Covariance components and genetic parameter estimation for 18 month weight in Nguni and Tuli cattle of Zimbabwe

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ARTICLE INFO

Article history:
Received 08 March 2013
Accepted 18 March 2013
Available online 27 March 2013

Keywords:
Direct
Maternal
Tuli
Nguni
Zimbabwe

ABSTRACT

An animal model was applied to estimate variance components and heritability estimates from weight at 18-months (18-mo) pedigree records of two experimental herds of Nguni and Tuli cattle maintained on range at Matopos Research Station. The fixed effects included were of year of birth, sex and age of dam. Random effects were direct and maternal genetic of the animal and dam with genetic covariance of direct and maternal effects, maternal permanent environment, and random residual. Estimates of direct heritability were 0.36 ±0.001 and 0.13±0.005 for Nguni and Tuli cattle, respectively. The maternal heritability was higher for Tuli cattle, 0.18 as compared to 0.02 for Nguni cattle. Estimates of maternal permanent environmental variance as a proportion of phenotypic variance were less than 1% in both Nguni and Tuli cattle. The direct-maternal genetic correlations were small and negative for Nguni cattle, and small and positive for Tuli cattle. Permanent environmental effects were found not to be important for 18-mo in both cattle breeds studied. The genetic variance is high in Nguni cattle that response to selection is expected to be high.

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1. Introduction

Indigenous livestock breeds have always played an important role in the lives of people of Sub Saharan Africa (Bosso et al., 2009), however information on genetic parameters which are population specific are scanty for Sanga cattle herds indigenous to East, Central and Southern Africa (Beffa, 2005). Such information on the nature and magnitude of population parameters (i.e. variance components and heritabilities) for these cattle herds are needed for effective designing of breeding programs and to estimate breeding values for traits of relevance to beef producers (Intaratham et al., 2008).

Maternal effects on post-weaning growth traits of beef cattle have been reported in some breeds (Macedo et al., 2009). Lee et al., (2000) reported estimates of heritability of 0.40 for 18-month weight in Korean Native cattle. Diop (1997) reported negative genetic correlations between direct and maternal genetic effects for 18-month weights of Gobra cattle in Senegal. Genetic models, including maternal effects and the covariances of direct and maternal effects fit data better than the simple additive model. In beef cattle post-weaning weights affects the economic success of producing slaughter animals and this is possible candidate trait for selection. Both negative and positive correlations between direct and maternal genetic effects have been reported for weight traits in literature (Plasse et al., 2002; Choi et al., 2000; Ferraz et al., 2000). Eighteen months weight has been given little consideration in cattle breeding programs, however as a postweaning growth trait, it has a potential value through its high correlation with mature weight and hence can increase the economic success of heavy animals at slaughter. The study would generate baseline information which will be of prime importance as the basis of any future proposal of establishment of open nucleus breeding herds with sampling of indigenous cattle still in newly resettled areas, as it is believed that some of the best genetic material adapted to harsh environments can be found in these areas. The objective of this study was to estimate covariance component and genetic parameters associated with direct and maternal genetic effects on 18-month weight of indigenous Nguni and Tuli cattle of Zimbabwe. Genetic parameters are specific for a particular population and environment and hence the need to estimate, in this case for the indigenous Nguni and Tuli cattle of Zimbabwe for the development of locally sound breeding programs and prediction of breeding values.

2. Materials and method

2.1. Study 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.

2.2. Herds history

In 1946 a Nguni herd was established at Tsholotsho sub-station and 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 and Nguni conservation herds were subsequently transferred to Matopos Research Station. Approximately 180 breeding females of each breed were maintained in single sired mating groups. The development and management of the herds were described by Brownlee (1977).

2.3. 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 years 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 (Tawonezvi 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.

2.4. Herd management

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.

2.5. Data collection and analysis

Records for 18-mo weight were obtained for two local experimental herds (Tuli and Nguni) kept at Matopos Research Station between 1983 to 1997. The data included a total of 2003 progeny records of 43 sires and 428 cows of Nguni, and 2122 progeny records from 40 bulls and 398 cows of Tuli cattle (Table 1). 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 an Animal Model. In matrix notation the univariate mixed linear model used was of the maternal form.

\[
Y = Xb + Zu + Wm + Spe + e
\]

where;

- \(Y\) = vector of 18-mo weight;
- \(b\) = vector of year of birth, sex and age of dam;
- \(u\) = vector of random animal effects;
- \(m\) = vector of random maternal (indirect) genetic effects;
- \(pe\) = vector of random permanent environmental maternal effects of dam;
- \(e\) = vector of random residual effects;
- \(X, Z, W\) and \(S\) are incidence matrices relating records to fixed, animal, maternal genetic and permanent environmental maternal effects, respectively.

2.5.1. Total heritability (\(\mathbf{h}^2\)) was calculated as: \(h^2 = (\sigma^2_a + 3/2 \sigma^2_{am} + 1/2 \sigma^2_m)/\sigma^2_p\) (Willham, 1972),

where:

- \(h^2\) = Total heritability (total genetic effects)
- \(\sigma^2_a\) = additive direct variance;
- \(\sigma^2_m\) = additive maternal genetic variance;
- \(\sigma^2_{am}\) = direct-maternal additive variance;
- \(\sigma^2_p\) = phenotypic variance = sum of variance and covariance components

2.5.2. Response to selection (\(\mathbf{R}\)) was calculated using the formula:

Annual \(R = \left(\frac{i_m + i_f}{L_m + L_f}\right) \times h^2 \times \sigma_p\)

where:

- \(R\) = annual rate of response to selection;
- \(i_m + i_f\) = selection intensity for males and females respectively;
- \(L_m + L_f\) = generation interval for males and females respectively;
- \(h^2\) = heritability for the important trait.
\[ \sigma_p = \text{standard deviation for the trait;} \]

The selection intensity \((i)\) is a function of the proportion of animals selected to be the future parents \((p)\). To calculate annual response the following assumptions were made on selection intensity on bulls: \(i_m = 1.755\) \((p=10\%)\) and for dams was \(i_f = 0.424\) \((p=75\%)\). The average calculated generation intervals were 4.9 years for males and 6.8 years for females for both breeds. The standard deviations for 18-mo weights were 31.86 kg and 33.64 kg for indigenous Nguni and Tuli cattle, respectively.

### 3. Results and discussion

Estimates of variance component and genetic parameters for 18-month (18-mo) weight for Nguni and Tuli cattle are presented in Table 2. The variance components for direct genetic effects for 18-mo weights were twice as large for Nguni as for Tuli cattle (367.1 vs 148.9 kg) despite the two populations being managed the same. The maternal genetic variance accounted for 2% and 18% of total phenotypic variation for Nguni and Tuli cattle, respectively. Variance due to permanent environmental effects as associated with the dam for 18-mo weight in both breeds of cattle were not important explaining proportionally less than 1% of the total phenotypic variance. The estimates of direct heritability for 18-mo weight were moderate, \((0.36\pm0.001)\) for Nguni cattle, but small for Tuli cattle, \(0.13\pm0.001\) (Table 3).

### Table 1

Descriptive statistics for 18 months weight in Nguni and Tuli cattle of Zimbabwe.

<table>
<thead>
<tr>
<th>Component</th>
<th>Nguni</th>
<th>Tuli</th>
</tr>
</thead>
<tbody>
<tr>
<td>Records</td>
<td>2003</td>
<td>2122</td>
</tr>
<tr>
<td>Sires</td>
<td>43</td>
<td>40</td>
</tr>
<tr>
<td>Dams</td>
<td>428</td>
<td>398</td>
</tr>
<tr>
<td>SD</td>
<td>31.86</td>
<td>33.64</td>
</tr>
<tr>
<td>Mean</td>
<td>263.58 ±1.45</td>
<td>258.25 ±1.47</td>
</tr>
<tr>
<td>CV</td>
<td>11.5</td>
<td>12.76</td>
</tr>
<tr>
<td>R-square</td>
<td>0.55</td>
<td>0.47</td>
</tr>
</tbody>
</table>

SD=standard deviation  CV=coefficient of variation

### Table 2

Estimates of genetic and environmental variances and (co)variances (kg \(^2\)) for 18-month weight in Nguni and Tuli cattle of Zimbabwe.

<table>
<thead>
<tr>
<th>Breed</th>
<th>(\sigma^2_A)</th>
<th>(\sigma^2_M)</th>
<th>(\sigma^2_{AM})</th>
<th>(\sigma^2_{PE})</th>
<th>(\sigma^2_E)</th>
<th>(\sigma^2_P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nguni</td>
<td>367.10</td>
<td>17.12</td>
<td>-3.15</td>
<td>0.17</td>
<td>633.90</td>
<td>1015.14</td>
</tr>
<tr>
<td>Tuli</td>
<td>148.90</td>
<td>205.90</td>
<td>48.26</td>
<td>0.12</td>
<td>728.90</td>
<td>1132.08</td>
</tr>
</tbody>
</table>

\(\sigma^2_A=\) direct additive genetic; \(\sigma^2_M=\) maternal additive genetic variance; \(\sigma^2_{AM}=\) direct and additive variance; \(\sigma^2_E=\) error variance; \(\sigma^2_P=\) phenotypic variance = sum of variance and covariance components.

### Table 3

Direct additive \((h^2_A)\), maternal \((h^2_M)\), total \((h^2_t)\) heritability estimates, standard errors (SE) and correlation between direct and maternal effects \((r_{AM})\), annual response, for 18-mo weight in Nguni and Tuli cattle of Zimbabwe.

<table>
<thead>
<tr>
<th>Breed</th>
<th>(h^2_A) SE</th>
<th>(h^2_M) SE</th>
<th>(h^2_t)</th>
<th>(r_{AM})</th>
<th>(R) (kg/yr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nguni</td>
<td>0.36±0.001</td>
<td>0.02±0.001</td>
<td>0.39</td>
<td>~0.04</td>
<td>1.2</td>
</tr>
<tr>
<td>Tuli</td>
<td>0.13±0.001</td>
<td>0.18±0.001</td>
<td>0.43</td>
<td>0.28</td>
<td>0.69</td>
</tr>
</tbody>
</table>

Lee et al. (1991) reported estimates for direct heritability of 0.04 for 18-mo weight in Korean Native cattle which were lower than those reported in the present study. The estimate of direct heritability in Tuli cattle agrees with those reported by Diop (1997) and Ferraz et al (2000) of 0.13. The direct heritability estimate of 18-mo weight in Nguni cattle were higher than those reported in literature (Lee et al., 2000) of 0.11 to 0.12. Denise reported an estimate of direct heritability for 20-mo weight of 0.29 for Hereford and Lobo et al (1994) reported a direct heritability of 0.26 for W550 in Nellore cattle, and both estimates are within the range of 0.13 to 0.36 found in the
present study. Elsewhere for body weight at 15 months, Bosso et al. (2009) observed a direct heritability of 0.48 which was three times higher than that reported in Tuli cattle in present study. Using polynomials and trigonometric functions in random regression models Macedo et al., (2009) observed direct heritability estimates of 0.29 to 0.31 which were closer to those reported for Nguni in the present study. On range working with another local cattle breed (Mashona) in Zimbabwe using paternal half sib methodology. Tawonezvi (1989) reported a heritability of slightly higher magnitude of 0.39 which is comparable to the 0.36 observed in Nguni cattle here.

Maternal effects on post weaning growth traits of beef cattle have been found in some cattle breeds (Meyer, 1992). Mackinnon et al., (1991) showed that maternal effects influence the post weaning growth in cattle, though the real magnitude of genetic effects is not clear. The maternal effects were present but not important in Nguni cattle which is in contrast to report by Diop (1997) who observed that maternal genetic effects accounted for a significant proportion of total variance for 18-mo (final) weight in Gobra beef cattle of Senegal. Surprising, maternal genetic effects seem very important in Tuli cattle even at this age, where the maternal heritability value is larger than direct effects. In contrary to the observation by Ferraz et al., (2000) who reported higher direct genetic effects than maternal effects in Santa Getrudis cattle in Brazil. The higher estimates of maternal effects than direct effects in Tuli cattle disagree with those of Lee et al. (2000), who reported that maternal heritability estimates were higher than direct heritability estimates for post-weaning growth traits. In this study the direct heritability for Tuli cattle was lower (0.13) than the maternal heritability estimates (0.18). Pre-weaning weight reflects that suckling calves are still dependent on their dams, where as after weaning a calf growth rate is dependant on its own genetic potential for growth, and subsequent weights are only minimally influenced by either maternal genetic or maternal permanent environmental effects, except for carryover effects which may be in contrast with the finding in Tuli cattle. The relatively high maternal component, that explains 18% of the total variation indicates that this effect should be kept in the model of analysis, even for 18-mo in such a Tuli population. On the other hand a plausible explanation for higher maternal effects (0.18) than direct effects (0.13) in Tuli cattle (Table 3) is the success on selection emphasis which was on maternal traits-fertility and calf survival and weaning weight over many generations. At post weaning stages expect individual animals to no longer depend on their dam for growth. The weight at this age should reflect only direct effects of the genes for growth, except if the carry over effects from weaning weight is present. The wide differences in magnitude of genetic parameters of the two populations, somehow may not have be expected because of taking into account the importance of environmental effects which are important in the tropics, expecting these to affect different populations in similar ways and importance. This may cause a decrease in heritability in all breeds. The environmental factors might have had a smaller effect on the populations studied

Eler et al., (1995) argued that for animals raised on range with little or no supplementation feeding, the length of time between weaning and yearling may not be enough to buffer maternal effects existing at weaning which may be contradictory with the observation in present study for Tuli cattle. Estimate of maternal heritability for indigenous Nguni and Tuli cattle were within the range of 0.005 to 0.36 reported by Meyer (1994) in Zebu crosses. The magnitude of maternal effects in Tuli may be as a result of selection of dams on their heavier calves at weaning weight. The smaller estimates of maternal heritability for 18-mo weight in Nguni cattle supports the report by Robison (1981) that maternal genetic effects generally are important for measurements of weight trait at younger ages and diminish with increasing age. Meyer (1992) suggested that the maternal effects identified in Zebu crosses for post weaning growth traits are a carry-over effect of those affecting weaning weight. Future studies need to investigate the magnitude of the maternal carry-over effects in different breeds under different management systems. In the present study, Tuli and Nguni cattle were kept under the same management and being influenced by the same environmental effects however the differences in magnitude of maternal effects were large.

The genetic correlation between direct and maternal effects was negative, but low for Nguni cattle, indicating a mild genetic antagonism between genes and should be considered in selection criteria. This agrees with results reported by Ferraz et al., (2000) in Santa Getrudis cattle in Brazil. Sarmiento and Garcia, (2007) reported a closer genetic correlation between direct and maternal effects which was negative, but low (-0.05) for 480-day in Romosinuano cattle. In Tuli cattle, the genetic correlation between direct and maternal effects was positive, but low for 18-mo. 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 for Nguni (-0.04) and Tuli (0.28), respectively, were in conformity with those reported in literature for postweaning weight traits using bivariate and univariate analysis (Meyer, 1994; Kaps, 2000). Lee and Pollak (1997) and Robinson (1994) reported that negative direct-maternal genetic correlations were inflated when the effects of sire*year interaction were not included in the model. In the present study the sire*year interaction was not accounted for in the model however year was fitted as a fixed effect. Diop (1997) reported negative genetic correlation between direct-maternal effects for 18-mo weights of Gobra in Senegal to be −0.28.

Fig. 1. Trends on age of dam environmental values for 18-mo weight in Nguni and Tuli cattle of Zimbabwe.

Fig. 2. Trends on age of dam environmental values for 18-mo weight in Nguni and Tuli cattle using a second order polynomial regression.
A quantity of interest when maternal genetic effects are present as in Tuli cattle in this study is the ‘total’ genetic variance, defined as $\sigma^2_G = \sigma^2_A + 0.5 \sigma^2_M + 1.5 \sigma^2_{AM}$. Total heritability defines as the covariance between an animal’s phenotype and the sum of its genetic effects, is $h^2_T = \sigma^2_G / \sigma^2_p$ (Willham, 1972) and it is directly proportional to selection response/expected genetic progress. The expected genetic progress was high in Nguni because of the high additive genetic variance. The populations have been closed nucleus herds since the 1940’s, low genetic progress in Tuli cattle might be due to inbreeding and small size of breeding groups which may have reduced the genetic variation at some point. The year effects were accounted for and the herds were kept under similar management and within the same environment the environmental effects may have influenced these herds differently. The total heritability was moderate. The annual selection response was higher in Nguni (1.2 kg/year) than in Tuli cattle (0.69 kg/year) possibly due to higher additive genetic variance in Nguni cattle. Use of total genetic effects on selection ($h^2_T$) for 18-mo weight would optimize genetic progress in both herds.

The age of dam environmental values trends for 18-mo weight of first order regression were highly significant in both cattle breeds studied. This partially agree with trends and findings of other workers that age of dam had an influence on weaning weight (Beffa, 1991) in Afrikaner. It may be reasonable to suggest that the effects of age of dam on 18-mo weight are a carry over effect from weaning weight. There was a positive effects of age of dam on 18-mo which increased as dam age increases to about 6 to 8 years the peak of milk production of the dam (Lobo et al., 1984), which indicates that good dams can influence the 18-mo weight of their progeny. The positive trends were 2.316 kg/yr ($R^2 = 0.32$) and 2.498 kg/yr ($R^2 = 0.88$) (Fig. 1) for Tuli and Nguni cattle, respectively, which may indicate that the age of the dam of Nguni cattle had much more carry over influence on 18-mo weight. The decline in the carry over effects of the dam were more pronounced after the age of eight years with a decline of –3.5832 kg/yr ($R^2 = 0.42$) and -5.9567 kg/yr ($R^2 = 0.95$) for Tuli and Nguni cattle, respectively. This may indicate that the indigenous Nguni cattle had much more dam age influence on 18-mo weight than Tuli cattle. For the whole period of study a second order polynomial regression improved the coefficient of determination ($R^2$) from 45% to 51% and 0.61% to 0.94% for 18-mo weight in indigenous Tuli and Nguni respectively (Fig. 2), which could probably mean higher order polynomial regressions could improve data fit for environmental values (Fig. 1 vs 2).

4. Conclusion

The study suggest that the maternal effects identified for 18-mo weight are as a result of a total carry over effect of those affecting weaning weight. The relatively high maternal component that explains 18% of total variation indicates that this effect should be kept in the model of analysis even for 18-mo weight in Tuli cattle. Maternal permanent environmental effects are not important for 18-mo weight in both Nguni and Tuli cattle. Therefore it is suggested that selection programs on 18-mo weight should consider using the total genetic variance to optimize genetic progress in both herds.

Acknowledgement

Efforts of past and present staff, particularly those employed at West Acre section, for care and maintenance of animals and collection of data is gratefully acknowledged.

References


