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ESTIMATES OF DIRECT, MATERNAL AND GRANDMATERNAL GENETIC EFFECTS FOR GROWTH TRAITS IN GOBRA CATTLE

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ABSTRACT

Estimates of genetic parameters for birth (N = 3909), weaning (N = 3425), yearling (N = 2764) and final (N = 2144) weights were obtained from the records of Gobra cattle collected at the Centre de Recherches Zootechniques de Dahra, Senegal. Three animal models were fitted to obtain estimates by REML using an average information (AI) approach. Model 1 considered random direct, maternal genetic and maternal permanent environmental effects. In model 2, a general grandmaternal effect was added to the random effects considered in model 1, and in model 3, the general grandmaternal effect was divided into grandmaternal genetic and grandmaternal permanent environmental effects. All models allowed covariances among genetic effects. The inclusion of grandmaternal effects in models 2 and 3 did not change the estimates of the genetic parameters compared to model 1. Variances attributable to grandmaternal effects became negative and were set close to zero, except for yearling weight for which grandmaternal heritability was 0.03 ± 0.03. The estimates for direct and maternal heritabilities were, respectively, 0.08 ± 0.03 and 0.03 ± 0.02 for birth, 0.20 ± 0.05 and 0.21 ± 0.05 for weaning, 0.26 ± 0.07 and 0.16 ± 0.07 for yearling and 0.14 ± 0.06 and 0.16 ± 0.06 for final weights. The estimates of the genetic correlation between direct and maternal effects for birth, weaning, yearling and final weights were -0.17 ± 0.40, -0.58 ± 0.32, -0.52 ± 0.34 and -0.34 ± 0.37, respectively. For yearling weight with grandmaternal heritability estimated to be only 0.03, model 3 gave estimates of the genetic correlation between direct and grandmaternal effects and between maternal and grandmaternal effects of 0.28 ± 0.48 and -0.33 ± 0.67, respectively. Estimates of direct and maternal heritabilities were unchanged when grandmaternal effects were not included in the model.

INTRODUCTION

Growth traits of beef cattle are known to be influenced by maternal effects. Early reports (Koch and Clark, 1955; Willham, 1963) mentioned the possible influence of grandmaternal effects. Falconer (1965) considered the maternal effect as a linear function of a mother's phenotypic value influenced by all maternal ancestors. The so-called 'fatty udder syndrome' is an example of a grandmaternal effect: a granddam with a high maternal ability may over-feed her daughter and thereby have a negative influence on her daughter's maternal ability by inhibiting development of her udder tissue (Totusek *et al.*, 1971). The importance of maternal effects in beef cattle has been widely reported (Koch, 1972; Baker, 1980; Robison, 1981; Meyer, 1992). Studies on African cattle populations have reported a strong maternal influence on growth traits (Tawah *et al.*, 1993; Khombe *et al.*, 1995; Diop and Van Vleck, 1998).

Animal models used to estimate maternal effects typically include direct and maternal genetic effects and maternal permanent environmental effects and consider the covariance between genetic effects. Meyer (1992) pointed out that such models may be suboptimal and need to be improved. The objective of this study was to evaluate the influence of including grandmaternal effects in a model for estimating genetic parameters for growth traits in Gobra cattle for which maternal effects have previously been shown to be important.

MATERIAL AND METHODS

The records of weight at birth, 6, 12, and 18 months were obtained from the Gobra herd at the Centre de Recherches Zootechniques de Dahra, Senegal. 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 July to September. The mean annual rainfall from 1964 to 1988 was 360 mm. The mean annual temperature is 28°C. The vegetation is described as savanna type dominated by *Acacia* sp. and annual grasses. Annual biomass production is closely related to the amount of rainfall the area receives each year.

Native pasture is the main source of feed. The quantity and quality of the pasture vary considerably during the year. During the rainy season, pastures are of good quality and abundant. During the dry season, the nutritive value of the forage decreases and supplemental feeding with ground nutcake or cottonseed is provided, especially for suckling cows and weaned calves.

Breeding females were randomly assigned to sires (30-50 cows/sire) for a breeding season from December to March. Cows that were not pregnant 3 months after the breeding season started were reassigned to a different bull.

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Over the years, the size of the herd has fluctuated around 300 cows. Males and females were selected based on weight at 6 months (weaning). Males were again selected based on their weight at 18 months after which the 10 best males underwent a growth performance test before final selection for the two or three bulls to be used as replacement bulls. Replacement females were selected at 24 months based on their weight. About 5% of the males and 80% of the females selected after weaning were used as replacements. Culling of the cows was based on poor reproductive performance (long calving interval or failure to calve after two breeding seasons) or poor growth performance of offspring.

The data for the present analyses consisted of the records of animals born from 1963 to 1989. Consistency checks were performed upon the identification of the animals and their pedigrees. Records of the progeny of sires with less than five progeny were deleted from the analysis. The PROC MIXED option of SAS (SAS, 1992) was used to test the significance of the fixed effects of month of birth, year of birth, sex and parity in a model with sire considered to be a random effect.

For estimation of the genetic parameters, three animal models were fitted for the four traits considered :

Model 1: $\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}_1\,\mathbf{a} + \mathbf{Z}_2\,\mathbf{m} + \mathbf{W}_1\,\mathbf{c} + \mathbf{e}$
Model 2: $\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}_1\,\mathbf{a} + \mathbf{Z}_2\,\mathbf{m} + \mathbf{W}_1\,\mathbf{c} + \mathbf{W}_2\,\mathbf{q} + \mathbf{e}$
Model 3: $\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}_1\,\mathbf{a} + \mathbf{Z}_2\,\mathbf{m} + \mathbf{Z}_3\,\mathbf{g} + \mathbf{W}_1\,\mathbf{c} + \mathbf{W}_2\,\mathbf{q} + \mathbf{e}$

where **y** is an N x 1 vector of observations, β is the vector of fixed effects of year of birth, month of birth, sex and parity of dam, **a**, **m** and **g** are vectors of breeding values for direct, maternal and grandmaternal genetic effects, **c** and **q** are vectors of maternal permanent environmental and grandmaternal permanent environmental effects and **e** is an N x 1 vector of residual random effects, and $\mathbf{X}$, $\mathbf{Z}_1$, $\mathbf{Z}_2$, $\mathbf{Z}_3$, $\mathbf{W}_1$ and $\mathbf{W}_2$ are known incidence matrices relating observations to their respective fixed and random effects. Matrices $\mathbf{Z}_1$, $\mathbf{Z}_2$ and $\mathbf{Z}_3$ were augmented for animals without records that were included in the relationship matrix.

For the most complete model (model 3), E (**y**) = $\mathbf{X}\beta$ and

$$V\begin{bmatrix}\mathbf{a}\\ \mathbf{m}\\ \mathbf{g}\\ \mathbf{c}\\ \mathbf{q}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & A\sigma_{ag} & 0 & 0 & 0\\ A\sigma_{am} & A\sigma_m^2 & A\sigma_{mg} & 0 & 0 & 0\\ A\sigma_{ag} & A\sigma_{mg} & A\sigma_g^2 & 0 & 0 & 0\\ 0 & 0 & 0 & I_{Nd}\sigma_c^2 & 0 & 0\\ 0 & 0 & 0 & 0 & I_{Ng}\sigma_q^2 & 0\\ 0 & 0 & 0 & 0 & 0 & I_N\sigma_e^2 \end{bmatrix}$$

where Nd and Ng are numbers of dams and granddams, respectively, and N is the number of records, **A** is the numerator relationship matrix among animals in the pedigree file, and the **I** matrices are identity matrices of specified order. Models 2 and 3 require each animal with a record to have a granddam. Therefore, "dummy" granddam identification was assigned for records with unknown granddam implying the assumption that these granddams are unrelated among themselves and unrelated to those with known identification. Table I summarizes the data used in the analyses.

Table I - Characteristics of the data including weights of Gobra cattle at different ages.

Numbers	Birth	Weaning	Yearling	Final
Records	3909	3425	2764	2144
Sires	64	64	63	62
Dams	1340	1203	1077	939
Maternal granddams	1038	908	805	700
Assigned granddams	493	384	308	240
Records with assigned granddams	1258	944	701	537
Mean (kg)	24.9	108.5	158.1	202.4
Unadjusted standard deviation (kg)	4.6	23.8	30.0	35.7

Components of variance were estimated by restricted maximum likelihood (REML) using an average information algorithm (Johnson and Thompson, 1995). The algorithm is a Newton method which uses first and second derivatives of the logarithm of the likelihood given the data to find estimates of variance components that maximize the likelihood function.

A preliminary analysis of variance showed that the fixed effects of month and year of birth, sex, and parity were significant. Consequently, these effects were included in all three models.

Estimates of relative variances attributable to additive direct (h_a^2), maternal (h_m^2) and grandmaternal (h_g^2) genetic effects were calculated as ratios of the estimates of additive direct (σ_a^2), maternal genetic (σ_m^2) and grandmaternal genetic (σ_g^2) variances, respectively, to the phenotypic variance (σ_p^2). The direct-maternal (r_{am}), direct-grandmaternal (r_{ag}) and maternal-grandmaternal (r_{mg}) genetic correlations were estimated as ratios of the direct-maternal (σ_{am}), direct-grandmaternal (σ_{ag}) and maternal-grandmaternal (σ_{mg}) genetic covariances to the square roots of the products of σ_a^2 and σ_m^2, σ_a^2 and σ_g^2, and σ_m^2, and σ_g^2, respectively. The estimates of relative variances attributable to maternal permanent environmental effects (c^2) and grandmaternal permanent environmental effects (q^2) were calculated as the ratios of the estimates of maternal (σ_c^2) and grandmaternal (σ_q^2) permanent environmental variances to the phenotypic variance (σ_p^2).

RESULTS

The variance components and estimates of genetic parameters (ratios and correlations) for birth weight are

presented in Table II. The direct (h^2_a) and maternal (h^2_m) heritabilities were 0.08 ± 0.03 and 0.03 ± 0.02, respectively, for the three models. The estimates were similar for all effects included in all models. The estimates of variances attributable to grandmaternal genetic and/or grandmaternal permanent environmental effects were close to zero in models 2 and 3. The estimate of the correlation between direct and maternal genetic effects was -0.17 ± 0.41. The estimate of c^2 was 0.04 ± 0.02 for all models. As expected from the estimates associated with grandmaternal effects, the three models resulted in essentially the same value for the log likelihood.

The pattern of the estimates for weaning weight (Table II) was similar to that pattern of estimates for birth weight, i.e., the estimates of the variance and covariance components for included effects were of the same magnitude in the different models. Variances attributable to grandmaternal effects were small, with values near zero. The estimates of direct and maternal heritabilities were 0.20 ± 0.05 and 0.21 ± 0.05, respectively. The direct-maternal genetic correlation was -0.58 ± 0.32 and c^2 was 0.15 ± 0.04.

The estimates for yearling weight (Table III) showed that the inclusion of grandmaternal genetic effects in model 3 slightly increased the additive direct genetic variance with an estimate of grandmaternal genetic heritability (h^2_g) of 0.03 ± 0.03. The estimated values of the genetic correlations between the direct and grandmaternal genetic effects (r_{ag}) and between the maternal and grandmaternal effects (r_{mg}) were small to moderate with large standard errors (0.28 ± 0.48 and -0.33 ± 0.67, respectively). The estimates of variance components attributable to direct and maternal effects and their correlation were similar for the three models. The estimates of h^2_a and h^2_m were 0.26 ± 0.07 and 0.16 ± 0.07, respectively. The estimate of r_{am} was -0.55 ± 0.37 for model 3. The estimates of c^2 were 0.09 ± 0.03 for model 1 and 0.07 ± 0.04 for model 3.

The estimate of variance for final weight attributable to grandmaternal effects was near zero (Table III). The estimates of direct (h^2_a) and maternal (h^2_m) heritabilities were 0.14 ± 0.06 and 0.16 ± 0.06, respectively. The estimate of c^2 was 0.04 ± 0.05. The correlation between the direct and maternal genetic effects was -0.34 ± 0.37.

Table II - Estimates of the components of variance and genetic parameters for birth and weaning weights of Gobra cattle.

	Birth weight			Weaning weight		
Parameters[a]	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
σ^2_a	1.24	1.24	1.24	82.0	82.1	82.1
σ^2_m	0.54	0.53	0.53	87.8	86.5	86.6
σ^2_g			0.0			0.0
σ_{am}	-0.14	-0.14	-0.14	-49.4	-49.2	-49.2
σ_{ag}			0.0			0.0
σ_{mg}			0.0			0.0
σ^2_c	0.65	0.61	0.61	61.9	60.3	60.2
σ^2_q		0.04	0.04		2.4	2.4
σ^2_e	13.68	13.68	13.68	228.6	228.6	228.6
σ^2_p	15.97	15.96	15.96	410.9	410.7	410.8
h^2_a	0.08 ± 0.03	0.08 ± 0.03	0.08 ± 0.03	0.20 ± 0.05	0.20 ± 0.05	0.20 ± 0.05
h^2_m	0.03 ± 0.02	0.03 ± 0.02	0.03 ± 0.02	0.21 ± 0.05	0.21 ± 0.05	0.21 ± 0.05
h^2_g			0.00 ± 0.00			0.00 ± 0.00
r_{am}	-0.17 ± 0.40	-0.17 ± 0.40	-0.17 ± 0.40	-0.58 ± 0.32	-0.58 ± 0.32	-0.58 ± 0.32
r_{ag}			0.00 ± 0.00			0.00 ± 0.00
r_{mg}			0.00 ± 0.00			0.00 ± 0.00
c^2	0.04 ± 0.02	0.04 ± 0.02	0.04 ± 0.02	0.15 ± 0.03	0.15 ± 0.04	0.15 ± 0.04
q^2		0.00 ± 0.02	0.00 ± 0.02		0.01 ± 0.02	0.01 ± 0.02
-2 log L[b]	14714.3	14714.3	14714.3	23477.7	23477.7	23477.7

[a]σ^2_a, Direct genetic variance; σ^2_m, maternal genetic variance; σ^2_g, grandmaternal genetic variance; σ_{am}, direct and maternal genetic covariance; σ_{ag}, direct and grandmaternal genetic covariance; σ_{mg}, maternal and grandmaternal genetic covariance; σ^2_c, maternal permanent environmental variance; σ^2_q, grandmaternal permanent environmental variance; σ^2_e, temporary environmental variance; σ^2_p, phenotypic variance; h^2_a, direct heritability; h^2_m, maternal heritability; h^2_g, grandmaternal heritability; r_{am}, direct-maternal genetic correlation; r_{ag}, direct-grandmaternal genetic correlation; r_{mg}, maternal-grandmaternal genetic correlation; $c^2 = \sigma^2_c / \sigma^2_p$, $q^2 = \sigma^2_q / \sigma^2_p$. [b]-2 log L = Minus twice the log likelihood given the data.

Table III - Estimates of components of variance and genetic parameters for yearling and final weights for Gobra cattle.

	Yearling weight			Final weight		
Parameters[a]	Model 1	Model 2	Model 3	Model 1	Model 2	Model 3
σ_a^2	169.7	169.4	177.3	129.3	129.1	129.1
σ_m^2	108.7	106.9	107.8	144.9	140.5	140.5
σ_g^2			20.8			0.0
σ_{am}	-70.4	-70.0	-76.6	-46.7	-45.3	-45.3
σ_{ag}			16.8			0.0
σ_{mg}			-15.4			0.0
σ_c^2	57.1	53.2	48.5	42.9	35.1	35.2
σ_q^2		5.2	0.0		10.3	10.2
σ_e^2	398.4	398.5	394.1	633.0	633.3	633.3
σ_p^2	663.5	663.2	663.2	903.4	903.0	902.9
h_a^2	0.26 ± 0.07	0.26 ± 0.07	0.26 ± 0.07	0.14 ± 0.06	0.14 ± 0.06	0.14 ± 0.06
h_m^2	0.16 ± 0.05	0.16 ± 0.05	0.16 ± 0.07	0.16 ± 0.06	0.16 ± 0.06	0.16 ± 0.06
h_g^2			0.03 ± 0.03			0.00 ± 0.00
r_{am}	-0.52 ± 0.34	-0.52 ± 0.35	-0.55 ± 0.37	-0.34 ± 0.37	-0.34 ± 0.37	-0.34 ± 0.37
r_{ag}			0.28 ± 0.48			0.00 ± 0.00
r_{mg}			-0.33 ± 0.67			0.00 ± 0.00
c^2	0.09 ± 0.03	0.08 ± 0.04	0.07 ± 0.04	0.05 ± 0.04	0.04 ± 0.05	0.04 ± 0.05
q^2		0.01 ± 0.02	0.00 ± 0.00		0.01 ± 0.03	0.01 ± 0.03
-2 log L[b]	20335.2	20335.1	20334.2	16445.6	16445.4	16445.4

[a]σ_a^2, Direct genetic variance; σ_m^2, maternal genetic variance; σ_g^2, grandmaternal genetic variance; σ_{am}, direct and maternal genetic covariance; σ_{ag}, direct and grandmaternal genetic covariance; σ_{mg}, maternal and grandmaternal genetic covariance; σ_c^2, maternal permanent environmental variance; σ_q^2, grandmaternal permanent environmental variance; σ_e^2, temporary environmental variance; σ_p^2, phenotypic variance; h_a^2, direct heritability; h_m^2, maternal heritability; h_g^2, grandmaternal heritability; r_{am}, direct-maternal genetic correlation; r_{ag}, direct-grandmaternal genetic correlation; r_{mg}, maternal-grandmaternal genetic correlation; $c^2 = \sigma_c^2/\sigma_p^2$; $q^2 = \sigma_q^2/\sigma_p^2$. [b]-2 log L = Minus twice the log likelihood given the data.

DISCUSSION

The inclusion of grandmaternal effects in the model did not change the estimates of the direct and maternal heritabilities or of the genetic correlation between the direct and maternal genetic effects for the four traits analyzed. However, for yearling weight, the inclusion of grandmaternal genetic effects in model 3 slightly increased the additive direct genetic variance. The estimates of variance attributable to grandmaternal effects were very small or zero, suggesting that these effects did not play an important role in these traits in this population of cattle which exhibits large differences in maternal genetic effects. Similar results were found with native Korean cattle (Lee *et al.*, 1998) which also exhibit large differences in 4 month and 6 month weights as a result of maternal genetic effects. Dodenhoff *et al.* (1998) reported significant variation in weaning weight attributable to grandmaternal effects in a population of Hereford cattle with moderate expression of maternal effects and a large negative correlation between direct and maternal genetic effects. These authors noted that when estimates of grandmaternal heritability were not zero, the estimates of maternal heritability increased, whereas direct heritability was not affected. A similar pattern was also observed in another population of Hereford cattle that had undergone long-term selection in Montana (USA) (Ferreira, G.B., MacNeil, M.D., and Van Vleck, L.D., unpublished results).

For yearling weight, there was a small, positive correlation between direct and grandmaternal genetic effects (r_{ag}) and a moderate, negative correlation between the maternal and grandmaternal genetic effects (r_{mg}). The standard errors associated with these estimates were large which means they are not significantly different from zero. Dodenhoff *et al.* (1998) reported small to large positive estimates of r_{ag} at weaning for different lines of Hereford cattle. The estimates for r_{mg} were negative and large for weaning weight in these lines. The negative correlation between direct and maternal and between maternal and grandmaternal genetic effects may be explained as the negative influence of dams on the maternal ability of their female offspring through overfeeding (Koch, 1972). Tawah *et al.* (1993) suggested that these negative correlations may reflect adaptation of the animals to a dry tropical environment where food resources are scarce. In such an environment, small cows tend to meet their nutritional requirements for maintenance and growth of their calves more easily than larger cows. The latter would produce smaller calves, especially at weaning, than would smaller cows of similar age.

Maternal heritability was important in all cases, except birth weight, with estimates of the same magnitude as for direct heritability. The estimates for weaning weight agreed with values reported for Hereford cattle (Meyer,

1992), Nelore cattle (Eler *et al.*, 1995), Wakwa and Gudali cattle (Tawah *et al.*, 1993), and Mashona cattle (Khombe *et al.*, 1995). For yearling and final weights, the estimates of direct, but not maternal, heritability were consistent with most published estimates. Maternal effects would be expected to diminish at these ages because the animals no longer depend on their mothers. Relatively high estimates of h^2_m were also reported by Eler *et al*. (1995) and Mackinnon *et al.* (1991) at yearling and later ages, respectively. These authors both also suggested that for animals raised on pasture with little or no feed supplement, the length of time between weaning and yearling ages may not be enough to buffer maternal effects present at weaning.

The estimate of the ratio of maternal permanent environmental variance to the phenotypic variance, c^2, was larger for weaning weight than for the other traits, as also reported by Eler *et al.* (1995) and Meyer (1992). Permanent environmental effects result from incidents that affect all progeny of the same cow. The effects before weaning may be caused by sequels of diseases or accidents to the udder, which will affect the milk production of the dam, whereas the estimate of c^2 at later ages may reflect a carryover effect on weaning weight.

CONCLUSIONS

Grandmaternal effects do not play an important role in the weight of Gobra cattle at birth, weaning (6 months), yearling (12 months) and 18 months of age. In contrast, maternal effects are important, even at 18 months of age. Models for the genetic evaluation of Gobra cattle could safely ignore grandmaternal effects but should include direct and maternal genetic effects with the corresponding direct-maternal genetic covariance.

RESUMO

Foram obtidas as estimativas dos pesos ao nascimento (N = 3909), ao desmame (N = 3425), com 1 ano de idade (N = 2764) e final (N = 2144) a partir dos registros de gado Gobra coletados no Centro de Pesquisas em Zootecnia de Dahra, Senegal. Três modelos animais foram adaptados para obter estimativas por REML usando uma abordagem de informação média (AI). O modelo 1 considerou os efeitos ambientais aleatórios direto, genético maternal e maternal permanente. No modelo 2, um efeito geral relativo às avós foi adicionado aos efeitos aleatórios considerados no modelo 1, e no modelo 3 o efeito geral relativo às avós foi dividido em efeitos ambientais genético e permanente. Todos os modelos admitiram covariâncias entre os efeitos genéticos. A inclusão dos efeitos relativos às avós nos modelos 2 e 3 não alterou as estimativas dos parâmetros genéticos comparados com o modelo 1. As variâncias atribuíveis aos efeitos relativos às avós tornaram-se negativas e foram posicionadas próximas a zero, exceto para o peso com 1 ano, para o qual a herdabilidade relativa à avo foi 0,03 ± 0,03. As estimativas para as herdabilidades direta e maternal foram, respectivamente, 0,08 ± 0,03 e 0,03 ± 0,02 para peso ao nascimento, 0,20 ± 0,05 e 0,21 ± 0,05 para peso ao desmame, 0,26 ± 0,07 e 0,16 ± 0,07 para peso com 1 ano e 0,14 ± 0,06 e 0,16 ± 0,06 para o peso final. As estimativas da correlação genética entre os efeitos direto e maternal para os pesos ao nascimento, ao desmame, com 1 ano e final foram -0,17 ± 0,40, -0,58 ± 0,32, -0,52 ± 0,34 e -0,34 ± 0,37, respectivamente. Para o peso com 1 ano com herdabilidade relativa à avó estimada como sendo apenas 0,03, o modelo 3 deu estimativas da correlação genética entre os efeitos direto e relativo à avó e entre os efeitos maternal e relativo à avó de 0,28 ± 0,48 e -0,33 ± 0,67, respectivamente. As estimativas de herdabilidade direta e maternal não se alteraram quando os efeitos relativos à avó não foram incluídos no modelo.

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