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Impact of maternal effects on ranking of animal models for genetic parameter estimation for birth weight in male Afrikaner cattle in Zimbabwe

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A B S T R A C T

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 four animal models from 1359 pedigree male birth weight records of Afrikaner 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 direct-maternal genetic covariance. The direct heritability (h^2_a) ranged from 0.40 to 0.43 when the maternal genetic effects were included in the model, whereas h^2_a was highest 0.45 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 0.09 and 0.09 when the permanent environmental effect of the dam was added. The permanent environmental effect of the dam was negligible. Weak negative covariances between direct and maternal genetic effects (σ^2_{am}) was observed in model which had all the random effects fitted and proved to the appropriate among the four models using the log likelihood ration test.

1. Introduction

The Afrikaner is a predominant cattle breed in southern Africa (Oliver, 1983) and was developed as a draft animal with little attention being given to fertility. Numerous studies have investigated the importance of maternal effects for pre weaning weight in a mixed model setting for various livestock species (Maniatis and Pollot, 2003). Birth is an early measurable trait which is influenced by the individual's genotype and environment and by the maternal ability of the dam, which is also influenced by the genotype and environment each is a source of variation which has been studied independently (Burferning and Kress). Birth weight could be utilized to choose among populations or a criteria preliminary selection in a given population. For birth weight maternal breeding values takes into account uterine environment which has been found significantly affecting birth weight (Joubert and Hammond, 1958). Ferrell (1991) showed that uterine environment can both restrict and allow for optimum growth of a fetus.

An animal model used to estimate maternal effects typically include direct and maternal genetic effects and maternal permanent environmental effects and considers the covariance between direct and maternal effects (Diop et al 1999; Waldron et al 1993). Genetic models including maternal effects and the covariance of direct and maternal genetic effect, fit data better than simple additive model (Dodenhoff et al 1999). However Meyer (1992b) pointed out that such model may be suboptimal and need to be improved. Although selection schemes for early growth that ignore maternal effects are likely to produce suboptimal genetic response (Gerstmayr, 1992). High negative correlations between direct and maternal genetic effects for early weight trait are common but biologically impossible (Meyer, 1994). Therefore the interpretation of results is not straight forward, reflecting the difficulty in separating these effects from the permanent environmental components when all are estimated in the same analysis (Maniatis and Pollot, 2003). The confusion between these effects leads to high sampling errors and strong sampling correlations between the estimates and often the quantity and quality of data available are insufficient to separate them adequately (Meyer, 1992a).

2. Materials and methods

2.1. 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 (Homann et al., 2007). 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 (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 (Ncube, 2005) and other livestock (Van Rooyen et al., 2004). 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 history and management

In 1957 two lines of grade Afrikaner cows each were established from a common gene pool and subjected to different nutritional and regimes, termed environments. The supplemented line cows were offered supplements during the dry season (9 kg silage and 1 kg cotton seed meal per head per day) and were mated to calve early (October to December) relative to the expected onset of rains. The non supplemented line cows were mated to bulls two months later than those in supplemented line. Selection within line was based on weight at weaning for bulls and weight prior to mating for replacement heifers. Cows were culled for poor productivity (infertility and low calf weaning weight)

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 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 and weaned at an average age of 210 days.

2.3. Statistical methods

Data on birth weight in male Afrikaner cattle were obtained from Matopos Research Station, Bulawayo, Zimbabwe. The data included a total of 1359 male's pedigree birth weight records from 32 sires and 346 dams of male Afrikaner cattle of Zimbabwe. 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 year of birth and age of dam. 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.

A simplex algorithm is used to search for variance components to minimize the function, -2log likelihood (L). Convergence was assumed when the variance of the function values (-2logL) of the simplex was $<10^{-8}$. A log likelihood ratio test was used to choose the most suitable random effects model for post weaning growth. The reduction in -2 logs L when a random effect was added to the model was calculated. If this reduction was greater than the value of the Chi-square distribution with one degree of freedom ($p<0.05$) the additional random effect fitted was considered significant. When log likelihood did not differ significantly ($p>0.05$), the model that had the fewer number of parameters was selected as the most appropriate. Four different animal models were fitted for male birth weight by ignoring or including maternal genetic effect, covariance between direct-maternal effects, maternal environmental effect that the four different models were:

Model 1 was a model with animal additive genetic effects and maternal genetic effect as the random effect other than the residuals:

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

Model 2 included random effect of permanent maternal environment

$$y=Xb + Z_a a + Z_c c + e \qquad (2)$$

Model 3 included both permanent environmental and genetic maternal effects but did not allowed correlation between direct and maternal genetic random effects.

$$y=Xb + Z_a a + Z_m m + Z_c c + e \qquad Cov(a,m)\neq A\sigma_a m \qquad (3)$$

Model 4 was the same as model 3 but assumed correlation between direct and maternal genetic random effects.

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

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) = σ^2_m A, V(c) = σ^2_c I, V (e) = $\sigma^2_e I$ and Cov (a,m) = σ_{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 at slaughter, sex and year of slaughter of progeny. Heritability of total additive genetic contribution to a maternally influenced trait was calculated according to the following equation (Willham, 1972).

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

3. Results and Discussion

Means, standard deviation and characteristics of the data structure and covariance components are summarized in Table 1 and 2. It was noted 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 birth weight in male Afrikaner cattle. Comparison of Model 1 and 2 showed that exclusion of permanent environment maternal effects slightly increased the direct heritability by 5%, however the direct heritability deceased by 7% when both maternal genetic and permanent environmental effects were take into account.

Table 1
Structure and descriptive statistics of the data set of male Afrikaner cattle of Zimbabwe.

Item	Magnitude
Pedigree records	1359
No base parents	161
No animals	2266
No sires	32
No dams	346
Mean (kg)	30.54
Coefficient of Variation (%)	13.30
Standard Deviation (kg)	4.86
Coefficient of Determination (%)	0.50

Table 2
Estimates of covariance components and genetic parameters of birth weight in male Afrikaner cattle of Zimbabwe.

Item	Model 1	Model 2	Model 3	Model 4
σ^2_a	22.11	23.11	21.14	21.40
σ^2_m	0.45		4.77	4.80
σ^2_{am}				-0.27
σ^2_{pe}		0.80	0.36	0.14
σ^2_e	28.85	28.01	26.46	26.25
σ^2_p	51.41	51.93	52.74	52.32
h^2_a	0.43	0.45	0.40	0.41
h^2_m	0.00		0.09	0.09
r_{am}				-0.003
c^2		0.02	0.01	0.00
h^2_T	0.43	0.45	0.45	0.36
-2Log L	15574	15563	15350	15248

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
r_{am} = direct and maternal genetic correlation
h^2_T = total heritability (total genetic effect)

Estimates of relative variance due to maternal permanent environmental effects decreased by 55% when both maternal genetic and permanent environmental effects were included in Model 3, and decreased by 83% when a genetic correlation between direct and maternal effects was assumed. The log likelihood showed a better fit with the full model (Model 4). In agreement with the review of Robison (1981), on the whole estimates of heritability and relative values due to permanent environmental effects for Model 3 were well within the range of comparable literature values. Koch et al., (1973) reported that genetic and permanent environmental component of maternal ability and covariance of individual and maternal effects account for 15 to 20 % of variation in birth weight which may be closer to our observation of 10%. The present study indicates that the maternal component for birth weight in the population is much of maternal genetic than maternal environmental. Inclusion of a covariance between direct and maternal genetic effects in Model 4 did not change the magnitude of maternal genetic effects. The range of maternal heritability of birth weight in male Afrikaner cattle in the present study were within the range reported by several authors. Comparable maternal heritability estimates range of 0.05 – 0.14 were reported in literature (Bertrand et al., 1987; Trus et al., 1988; Meyer, 1992) .Brown et al., (1969); Nelsen et al., (1984); Cantent et al., (1988) and Trus et al., (1988) reported higher birth weight maternal heritability estimates of 0.30, 0.82, 0.27 and 0.42, respectively in beef cattle. The maternal heritability estimates were lower than direct heritability which coincides with the findings of several authors(Meyer, 1992; Brown et al., 1996; Trus et al., 1988) however in contrary with what was reported elsewhere (Cantet et al., 1993; Nelsen et al., 1984,) who suggested that estimates before 1984 direct heritability were smaller than maternal heritability and genetic correlation between direct and maternal were highly negative, whereas more recent reports suggest that direct heritability estimates are larger than maternal heritability estimates with correlation between direct and maternal being also negative. Therefore the estimate in the present study are in the lower range as compared to those report din literature but agrees quite well with the notion that recent estimates of direct heritability are higher than maternal heritability estimates.

The proportion of variance due to permanent environmental maternal effects were negligible however in other species high estimates of permanent environmental maternal effects have been associated with permanent environmental effects of the uterus and the effects of multiple birth in small ruminants (Snyman et al., 1995). The estimates of ratio of maternal permanent environment variance to phenotypic variance, c^2 was of the same magnitude reported in Gobra cattle (Diop et al., 1999). Permanent environment effects results from incidence that affects all progeny of the same cow in case of birth weight (Joubert and Hammond, 1958; Ferrell 1991). The negative correlation of direct and maternal genetic effects in the present study could be explained from evolutionary point of view that it prevents species to becoming increasingly larger (Cundiff, 1972). However several workers mentioned that a possible existence of a negative environmental covariance between dam and offspring could result in a biased estimation of genetic correlation between direct and maternal genetic effects (Meyer, 1992). In this population it seemed the correlation between direct and maternal genetic effects was weak and not important. The inclusion of correlation between direct and maternal genetic in Model 4 did not change the magnitude of maternal heritability as compared to Model 3. Modeling different non genetic factors has influenced the negativity of covariance between direct and maternal genet effects in beef cattle (Robbinson, 1996a, b; Lee and Pollak, 1997; Meyer, 1997; Dodenhoff et al., 1999). The total genetic effects for birth weight in this population was high hence genetic response could be high.

4. Conclusion

Inclusion and /or exclusion of the direct and indirect maternal genetic effects in a model may influence the magnitude of direct heritability, however the permanent environmental effects of the dam was negligible in this population. A full animal model must be used for genetic evaluation of birth weight of male Afrikaner cattle

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