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INFLUENCE OF MATERNAL EFFECTS ON RANKING OF ANIMAL MODELS FOR GENETIC PARAMETER ESTIMATION FOR COLD CARCASS MASS IN GOATS

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ABSTRACT
Genetic parameters for simple carcass traits in developing countries where goats are numerous are scarce. 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 2341 cold carcass mass pedigree records of indigenous Matebele goat 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 direct-maternal genetic covariance. The direct heritability (h^2_a) ranged from 0.14 to 0.25 when the maternal genetic effects were included in the model, whereas h^2_a estimation was 0.26 when maternal effects were excluded. The maternal heritability (h^2_m) was 0.00 when only maternal genetic effects were included in the model and were 0.05 and 0.10 when the permanent environmental effect of the dam was added. The permanent environmental effect of the dam was negligible. A positive covariances between direct and maternal genetic effects (σ^2_{am}) was observed in Model 4 which had all the random effects fitted proved to the 'best' among the four models using the Cp statistic ranking.

KEY WORDS: Variance Components*,* Animal Model, AIREML, Cold Carcass, Goat, Mallows Cp.

INTRODUCTION
There are more than two million goats in Zimbabwe, consisting 32 per cent of the total ruminant livestock population (CSO, 1999). About 90 per cent of these are found in the communal areas and of the 90 percent, 30 percent is in high rainfall areas. No attempts have been made to improve the genetic potential for meat production in the indigenous goats of Zimbabwe. Considerable research effort has been directed towards general management (*e.g.,* housing, feeding, health management etc) of goats. Carcass genetic evaluation work is expensive, and studies to derive accurate genetic parameters require a considerable number of animals. There are very few or no reports of comprehensive studies in this area on indigenous goats in Zimbabwe. The present study is of the few known studies that address the limited effort that has been made in carcass evaluation and estimation of genetic parameters in indigenous Matebele goats in Zimbabwe.

Estimates of genetic parameters for cold carcass mass using different animal models in the tropics for indigenous goats are scarce in literature. Models with maternal effects and corresponding genetic parameters have always been considered problematic (Meyer, 1997) due to the confounding contributions of direct and maternal effects. The animal models commonly used to estimate maternal effects include maternal genetic and permanent environmental effects (Willham, 1963). Genetic models, including maternal effects and the covariance of direct and maternal genetic effects, fit data better than the simple additive model. The aim of this study was to investigate the importance of maternal effects on cold carcass mass of the indigenous Matebele goat, using different animal models including both maternal and permanent environmental effects.

MATERIALS AND METHODS
Study Location
Matopos Research Station (20º 23' S, 31º 30' E) situated 30 km South West of Bulawayo in Zimbabwe on an altitude of 800m above sea level which experiences low erratic rainfall of less than 450 per annum (Homann *et al*., 2007). High summer temperatures, maximum and minimum mean temperatures of hottest months are 31.6 ºC and 21.4 ºC, respectively with a possibility of severe droughts (Hagreveas *et al*., 2004). The most common type of vegetation is sweet veld with comparatively high nutritional value of browse and annual grass species (Ward *et al*., 1968). Detailed description of the climate and vegetation type were given by Day *et al* (2003) and Gambiza and Nyama (2000), respectively.

Flock management
The does plus their progeny were grazed on an extensively managed dry land veld during the day from 0800 hours to 1500 hours and were penned at night. The major grass species in these pastures are *Hyparrhenia* spp., *Andropogon* spp., *Pennisetum purpur* and *Brachiaria mutica*. Depending on the availability of food and the severity of dry season, varying quantities of energy (maize stover) and protein (cotton seed cake) supplements were given when does grazed on standing hay or cut and

stacked hay. The does were fed 0.3 kg and kids 0.2 kg of cottonseed cake meal each per day from the end of May each year until the onset of the rainy season. The nutrient composition of cotton seed cake was 930g/kg dry matter, 730g/kg total digestible nutrient, 390-450g/kg protein, 300-360g/kg digestible protein and metabolizable Energy value 10.9 megajoules/kg. Water was constantly available. Mineral licks were often *ad libitum* in the dry season. Prophylaxis deworming and de-ticking in a plunge dip were regularly carried out using organophosphates. All animals were vaccinated against Pulpy Kidney and Rift Valley Fever. Does were assigned into mating flocks each year but mating of close relatives was avoided. Does of all age categories were represented in each single buck-mating group. The breeding season was between May and June. Single sire flocks comprised of one buck to 30 does. Females were introduced to the breeding flock for mating when they attained one and half years of age and bucks were not used for service until they were over one and half years. Initial buck selection was based on birth weights with male singles of over 3 kg and twins over 2.5 kg weight being retained entire, while the rest of the males were castrated using rubber ring. Most kids were born between late October and early November, which is the start of the rainy season. Kids were weighed using an electronic scale and ear tagged soon after birth and left to suckle their dams during grazing until weaning at approximately 3 months of age. Kids were separated by sex at weaning into different weaner flocks.

Slaughter Method

All slaughtered goats fasted for about 24 hours before slaughter. They were provided only with fresh drinking water. The animals were weighed individually before fasting (preslaughter weight) and 24-hour fasting (empty live weight just before slaughter. Heart girth was also measured at the time of slaughter. Slaughtering was performed according to the local method of severing jugular veins, throat and trachea without stunning. The slaughtered animals were allowed to bleed to their end usually for 10 minutes and the head was then removed at its atlanto-occipital articulation followed by flaying, evisceration and disjoining of cannons. The weight of the head, feet and skins were recorded separately. The entire gastro-intestinal tract was removed from each slaughtered goat and weighed with and without contents. A hot carcass of each animal was prepared by removing head, feet, skin, thoracic cavity contents, abdominal cavity contents, pleural cavity contents and cannons. This was weighed within one hour of slaughter. Liver, lungs, heart, kidneys, kidney fat were removed from the body cavity and weighed separately. The dressed carcasses were chilled at –200c for 24 hours which led to shrinkage in carcass. Cold carcass was obtained before cutting the carcass into different prime cuts. The weight of prime cuts (front barrel and hind barrel) was also recorded. The last rib was left attached to the hind barrel. The chilled carcass was split between the 6th and 7th ribs to obtain the rib barrel. Fat score on back fat was done by visual assessment using a scale of 1 to 3.5 designed by ILCA.

Statistical methods

Data on cold carcass mass were obtained from Matopos Research Station, Bulawayo, Zimbabwe on indigenous Matebele goat. The data included a total of 2341 pedigree cold carcass mass records from 37 sires and 218 dams of the indigenous Matebele goat. Genetic parameters were estimated using the Average Information Restricted Maximum Likelihood (AIREML) methodology (Gilmour, 1995) using an Animal Model. The analytical models included fixed effects of sex, age at slaughter and year of slaughter. Fixed factors for models for all traits were determined through preliminary analyses using procedure GLM of SAS (1996) (SAS Inst. Inc., Cary, NC). Fixed factors (main effects and interactions) and covariates were tested and removed from the model if found non-significant (P> 0.01), with non-significant effects rejected sequentially. Five animal models were used excluding a simple animal model with additive direct genetic effects as the only random effect because there is a tendency of overestimating direct heritability (Meyer, 1992). Model (1) used maternal effects as an uncorrelated random effect. Model (2) ignored maternal genetic effects and included permanent environmental maternal effect as the second random effect. Model (3) considered both maternal and permanent environmental maternal effect as uncorrelated to the additive direct genetic effect. Model (4) considered maternal effects as the second random effect but allowed for covariance between the direct and maternal effects. The following models were used:

$$y=Xb + Zaa + Zmm + e \quad (1)$$
$$y=Xb + Zaa + Zcc + e \quad (2)$$
$$y=Xb + Zaa + Zmm + Zcc + e \quad Cov(a,m) = A\sigma am= 0 \quad (3)$$
$$y=Xb + Zaa + Zmm + Zcc + e \quad Cov(a,m)=A\sigma am \quad (4)$$

where Y is the vector of observations b, a, m, c and e are the vectors of fixed effects, direct additive genetic effects (animal), maternal genetic effects, permanent environmental effect of dam and the residual, respectively. X, Za, Zm, and Zc, are the incidence matrices of fixed effects, direct additive genetic effects, maternal genetic effects and permanent environmental effect of dam. (Co)variances were described as: $V(a) = \sigma^2_a A$, $V(m) = \sigma^2_m A$, $V(c) = \sigma^2_c I$, $V(e) = \sigma^2_e I$ and $Cov (a,m) = \sigma_{am} A$, 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 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 relationship matrix between animals, I the identity matrix. In the present study the fixed part of the model included age of dam, sex and year of birth of progeny. Heritability of total additive genetic contribution to a maternally influenced trait was calculated according to the following equation (Willham, 1972).

$$h^2_T = \frac{\sigma^2_a + 0.5\sigma^2_m + 1.5\sigma^2_{am}}{\sigma^2_p}$$

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 β_0, s^2 is the residual mean square from the largest postulated containing all the effects and n is the total number of records. s^2 is presumed to be a reliable unbiased estimate of the error of variance σ^2, i.e.

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

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

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

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 $E\left(C_p\right) = p$, 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 fall below the $C_p = p$ line because of random variation.

RESULTS AND DISCUSSION

The descriptive statistics of the data set, covariance components and Mallows C_p statistic values under five different single trait models with most appropriate model (in bold) determined using Mallows Cp statistic test regarding cold carcass mass are shown table 1, 2 and 3, respectively. It is evident that the model used in the analysis influenced the relative values of direct heritability and maternal heritability. Estimates of the direct heritability had a range of 0.05 to 0.26 and estimates of the maternal heritability were 0.01 to 0.10. Maternal heritability were lower than direct heritability in all models which was an indication that cold carcass was largely be influenced by the individual genetic potential than the maternal genetic potential. In current study on cold carcass mass of Matebele goat the inclusion of both maternal genetic and permanent environmental maternal effects, with a covariance between direct and maternal effects reduced the Cp function as compared with other models.

TABLE 1. Structure and descriptive statistics of the data set of cold carcass mass of Matebele goats of Zimbabwe

Item	
Pedigree records	2341
No base parents	255
No animals	2596
No sires	37
No dams	218
Mean (kg)	12.16
Coefficient of Determination (%)	42
Coefficient of Variation (%)	27.40
Standard Deviation (kg)	4.30

TABLE 2. Estimates of covariance components and genetic parameters of cold carcass mass in Matebele goat of Zimbabwe.

Item	Model 1	Model 2	Model 3	Model 4
σ^2_a	2.46		1.67	3.35
σ^2_m	0.10	3.17	0.58	1.28
σ^2_{am}				0.48
σ^2_{pe}		0.24	0.38	0.49
σ^2_e	9.50	9.02	9.69	8.19
σ^2_p	12.06	12.43	12.32	13.79
h^2_a	0.21	0.26	0.14	0.25
se	0.002	0.002	0.001	0.001
h^2_m	0.000		0.05	0.10
c_{am}				0.04
h^2_T	0.21	0.26	0.16	0.34
r_{am}				0.23
c^2		0.00	0.00	0.00

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

TABLE 3. The computed Mallows C_P statistic used to rank animal models

Model	C_P	Ranking
4	8.23	1
2	9.06	2
1	9.55	3
3	9.75	4

On the other hand in model 4 the maternal heritability effects (h^2_m) was significant and therefore this model was considered the most fit for cold carcass mass. Including permanent environmental maternal effects in Model 2 resulted in an increase in direct heritability by 23% compared to Model 1 with maternal genetic effects alone. In fact in Model 3 in which both direct and maternal genetic effects were taken into account, 5% and 4% of the total phenotypic variance was attributable to direct and maternal effects, respectively. When one of the maternal effects was ignored the total variance was more attributed to the direct genetic variance resulting in overestimating of direct heritability. Inclusion of a covariance between direct and maternal effects in Model 4 resulted in highest total genetic effects. However this could have been caused by the positive correlation (r_{AM}) of direct and maternal genetic effects. The nature of the correlations which may be positive or negative can sometimes be attributed to structure of the data (Lee and Pollack, 1997; Robinson, 1996b). Hence the use of this model would maximize total genetic effects for maximum selection response. Authors could not explain the negative covariance between direct and maternal genetic effects while excluding maternal effects in Model 5. However, this could be an indication that the maternal effect could be important. The results of Mallows C_p statistic is as shown in Table 3 and. Unfortunately there is no point falling below the C_p=p line but that point from model (4) is fairly closest one. As a result model (4) 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

CONCLUSION

The study shows that including maternal effects for cold carcass mass of indigenous Matebele goat will improve estimates of direct heritability, especially where permanent environmental effects are accounted for. Maternal heritability were lower than direct heritability estimates, indicating a greater genetic influence of individual animals genetic potential than the influence on this trait Can conclude that inclusion of maternal genetic effects and/or maternal environmental effects would have a bearing on the ranking of models, where in the present study Model 4 fit data better than the other models.

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