was measured has shown that the extent to which covariance affect genetic parameter estimation could be different amongst herds/breeds, data structure and management systems (Dees and Koger, 1967). In the present study the herd was kept under veld management without a provision of supplement unless during drought years. However the results of genetic covariance between direct and maternal are similar to those reported for cattle under intensive management (Bertrand and Benyshek, 1987). It is reasonable to suggest that comparison of genetic covariance of direct and maternal effects estimates from the present study with previously reported estimates may be difficult taking into account differences in environment, type of recording, data structure, worse part of it the models and methods used for estimation of covariances were different. Inclusions of different sets of fixed effects have an impact on the negativity and positivity of the resultant covariance. This means the negative direct-maternal correlation magnitude could vary due to models differing in accounting for sources of variation. A non genetic factor fitted influences the negativity of covariance between direct and maternal genetic effects in cattle (Robinson, 1996a; Lee and Pollack, 1997; Meyer, 1997; Dodenhoff, et al., 1999). In the present study sex, year of birth and age of dam were fitted as fixed effects were interactions such as herd\*year\*seasonal effects may not be considered important.

The total heritability was lower than those reported by other authors (Dees and Koger, 1967; Hohenboken and Brinks, 1971) however were within the same range as those reported by Meyer (1992). Maternal across year repeatability for dam performance were low to medium which suggest that it would be difficult to select on their offspring weaning weight repeated records.

The results of Mallows  $C_p$  statistic are as shown Table 3. Unfortunately there is no point falling below the  $C_p=p$  line but that value from model (5) is fairly the closest and it gives the least Mallows  $C_p$  statistic. As a result model (5) becomes the 'best' amongst the five models. That is, if maternal effects are considered as the second random effect but allowed for covariance between the direct and maternal effects.

#### 4. Conclusion

The magnitude of covariance components and genetic parameters depended on the model used. The estimates of direct additive genetic variance components were larger than those of maternal additive variances consequently estimate for direct heritability were higher than maternal heritability for most models. The permanent environmental effects of the dam as a proportion of total the total phenotypic variance were low as a result were not important in this herd. The strong and negative genetic correlation between direct and maternal effects was of much interest in the sense that it could limit the utilization of aggregate breeding values for improvement of weaning weight in indigenous Nguni cattle. Using the Mallows  $C_p$  statistics test it showed that model 5 could be appropriate for genetic evaluation of weaning weight in this population, which mean because of negative genetic correlation between direct and maternal effects for weaning weight, methods of selection accounting for both direct and maternal genetic effects would result in greater economic selection response than selection based only on direct genetic effect.

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