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Estimation of genetic parameters for preweaning and postweaning growth traits in the Gudali beef cattle using multiple trait derivative free restricted maximum likelihood

Ndofor-Foleng, H. M.^{1*}, Ebangi, A. L.², Agu, C. I.¹ and Okenyi, N.¹

¹Department of Animal Science, University of Nigeria, Nsukka, Enugu State, Nigeria.

²Regional Centre for Agricultural Research for Development, Bambui, Bamenda, Cameroon.

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Records on pedigree information and growth traits of Gudali beef calves were obtained from the Institute of Agricultural Research for Development, Cameroon. Data were edited to have complete information on calf, sire and dam identity, sex, dates and season of birth, herd and weights at birth (BWT), 6 months (6 MWT), weaning (WWT), 12 months (12 MWT), yearling (YWT), 18 months (18 MWT), 24 months (24 MWT) and 36 months (36 MWT). Genetic parameters were estimated using multiple trait derivative free restricted maximum likelihood (MTDFRML) program. The estimated direct (h^2_a) and maternal (h^2_m) heritabilities for BWT, 6 MWT, WWT, YWT, 18 MWT, 24 MWT and 36 MWT obtained were 0.39, 0.10, 0.25, 0.21, 0.18, 0.25, 0.18 and 0.05, 0.07, 0.11, 0.10, 0.05, 0.09, 0.07, respectively. Estimates of maternal genetic variance and corresponding heritabilities (h^2_m) were lower than estimates for direct additive variance and heritability (h^2_a). The genetic correlation between direct and maternal influence were negative. The across-trait direct and maternal genetic correlation estimates were medium to high with the exception of BWT and 18 MWT; BWT and 36 MWT, had negative values. The positive values reported for the additive and maternal correlations between the growth parameters indicate that selection for one trait resulted in genetic improvement in the other. The moderate values of heritabilities indicate that selection for growth traits was effective.

Key words: Covariance, heritability, genetic correlation, growth traits.

INTRODUCTION

Africa is endowed with a diversity of indigenous breeds that have proven remarkably suitable to survive and produce under the prevailing environmental rigors (Scholtz, 1988). The importance of using livestock breeds adapted to specific environments cannot be overemphasized. This is particularly so for tropical environments where, in the absence of resources for substantial improvement of the production environment,

the most viable and widely available option is the utilization of adapted animal genetic resources (Rege, 1993). The Gudali cattle survive and even reproduce under conditions where other breeds (mostly exotic) simply perished. With these facts in mind, an effort to conserve this valuable resource, the hardy animals of unique genetic origin has been made in Cameroon. The development of the livestock industry in Wakwa, Cameroon was identified as a high priority because of the high cattle population. Therefore, a good strategic plan had to be designed to promote the development of the livestock industry so that it could become a contributor to the economic welfare of the people of Cameroon. A selection experiment was conducted which led to the

*Corresponding author. E-mail: harriet.ndoforfoleng@unn.edu.ng or harrietndo@yahoo.co.uk.
Tel: +2347039222080 or +23775316263.

development and establishment of data on pedigree and performance traits on the Gudali cattle.

The potential for genetic change in economically important traits (preweaning and postweaning growth trait) of livestock such as Gudali beef cattle depends on the magnitude of the genetic and maternal heritability of each trait considered in selection. Preweaning and postweaning growth rate has been recognized as one of the most important traits that determine economic efficiency of beef cattle production and also as an important selection criterion because of the ease with which it can be measured (Prayaga, 2003). These traits are influenced by direct and maternal covariance and heritabilities. Heritability is a fundamental population parameter since it largely determines the prospect for changing a population by selection. Many economically important traits such as growth traits have a relationship whereby a change in the value of one trait is accompanied by a change in the value of the other. This is the concept of genetic correlation. Genetic correlations between traits are equally essential for determining the optimum weighting and expected response to selection in a multi-trait selection programme (Falconer, 1996).

However, there is paucity of information on the estimates of genetic parameters for body weights, the extent of between and within breed variation in the tropics. Estimates available are mainly for temperate breeds or their crosses in tropical environments (Meyer, 1997; Plasse et al., 2002a; Pico et al., 2004; Rasali et al., 2005).

The parameter estimates reported in literature for growth traits in tropical cattle are quite variable being estimated from small datasets (Iloeje, 1986; Tawah and Rege, 1996; Corbet et al., 2006). Considerable research efforts have also been directed towards estimating genetic parameters for various growth traits in beef cattle. Review articles by Koots et al. (1994) and Lobo et al. (2000) described many of the parameters estimates for several preweaning and postweaning growth traits in different beef cattle breeds from different countries. Genetic parameters are unique to the population in which they are estimated and they may change over time due to selection and management decisions. Thus, this paper presents estimates of genetic parameters for growth traits of Gudali beef cattle extensive grazing management systems in Wakwa, Adamawa region of Cameroon.

MATERIALS AND METHODS

The study area

The study was carried out in the Beef Herd Unit, Wakwa Centre of the Institute of the Agricultural Research for Development, which is located on the Adamawa region of Cameroon. Man has shaped the Adamawa's vegetation greatly. It was once highly forested, but repeated brush burning and cattle trampling have changed the terrain. It is a Derived-Savanna, which is interspersed with *Daniellia* and *Lophira* spp. of trees. Piot and Rippstein (1975) have described major grasses with predominant species being *Hyparrhenia* spp.

and *Panicum maximum*. The principal improved pastures developed on station are *Brachiaria* and *Stylosanthes* spp (Bayemi et al., 2005). The average annual rainfall is about 900 to 1,500 mm per year falling between March and October and the dry season is between November and February (Bayemi et al., 2005).

Breeding programme (Selection and mating)

With the exception of the foundation animals, and purchased replacement heifers, experimental animals were progeny of selected sires and dams. Purebred foundation bulls were purchased from the local farmers and were meticulously selected for breed standards including coat colour, age, size, conformation, adaptation, temperament and fertility as defined by Mandon (1957).

The selection scheme consisted of bull evaluation on individual and progeny performance and mass selection of females on phenotypic performance. According to Tawah et al. (1993), conformation and physical or structural soundness were additional criteria used for sires and heifers. At weaning, 12, 24 and 36 months, the animals were subjected to a selection scheme, which was based on individual and progeny performance (Ndofor-Foleng et al., 2011). The selection truncation point varied with numbers available, influenced by reproductive rate, deaths, sales, and emergency slaughter and replacement requirements. Based on this information, cows with proven performance in the herd were usually kept for breed replacements. Cows were regularly culled together with their progeny for poor calf, weaning weight or poor individual performance (age, conformation, agalactia, hardiness, and diseases) and failure to conceive after two successive mating (Tawah et al., 1993). Bayemi et al. (2005) reported detailed description of the breed, breeding and management of the herd.

Data collection

The data used for the estimation of heritability, correlation between maternal and genetic effects, direct and maternal genetic correlations consisted of 3788 records of birth and weaning weights of purebred Gudali calves from 1137 dams and 93 sires. The data that were collected included pedigree information and performance records from birth to 36 months weight in the Gudali beef cattle. The following information were obtained: calf identity (CID), sire identity (SID), dam identity (DID), calf date of birth (day, month and year), season of birth, sex of calf, breed of the calf, the monthly body weights of the calf which included birth weight (BWT), 6 months weight (6 MWT), weaning weight (WWT), yearling weight (YWT), 18 months weight (18 MWT), 24 months weight (24 MWT), and 36 months weight (36 MWT). The raw data were edited such that the utilized records gave complete information on sex, dates, and weights at birth; 6 MWT, WWT, 12 MWT, YWT, 18 MWT, 24 MWT and 36 MWT, and proper identifications for herd, sire, dam, season and breed. After editing, only data of 1968 and 1988 were considered in the analysis. Actual weights were adjusted to 180, 240, 365, 540, 720 and 1080 days, corresponding to 6 YWT, 8 YWT, 18 MWT, 24 MWT and 36 MWT, respectively.

Statistical model

The general linear model procedure of SAS (2002) was used to test the significance of non-genetic (fixed) effects, with sire effect considered as random; birth month and birth year of calf, season of birth, sex of calf, herd, sire year, dam month and year of birth and cow age group and herd-year-season fitted as fixed effect and exact ages at 3, 4, 6, WWT, YWT, 18, 24, 30 and 36 MWT as linear covariates. The following model was fitted for birth weight, 3 MWT, 4 MWT, WWT, YWT, 18 MWT, 24 MWT, 30 MWT and 36 MWT:

$$Y_{ijklmnopq} = \mu + A_i + B_j + C_k + D_l + E_m + F_n + G_o + H_p + HYS_q + e_{ijklmnopq}$$

where, $Y_{ijklmnopq}$, is an observation of a trait on the i 'th sire of the j 'th breed, of the k 'th sex, born in the l 'th season, of the m 'th herd, of the n 'th year of birth of the dam, of the o 'th calf year of birth, of the p th cow age group and of the q th herd-year-season; μ , is the overall mean; A_i , is the random effects of the i th sire; B_j , is the fixed effects of the j 'th breed; C_k , is the fixed effects of the k 'th sex ($K= 1, 2$); D_l , is the fixed effects of the l 'th season ($l = 1, 2$); E_m , is the fixed effects of the m 'th herd ($m = 1, 2, 3, \dots, 21$); F_n , is the fixed effects of the n 'th year of the birth of dams ($n= 52, 53 \dots 83$); G_o , is the fixed effects of the o 'th calf birth year ($n= 67, 68, 69, \dots, 88$); H_p , is the fixed effect of the p th cow age group ($p= 1, 2, \dots, 5$); HYS_q is the fixed effects of k 'th herd-year-season; $e_{ijklmnopq}$, is the residual error variance, assumed to be normally, identically and independently distributed with a zero mean and variance (σ^2) (niid).

In order to determine the fixed effects to be included in the model, preliminary analyses were performed using general linear model procedure of SAS (2002). The fixed effects included in the analyses were birth month and birth year of calf, season of birth, sex of calf, herd, sire year, dam month and year of birth and cow age group and herd-year-season fitted as fixed effect and exact ages at 6, WWT, YWT, 18, 24 and 36 MWT as linear covariates. Variance components were estimated using the multiple trait derivative free restricted maximum likelihood (MTDFRML) program (Boldman et al., 1995), fitting an animal model throughout and incorporating all pedigree information available. Suitability of the model was considered when a significant ($P < 0.05$) increase in log likelihood occurred when adding an additional random effect.

For the analysis of the traits, the following model was used:

$$Y = X\beta + Z_1a + Z_2m + Z_3c + \epsilon \text{ (with cov (a, m) = 0)}$$

where, Y is the $N \times 1$ vector of records, X , Z_1 , Z_2 , and Z_3 are known incidence matrices that associate levels of β , a , m and c with Y , β denotes the vector of fixed effects (calf year of birth, season of birth of calf, sex of calf, herd, herd-year-season etc), a is the vector of breeding values for direct genetic effects, m is the vector of breeding values for maternal genetic effects, c is the vector of permanent environmental plus non-additive genetic effects contributed by dams to records of their progeny and ϵ is the residual effect.

Genetic analysis

All pedigree information available was included in the analysis in order to minimize bias due to selection and to increase the accuracy of estimation through additional ties between animals. Genetic parameters of the growth traits were analyzed using multivariate analysis with the software MDTFREML (Van Vleck, 2007), using as convergence criteria variation of 10^{-9} between log of likelihood function on different rounds. Each analysis was then restarted using the resulting estimates of the parameters as new priors until changes in the function value and estimates of the scaled parameters (variances as proportions of phenotypic variance and correlations) were less than 0.01 (Boldman et al., 1995). Depending on the model, the log likelihood function was maximized with respect to the direct heritability (h^2_a), and the maternal heritability (h^2_m), (Boldman et al., 1995). From these parameters estimates, heritabilities were derived at convergence. Genetic correlations between the growth traits were obtained as the covariance component estimate for the two traits by the geometric mean of the two family variance component estimates.

MTDFREML method of analysis has some unique attributes, which have made the method of choice. For example, it accounts for the loss in degrees of freedom due to fixed effects in the model;

it is an interactive procedure well suited for use with mixed model equations along with the expectation maximization algorithm; it eliminates the bias due to selection; and it takes into account all relationships present in the pedigree.

RESULTS AND DISCUSSION

Descriptive statistics of traits under study are shown in Table 1. Coefficient of variations of all the traits studied were low ranging between 11 to 17% and is consistent with values for growth traits in other studies (Tawah et al., 1993; Abassa et al., 1993).

Variance-covariance component

Variance-covariance component estimates for performance traits are shown in Table 2. Maternal variance for all traits studied was consistently lower than additive genetic variance in the Gudali. Similar results have been reported in the study of Australian beef cattle by Duangjinda et al. (2001) and Aziz et al. (2005) in Japanese Black cattle. However, Elzo et al. (1998), in a study of Romosinuano-Zebu cattle, observed that, the additive genetic variance was lower than maternal genetic variance for birth weight (2.04 and 2.32 kg^2 , respectively) and as well as for weaning weight (100.46 and 166.52 kg^2).

The phenotypic variance (σ^2_p) of the Gudali increased from birth to 36 months. On the other hand, the residual variance (σ^2_e) increased from birth to 36 months of age. The highest error variance was observed in 36 month and the lowest in birth weight. Lee et al. (1997) reported that error variance for estimated genetic values increases as the differences between true and estimated variance components decreases.

The covariance between direct and maternal additive genetic effects (σ_{am}) for weights at birth to 36 months of age was found to be negative in all traits studied. Nearly all comparable studies reported a negative covariance between direct and maternal effect (Alenda et al., 1980; Franke et al., 2001; Dadi et al., 2002). The antagonism between direct and maternal components of covariance appears to be common in beef cattle (Kars et al., 1994; Pico et al., 2004).

The estimate of the direct-maternal genetic correlation is shown in Table 2. The correlation between direct and maternal effects was high for BWT (-0.99) and 6 MWT (-0.99); moderate for WWT (-0.42), YWT, 24 MWT (-0.43), and low for 18 MWT (-0.19), and 36 MWT (-0.02). Generally, the genetic antagonism between maternal and direct effects obtained in this study for all traits was stronger than those seen in literature. These were stronger than estimate of -0.37 obtained for BWT for Brahman cattle (Plasse et al., 2002) and -0.17 obtained by Rios-Utrera (2008), -0.23 obtained for WWT (Rios-Utrera, 2008) and -0.39 obtained for YWT (Meyer, 1992). The highly negative results obtained in this study suggest

Table 1. Description of data used after editing.

Item	BWT	6 MWT	WWT	YWT	18 MWT	24 MWT	36 MWT
Number of animals	3788	2945	2731	1902	1902	1770	1390
Number of sire	93	93	93	93	82	82	79
Number of dam	1137	1137	1117	1112	1005	931	912
Average body weight (kg)	24.09	144.98	149.57	159.36	197.87	225.36	310.52
SD	2.95	29.30	29.18	29.94	36.45	40.69	46.63
R ² (%)	0.17	0.38	0.46	0.45	0.38	0.44	0.45
CV (%)	12.48	16.18	15.81	15.72	14.86	13.01	11.70
Min (kg)	12	80	90	89	73	97	167
Max (kg)	48	263	269	321	384	456	481

SD, Standard deviation; CV, coefficient of variation; R², coefficient of determination; Min, minimum; Max, maximum; R² values were fairly high, indicating relatively good fit.

Table 2. Estimates of heritabilities for growth traits in the Gudali cattle.

Trait	BWT	6 MWT	WWT	YWT	18 MWT	24 MWT	36 MWT
σ_a^2	3.11	70.28	180.00	226.71	230.01	360.27	262.71
σ_m^2	0.393	47.21	80.66	106.78	76.57	125.54	100.45
σ_e^2	5.33	547.64	548.96	763.47	764.59	1011.75	1016.77
σ_p^2	7.86	708.99	710.00	1058	1277	1443	1456
σ_{pe}^2	0.178E-01	101.01	39.92	28.20	29.79	79.69	55.80
σ_{am}	-1.10	-57.16	-23.16	-67.57	-21.71	-54.78	-3.69
h_a^2	0.39	0.10	0.25	0.21	0.18	0.25	0.18
h_m^2	0.05	0.07	0.11	0.10	0.05	0.09	0.07
r_{am}	-0.99	-0.99	-0.42	-0.43	-0.19	-0.26	-0.02

σ_a^2 , Direct additive genetic variance; σ_m^2 , maternal additive genetic variance; σ_e^2 , error variance; σ_p^2 , phenotypic variance; σ_{pe}^2 , permanent maternal environmental variance; σ_{am} , genetic covariance between direct and maternal effect; h_a^2 , direct heritability; h_m^2 , maternal heritability; r_{am} , genetic correlation between direct and maternal effects.

a genetic antagonism between a heifer's prenatal growth potential and the subsequent quality of her intrauterine environment (Norris et al., 2004). They also indicate that the probable reduction in maternal performance due to intense selection for individual growth may be substantial.

Heritability estimates of preweaning and postweaning growth traits

Direct additive genetic heritability (h_a^2) estimates for BWT (0.39), 6 months (0.10) WWT (0.25), YWT (0.21) 18 months (0.18), 24 months (0.25) and 36 months (0.18) was obtained for the Gudali cattle (Table 2). Moderate additive genetic heritability (h_a^2) estimates were obtained for BWT (0.39), WWT (0.24), YWT (0.21), 24 months (0.25) in the Gudali cattle. The direct heritability of BWT for in this work is equally higher than that reported for Brahman cattle (0.28) (Pico et al., 2004) in South Africa.

The lowly heritable traits includes 6 MWT (0.10), 18 MWT (0.18) and 36 MWT (0.18) for the Gudali cattle. The low heritability obtained for these traits in this study could be either due to deterioration in management resulting to

poor nutritional status of the animals, or due to the use of same sire for a number of years, which could decrease additive genetic variation.

The values of heritability obtained for 6 MWT were within the range of values reported in literature (Montaldo and Kinghorn, 2003). Direct heritability for WWT, YWT and 18 MWT in the present study were within the range of estimates reported on some tropical Zebu cattle (Tawah et al., 1993; Melis et al., 2009). The estimates reported by Mostert et al. (1998) for Brahman cattle (0.25 for WWT); Meyer (1992) for Hereford cattle (0.24 for YWT) and Kars et al. (1994) for Nguni cattle (0.19 for 18 MWT) are not different from the results obtained in this study for the Gudali cattle.

However, reported estimates for direct heritability only for mature weights in the present study are equally within range of reported estimates in summary reviews (Meyer, 1992) for Hereford cattle in Australia (0.22 for final weight); Meyer (1992) for Zebu cross (0.20 for 24 MWT) and Bosso (2006) for N'dama cattle (0.24 for 36 MWT).

The contribution of maternal effects to the phenotypic variance (h_m^2) in the preweaning traits were BWT (0.05), 6 MWT (0.07), WWT (0.11) and in the postweaning traits

Table 3. Direct additive genetic correlation (r_a), and maternal genetic correlation (r_m) between growth traits in Gudali.

Trait 1	BWT	BWT	BWT	BWT	WWT	WWT	WWT	YWT	YWT	EMWT
Trait 2	WWT	YWT	EMWT	36MWT	YWT	EMWT	36MWT	EMWT	36MWT	36MWT
$\sigma_a^2 1$	3.11	3.11	3.11	3.11	180.00	180.00	180.00	226.71	226.71	230.01
$\sigma_a^2 2$	180.00	226.71	230.01	262.71	226.71	230.01	262.71	230.01	262.71	262.71
$\sigma_a 1, 2$	12.54	10.36	-17.65	-6.00	177.77	177.02	152.22	159.84	146.42	122.90
$r_{a1, 2}$	0.53	0.39	-0.66	-0.21	0.88	0.87	0.70	0.70	0.60	0.50
$\sigma_m^2 1$	0.39	0.39	0.39	0.39	80.66	80.66	80.66	106.78	106.78	76.57
$\sigma_m^2 2$	80.66	106.78	76.57	100.45	106.78	76.57	100.45	76.57	100.45	100.45
$\sigma_m 1, 2$	4.04	2.52	-4.42	-5.57	92.81	77.80	87.31	54.25	72.49	43.85
$r_{m1, 2}$	0.72	0.39	-0.81	-0.89	1.00	0.99	0.97	0.60	0.70	0.50

$\sigma_a^2 1$, Direct additive genetic variance for trait 1; $\sigma_a^2 2$, direct additive genetic variance for trait 2; $\sigma_a 1, 2$, direct covariance between trait 1 and 2; $\sigma_m^2 1$, maternal additive genetic variance for trait 1; $\sigma_m^2 2$, maternal additive genetic variance for trait 2; $\sigma_m 1, 2$, maternal covariance between trait 1 and 2; $r_{a1, 2}$, additive genetic correlations between trait 1 and 2; $r_{m1, 2}$ = maternal genetic correlations between trait 1 and 2.

(YWT (0.10) 18 MWT (0.05), 24 MWT (0.09) and 36 MWT (0.07). High estimates of h_m^2 for postweaning traits were unexpected because at this age, the calves do not depend on their mother and the weight should reflect only the direct effect of the genes on growth except for carrying over maternal effects from before weaning. These results were consistent with estimates for BWT in Charolais cattle in Sweden (Eriksson et al., 2004); in Bonsmara in South Africa (Nephawe et al., 2006) and in Romosinuano cattle in the Colombian (Sarmiento and Garcia, 2007).

Genetic correlation between growth traits

The estimates of direct and maternal genetic correlations between all the preweaning and postweaning growth traits are shown in Table 3. The genetic and maternal correlations between all pairs of postweaning traits were consistently high and positive. They ranged between 0.50 and 1.00. The additive direct and the maternal genetic correlations between WWT and YWT, WWT and 18 MWT, WWT and 36 MWT, YWT and 18 MWT, and YWT and 36 MWT were high, indicating that selection for one trait should result in genetic improvement in the other trait. The high positive correlation between these traits indicate that there are many genes, which affect two traits simultaneously, as selection based on one trait caused the positive response for another trait. Plasse et al. (2002) reported a similar genetic correlation of 0.64 and a high maternal genetic correlation of 0.74 for the same traits in the South African Brahman cattle. On the other hand, Jung et al. (2004) reported a lower additive genetic correlation between these traits as 0.43 and 0.50 for South Gertrudis and German Holstein calves, respectively.

On the other hand, the correlations between BWT and mature body weights was high and negative ranging between -0.21 to -0.89. The same correlations when involving BWT and WWT, and BWT and YWT were low

while BWT and 18MWT, and BWT and 36MWT had a negative correlation. The generally low correlation between traits estimated in this study is in agreement with Meyer (1993), who found lower correlation between traits for Zebu cross than for Angus cattle. As a result, she suggested that the genetic determinants of growth at various ages are more diverse in tropical than temperate environments.

The present positive genetic and maternal correlations between BWT and WWT indicate that selection for BWT would be associated with genetic and maternal improvement in the growth traits from birth to weaning and indicates a positive genetic relationship between pre- and postnatal effects. Abdel-Glil and El-Banna (2001) arrived at the same conclusion.

The high and positive genetic correlations between all the growth traits in this study implies that they are all being controlled by similar genes and thus, selection for any one of these traits would lead to positive changes in the other. This agrees with the report of El-said et al. (2005) and supports the contention that both traits are essentially the same measure of growth and are thus, under the influence of similar genes. Thus, the two traits can be regarded as the same trait in a selection programme.

Conclusion

The magnitude of heritability estimates for growth traits derived from selection experiments carried out in the Gudali beef cattle suggests that selection can be highly effective in changing growth traits in beef cattle. It could be concluded that the genotype of the calf was more important than the genotype of the dam in determining preweaning and postweaning growth traits, as indicated by the moderate means of estimates of direct heritability and the low means of estimates of maternal heritability. It is, therefore, recommended that selection emphasis should be given to adaptability and functional efficiency of

the individual grade animals in Adamawa region, Cameroon. In addition, because of negative genetic correlation between direct and maternal effects for growth traits, 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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