Genetic Parameter estimates for growth traits in purebred gudali and two-breed synthetic wakwa beef cattle in a tropical environment

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ABSTRACT

Data collected between 1968 and 1988 from a selection experiment involving the purebred Gudali and a two-breed synthetic, the Wakwa, at the Animal Production and Research Stations of Wakwa in Ngaoundere, Cameroon, were analysed using mixed model procedures. Estimates for direct, maternal and total heritabilities were 0.37, 0.05 and 0.21 for birth weight (BWT); 0.24, 0.17 and 0.07 for pre-weaning average daily gain (ADG); 0.27, 0.19 and 0.11 for weaning weight (WWT); 0.51, 0.20 and 0.22 for yearling weight (YWT) and 0.18, 0.02 and 0.18 for eighteen month weight (EWT) in the Gudali. Corresponding estimates in the Wakwa were 0.55, 0.23 and 0.18 for BWT; 0.26, 0.07 and 0.12 for ADG; 0.28, 0.09 and 0.15 for WWT; 0.18, 0.00 and 0.17 for YWT and 0.14, 0.06 and 0.17 for EWT, respectively. Estimates for genetic correlation between the direct and maternal genetic effects were -0.88 and -0.90 for BWT; -0.80 and -0.83 for ADG; -0.77 and -0.76 for WWT and -0.81 and -0.98 for YWT in the Gudali and Wakwa, respectively. These estimates are indicative that there are possibilities of improving pre-weaning and/or post-weaning traits in both breeds through selection. However, the overall genetic progress might be lower when selection is concentrated on direct performance as a result of the genetic antagonism between the direct and maternal genetic effects.

Keywords: Growth traits, genetic parameters, Gudali, Wakwa, tropical environment

RESUME

Des données provennant d'une expérience de sélection massale de zébus Goudali de race pure et demi-sang Wakwa, collectées entre 1968 et 1988 aux Stations Zootechnique et Recherche Zootechnique de Wakwa (Ngaoundére, Cameroun) ont été analysées à l'aide de procédures de modèle mixte. Les héritabilités directe, maternelle et totale ont été estimées à 0,37, 0,05 et 0,21 pour le poids à la naissance (BWT); 0,24, 0,17 et 0.07 pour le gain pondéral moyen quotidien (ADG); 0,27, 0,9 et 0,11 pour le poids au sevrage (WWT); 0,51, 0,20 et 0,22 pour le poids à 12 mois (YWT); 0,18, 0,02 et 0,18 pour le poids à 18 mois (EWT) des Goudali. Les héritabilités correspondantes ont été respectivement estimées chez les Wakwa à 0,55, 0,23 et 0,18 pour BWT; 0,26, 0,07 et 0,12 pour ADG; 0,28, 0,09 et 0,15 pour WWT; 0,18, 0,00 et 0,17 pour YWT et 0,14, 0,06 et 0,17 pour EWT. Les valeurs estimées des correlations génétiques entre les effets directs et maternels étaient -0,88 et -0,90 pour BWT; -0,80 et -0,83 pour ADG; -0,77 et -0,76 pour WWT et -0,81 et -0,98 pour YWT respectivement chez les Goudali et Wakwa. Ces valeurs sont indicatives des possibilités d'amélioration par sélection des traits de caractère avant ou apres sevrage dans les deux races. Toutefois, le progress génétique serait plus lent si la sélection etait concentrée sur les performances directes en raisons de l'antagonisme entre les effets directs et maternels.

Mots clés:

Introduction

Whereas the annual meat production in Cameroon is about 105,052 tons, the annual demand is estimated at 161,000 tons (Tanya *et al.*, 1995). The shortfall is made for by importation of about 36,000 tons of beef from Tchad and Central African Republic and about 20,000 tons from Europe and Argentinia (World Bank, 1989). Given the trends, successive pre- and post-independent governments of Cameroon have put in place a number of research programmes since 1952, aimed at improving beef cattle productivity. The programmes include, amongst others, breed substitution, upgrading of the local Gudali (Mandon, 1957), crossbreeding between local and exotic breeds and improvement of the indigenous breeds through selection (Lhoste, 1968, 1969, 1977). The first two programmes based on breed substitution and upgrading however, were unsuccessful because no one breed is «best» for all reproductive attributes and also because of non-adaptability of exotic breeds to prevailing environmental and socio-economic conditions.

The Gudali beef improvement programme which started in 1952, firstly with the Wakwa project and subsequently in 1969 with the selection programmes (Wakwa and Gudali projects) has been more successful (Tawah *et al.*, 1996). Over the years, the Gudali beef improvement programme has accumulated substantial volumes of data on pre-weaning and post-weaning growth traits, which have not yet been comprehensively analysed. Abassa *et al.* (1993) quantified factors affecting birth and weaning weight of Gudali and Wakwa assuming that herd effect was not important. Tawah *et al.* (1993, 1994) estimated genetic parameters and trends for birth and weaning weights from data collected between 1971 and 1985. The model for these analyses assumed that herd effect and maternal permanent environmental effect were not important. Though genetic parameters on growth traits for various breeds of beef cattle exist in the literature,

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it is important that estimates for performance traits in these breeds be carried out under their specific management and production environment. The basic problem is the choice among alternative measures of growth performance such as daily weight gain over specified periods and age correlated weights at specified times for improvement strategies. The choice of any trait for improvement will depend on the genetic and economic importance. It is therefore necessary to obtain reliable information on genetic parameters of not only birth and weaning weight traits but also post-weaning traits.

The objective of the study was therefore to estimate pre-weaning and post-weaning genetic parameters for growth performance traits in Gudali and Wakwa beef cattle in the tropical highlands of Cameroon. This is important in drawing up future selection strategies.

MATERIALS AND METHODS

Foundation animals

The foundation population for the Wakwa project was composed of 45 purebred Brahman bulls imported from the USA between 1952 and 1958. The foundation population for the Gudali project consisted of 720 purebred Gudali heifers of ages two to four years selected between 1965 and 1969 (Tawah, 1992). Purebred foundation bulls (ages five to seven years) for the Gudali project were purchased from the local farmers and were meticulously selected for breed standards including coat colour, age, size, conformation, temperament, adaptation and fertility as defined by Mandon (1957).

Breed description

The Gudali and Wakwa breeds have been described by Lhoste (1969), Tawah and Mbah (1989) and Ebangi (1999). The Gudali is a short-horned West African zebu, which is a predominant subtype of the Adamawa Gudali that inhabits the Adamawa mountain ranges stretching from Nigeria to Cameroon (Tawah & Rege, 1996). This breed is of good temperament and of excellent beef conformation and possesses a natural ability to produce and reproduce optimally under prevailing local conditions without much additional inputs (Tawah *et al.*, 1993). It is predominantly found in Ngaoundere in the Adamawa Province of Cameroon with some strains found in Banyo. It is a popular breed, especially in the smallholder sector of the Adamawa highlands (Tawah *et al.*, 1996). The Wakwa is a two-breed synthetic which was developed from *inter se* matings of American Brahman x Gudali first filial generations and have been maintained at 0.50 exotic blood. Detailed description of its development has been reported by Mandon (1957).

Management

The animals were maintained at the Wakwa Animal Production Unit of the Ministry of Livestock, Fisheries and Animal Industry and at the Wakwa Research Unit of the Institute of Agricultural Research of the Ministry of Scientific and Technical Research. These Units are located on the Adamawa highlands of Cameroon. The management system, feeding, pastures and climatic conditions have been well documented (Duma & Lhoste, 1966; Lhoste, 1968 & 1977; Lhoste & Pierson, 1973; Piot & Rippstein, 1975; Pamo & Yonkeu, 1987; Tawah & Mbah, 1989; Tawah *et al.*, 1993).

Breeding females were annually reshuffled within breed into various breeding herds, and breeding bulls assigned randomly to about 30 to 40 females but ensuring that inbreeding was minimised. At birth, calves were ear-tagged and weighed and sire and dam recorded, as well as breed, sex, date, month and year of birth. They were weighed within 24 hours and subsequently, monthly. At weaning, 12, 24 and 36 months the animals were subjected to a selection scheme which was based on bull evaluation on individual and progeny performance and selection of females based on mass and phenotypic performance as documented by Lhoste (1977) and Tawah *et al.* (1994).

Data collection and editing

Data on calves born from 1968 to 1988 were compiled from the various herdbooks of Adamawa maintained at the Wakwa Animal and Veterinary Research Centre. The data collected included pedigree information on individual calves, sex, date, month and year of calving, birth years of sires and dams, birth weight (BWT) and weaning (WWT), yearling (YWT) and eighteen months (EWT) weights selected from monthly weights for dates closest to eight, twelve and eighteen months, respectively. Weaning age (WAGE), yearling age (YAGE), eighteen-month age (EAGE), cow age group (CAG) and preweaning daily gain (ADG) were derived from the data set as described by Ebangi (1999). Two seasons were defined according to Abassa *et al.* (1993) and Tawah *et al.* (1993): a five months dry season extending from November to March and a seven months rainy season from April to October.

The data were edited for valid pedigree information, consistency checks of dates, ages at weaning, yearling, eighteen months and for weight ranges considered unreasonable for the age and sex of the animal. As a result, all birth weights less than 15 kg or greater than 35 kg were discarded. Progeny not identified with herds were discarded. Weaning weights less than 100 kg and yearling and eighteen months weight less than 120 kg were omitted. The resulting summary structures for the two breeds are presented in Tables 1 and 2.

Statistical Model and Analytical Techniques

Restricted maximum likelihood estimates were obtained by the MTDFREML software (Boldman *et al.*, 1995). An animal model was used for each trait with the direct effect, maternal effect correlated to the direct effect, non-additive maternal permanent environmental effect, uncorrelated to direct and maternal effects and environmental effect, associated with the direct effect, fitted as random effects. Sex, season of calving, herd, calf birth year (CBY) and cow age group (CAG) were fitted as fixed effects. Ages at weaning (WAGE), yearling (YAGE) and eighteen months (EAGE) were fitted as linear covariates on weaning, yearling and

Table 1: Data summary structure for trait means and variation in Gudali beef cattle

ITEM	BWT	ADG	WWT	YWT	EWT	WAGE	YAGE	EAGE
No. of records	2886	2732	2899	2098	1957			
No. of animals	3728	3728	3728	2748	2569			
Dams	1137	1115	1181	1001	931			
Sires	93	93	93	82	79			
Progeny/dam	2.70	2.75	2.60	2.10	2.10			
Progeny/sire	32.99	32.99	32.99	25.59	24.80			
Dam/sire	12.23	11.99	12.70	12.21	12.08			
Inbred calves	78	78	78	26	22			
IC	0.08	0.08	0.08	0.10	0.08			
Mean	24.09	0.52	148.79	159.12	197.77	238.67	362.87	541.62
SD	2.73	0.12	28.49	28.04	36.50	28.49	13.85	13.22
CV (%)	11.34	23.14	19.15	17.62	18.45	3.83	7.32	2.44

BWT = birth weight (kg), ADG = pre-weaning gain (kg); WWT = weaning weight (kg); YWT = yearling weight (kg); EWT = eighteen months weight (kg); WAGE = weaning age (days), YAGE = yearling age (days), EAGE = eighteen months age (days)

Table 2: Data summary structure for trait means and variation in Wakwa beef cattle

ITEM	BWT	ADG	WWT	YWT	EWT	WAGE	YAGE	EAGE
No. records	1793	1656	1838	1372	1328			
No. animals	2391	2391	2391	1831	1731			
Dams	656	639	710	570	579			
Sires	60	60	60	53	53			
Progeny/dam	2.99	3.07	2.76	2.52	2.30			
Progeny/sire	32.68	32.68	32.68	27.08	25.17			
Dam/sire	10.93	10.65	11.83	10.75	11.13			
Inbred calves	58	58	58	29	22			
IC	0.07	0.07	0.07	0.07	0.07			
Mean	24.90	0.57	161.65	170.70	213.65	239.28	361.69	541.18
SD	3.14	0.12	29.54	27.71	37.38	14.84	11.50	12.29
CV (%)	12.62	21.11	18.27	16.23	17.50	6.20	3.18	2.37

BWT = birth weight (kg), ADG = pre-weaning gain (kg); WWT = weaning weight (kg); YWT = yearling weight (kg); EWT = eighteen months weight (kg); WAGE = weaning age (days), YAGE = yearling age (days), EAGE = eighteen months age (days)

eighteen months weights, respectively. The simplex method was used to search for a maximum of the residual likelihood function by evaluating likelihoods over a network of points determined from the simplexes with a 10E-9 used as stopping criterion. Where the search strategy did not converge to global maximum, the program was re-started until twice the logarithms changed no more by 0.00 to 0.02. Priors for (co)variance components were obtained from reported estimates by Tawah *et al.* (1993).

The model in matrix notation was presented as:

$\underline{y} = X\underline{b} + Z_1\underline{a}+ Z_2\underline{m} + Z_3\underline{c} + \underline{e}$, where

$\underline{y}$ was an observation vector for growth performance traits (BWT, ADG, WWT,YWT, EWT) records;

X, an incidence matrix relating observations to the fixed and covariate effects;

$\underline{b}$, a vector of identifiable non-random fixed (sex, herd, season and year of calving, CAG) and covariate (WAGE, YAGE, EAGE) effects;

Z_1, Z_2 and Z_3 known incidence matrices relating elements of direct, maternal and non-additive maternal permanent environmental effects to y;
a and m, nonobservable correlated random vectors for direct and maternal effects;
c, nonobservable uncorrelated random vector associated with the non-additive maternal permanent environmental effect and e, random vector associated with residual effect of error. The vectors a, m, c and e were assumed to be multivariate normal (MVN) with zero mean and variance, ó^2. Dams were assumed to be related only by their sires. The variance-covariance structure was presented as:

$$\mathrm{Var}\begin{bmatrix} a \\ m \\ c \\ e \end{bmatrix} = \begin{bmatrix} A\sigma^2_a & A\sigma_{am} & 0 & 0 \\ A\sigma_{am} & A\sigma^2_m & 0 & 0 \\ 0 & 0 & I\sigma^2_c & 0 \\ 0 & 0 & 0 & I\sigma^2_e \end{bmatrix}$$

where ó^2 is the direct genetic variance, ó^2_m the maternal genetic variance, ó$^2_{am}$ the covariance for direct-maternal genetic effects, ó^2_c the uncorrelated non-additive maternal permanent environmental effect, A the numerator relationship matrix, I the identity matrix and ó^2_e the error random variable for the trait.

RESULTS AND DISCUSSION

Inbreeding coefficient (IC) was quite low in the two breeds and ranged between 0.07 and 0.10. The weight differences at birth and average pre-weaning daily gain and ages at weaning, yearling and eighteen month between the two breeds were very slight. There were however marked differences in corresponding weights at weaning, yearling and eighteen months (Tables 1 & 2).

The estimates of (co)variance components for the growth traits in Gudali and Wakwa are presented in Tables 3 and 4, respectively.

In both tables, estimates for direct genetic variances were higher than corresponding maternal genetic variance components in all traits. There was a consistent increase in the (co)variance estimates from average daily weight gain (ADG) to weaning (WWT) in both breeds. The direct, maternal, residual and phenotypic variances decreased at yearling (YWT) and increased at eighteen months weight (EWT) in both breeds.

The direct-maternal covariance and permanent maternal environmental variance increased from ADG to YWT in Gudali but dropped at EWT, while in the Wakwa breed, they increased from ADG to WWT and then decreased at

Table 3: (Co)variance estimates for pre-weaning and post-weaning growth traits in Gudali cattle

Trait	Ó^2_A	Ó^2_M	Ó$_{AM}$	Ó$^2_{PE}$	Ó^2_e	Ó^2_P
BWT	2.624	0.371	-0.871	0.199E-05	5.033	7.156
ADG	0.003	0.002	-0.002	0.928E-03	0.008	0.012
WWT	188.277	127.367	-119.157	40.320	449.254	686.05
YWT	309.177	122.268	-156.686	57.339	273.014	605.112
EWT	171.945	16.049	0.119	0.211	787.622	975.946

Ó^2_A = direct additive genetic variance, Ó^2_M = maternal additive variance,
Ó$_{AM}$ = direct-maternal covariance, Ó$^2_{PE}$ = permanent maternal environmental variance,
Ó^2_e = residual variance, Ó^2_P = phenotypic variance

Table 4: (Co)variance estimates for pre-weaning and post-weaning growth traits in Wakwa cattle

Trait	Ó^2_A	Ó^2_M	Ó$_{AM}$	Ó$^2_{PE}$	Ó^2_e	Ó^2_P
BWT	4.633	1.976	-2.725	0.340E-05	4.612	8.496
ADG	0.003	0.001	-0.001	0.208E-02	0.008	0.013
WWT	214.452	67.990	-91.900	110.303	453.516	754.363
YWT	107.851	0.013	-1.168	71.710	434.339	612.746
EWT	157.682	64.520	0.012	0.174	878.551	1100.940

Ó^2_A = direct additive genetic variance, Ó^2_M = maternal additive variance,
Ó$_{AM}$ = direct-maternal covariance, Ó$^2_{PE}$ = permanent maternal environmental variance,
Ó^2_e = residual variance, Ó^2_P = phenotypic variance

YWT and EWT. The direct estimates in the Wakwa breed were higher than corresponding estimates in the Gudali for BWT and WWT. The trend was reversed for YWT and EWT. With the exception of BWT and EWT, the maternal variance components in Gudali for ADG, WWT and YWT were higher than corresponding estimates in the Wakwa. The higher direct and maternal variance components corresponded to the higher direct and maternal heritabilities (see Tables 3, 4, 5 & 6). The higher direct genetic variances as against lower variances are in agreement with reports by Trus and Wilton (1988) in birth and average pre-weaning daily gain in Angus, Herefords, Charolais, Simmental and Shorthorn calves; Burfening *et al.* (1981) in birth weight of Simmental calves and Bertrand and Benyshek (1987) in birth and weaning weight in Limousin and Brangus calves. Kars *et al.* (1994), Haile-Mariam and Kassa-Mersha (1995) and Meyer (1992) also reported higher estimates for direct variance components of pre-weaning and post-weaning growth traits in Nguni, Boran and Australian Herefords, Angus and Zebu cross calves, respectively. Wright *et al.* (1991) and Diop and Van Vleck (1998), however, reported higher estimates of maternal variances as against lower estimates of direct variance components for weaning and eighteen months weight in Senepol and Gobra calves, respectively. Negative permanent maternal environmental variances though not common in the literature have been reported by Wright *et al.* (1991) in Senepol calves.

The estimates for genetic parameters in Gudali and Wakwa are presented in Tables 5 and 6, respectively.

Apart from EWT in both breeds and YWT in Wakwa, estimates for all other traits were moderately to highly heritable. Lower estimates for total heritability were obtained for traits with corresponding negative direct-maternal genetic correlations. The estimates for direct heritabilities (h^2_A) were higher than corresponding maternal heritabilities (h^2_M) for all the performance traits. Similar trends have been reported by some researchers (Burfening *et al.*, 1981; Bertrand and Benyshek, 1987; Arnason & Kassa-Mersha, 1987; Trus and Wilton, 1988; Meyer, 1992; Shi *et al.*, 1993; Kar *et al.*, 1994; Koots *et al.*, 1994; Khombe *et al.*, 1995; Haile-Mariam and Kassa-Mersha, 1995; Van der Westhuizen, 1997). However, higher maternal heritabilities as against lower direct heritabilities are equally common in the literature (Wright *et al.*, 1991; Brown & Galvez, 1969;

Table 5: Estimates of genetic parameters for pre-weaning and post-weaning growth traits in Gudali cattle

Traits	h^2_A	h^2_M	h^2_T	C^2	C_{AM}	r_{AM}
BWT	0.37	0.05	0.21	0.28E-06	-0.12	-0.88
ADG	0.24	0.17	0.07	0.08	-0.16	-0.80
WWT	0.27	0.19	0.11	0.05	-0.17	-0.77
YWT	0.51	0.20	0.22	0.09	-0.26	-0.81
EWT	0.18	0.02	0.18	0.22E-03	0.12	0.00

h^2_A = direct heritability, h^2_M = maternal heritability, h^2_T = total heritability defined as $Ó^2_A + 1/2Ó^2_M + 3/2Ó_{AM}$ (Willham, 1972), C^2 = permanent maternal environmental variance as a proportion of the phenotypic variance, C_{AM} = direct-maternal covariance as a proportion of the total phenotypic variance, r_{AM} = genetic correlation between direct and maternal genetic effects

Table 6: Estimates of genetic parameters for pre-weaning and post-weaning growth traits in Wakwa cattle

Traits	h^2_A	h^2_M	h^2_T	C^2	C_{AM}	r_{AM}
BWT	0.55	0.23	0.18	0.41E-06	-0.32	-0.90
ADG	0.26	0.07	0.12	0.21E-02	-0.12	-0.83
WWT	0.28	0.09	0.15	0.15	-0.12	-0.76
YWT	0.18	0.00	0.17	0.12	-0.002	-0.98
EWT	0.14	0.06	0.17	0.16E-03	0.00001	0.00

h^2_A = direct heritability, h^2_M = maternal heritability, h^2_T = total heritability defined as $Ó^2_A + 1/2Ó^2_M + 3/2Ó_{AM}$ (Willham, 1972), C^2 = permanent maternal environmental variance as a proportion of the phenotypic variance, C_{AM} = direct-maternal covariance as a proportion of the total phenotypic variance, r_{AM} = genetic correlation between direct and maternal genetic effects

Nelsen *et al.*, 1984; Cantet *et al.*, 1988; Hohenboken & Brinks, 1971). In Tables 5 and 6, 18% (EWT) to 51% (YWT) and 14% (EWT) to 55% (BWT) of the total phenotypic variation for the growth traits were accounted for by the direct genetic effect associated with the genotype of the Gudali and Wakwa calves, respectively. Also, the contribution from maternal effect to the total phenotypic variation ranged from 2% (EWT) to 20% (YWT) and 00% (YWT) to 23% (BWT) in the Gudali and Wakwa genotypes, respectively.

The total heritability was lower than the direct heritability for traits with corresponding negative direct-maternal genetic correlations. Total heritability ranged from 0.07 (ADG) to 0.22 (YWT) for the Gudali and from 0.12 (ADG) to 0.18 (BWT) for the Wakwa. With the exception of eighteen months weight where direct-maternal genetic correlation was zero, and highly negative, it ranged from -0.77 to -0.88, in Gudali and -0.76 to -0.98, in Wakwa. With the exception of yearling weight, where maternal heritability was zero in Wakwa, maternal and permanent maternal environmental effects were present though at variable magnitudes in the traits studied in both breeds.

The results from the present study are generally in agreement with those for the same breeds by Tawah *et al.* (1993) but for the higher birth weight direct heritability estimate (0.65), higher weaning weight maternal heritability estimate (0.27) and lower birth weight genetic correlation estimate between direct and maternal effects (-0.39) for the Wakwa breed. The differences might have been caused by the inclusion of herd and permanent maternal environmental effects in the model used for the present study. With the exception of the high yearling weight direct heritability (0.51), direct heritabilities reported for birth weight, average pre-weaning daily gain, weaning and eighteen-month weights in the present study for Gudali were within range of estimates reported on some other tropical zebu cattle (Ilοeje, 1986; Kars *et al.*, 1994; Haile-Mariam & Kassa-Mersha, 1995; Khombe *et al.*, 1995). The estimates reported by Diop & Van Vleck (1998) for the Gobra breed, however, differed from those reported in this study. Reported estimates for direct heritabilities for birth weight, average pre-weaning daily gain and weaning weight in the present study are equally within range of reported estimates in some summary reviews (Barlow, 1978; Mohiudden, 1993; Koots *et al.*, 1994). The direct heritability for yearling weight from the present study was, however, higher than those reported by Mohiudden (1993). The estimate for maternal heritability obtained in this study for birth, weaning and yearling weights differed from estimates reported in literature reviews (Mohiudden, 1993; Koots *et al.*, 1994).

Genetic parameter estimates for tropical crossbred zebu are few in the literature. However, the estimates of 0.61 and 0.11; 0.20 and 0.32; 0.25 and 0.20 and 0.26 and 0.09 for direct and maternal heritabilities for birth, weaning, yearling and eighteen-month weights obtained by Mackinnon *et al.* (1991) for Africander crosses are within the range of Wakwa estimates. However, the estimates of 0.40, 0.46 and 0.17 for direct, maternal and total heritabilities for weaning weight in crossbred Brahman x Shorthorn registered by Deese and Koger (1967) are different from those of the present study. The variation in the genetic estimates of the crossbreds could be attributed to additive breed differences, heterosis, breed complementarity and genotype-environment interactions.

Although the estimates reported by Kars *et al.* (1994), Khombe *et al.* (1995), Haile-Mariam & Kassa-Mersha (1995), Neser *et al.* (1996), Diop & Van Vleck (1998) for direct-maternal genetic correlations for pre-weaning and/ or post-weaning traits in tropical beef cattle are also highly negative, those obtained in the present study were much higher. The estimates for pre-weaning weights were higher than those reported by Koch (1972). These highly negative direct-maternal genetic correlations are, however, within range of other estimates in the literature. Estimates of -1.05 and -0.61 have been reported by Cantet *et al.* (1988) and Robinson (1996) for birth weight of Herefords and Angus calves, respectively. Hohenboken and Brinks (1971), Thompson (1976), Meyer (1992) and Cantet *et al.* (1988) reported estimates of -0.79, -0.78, -0.59 and -0.57 for weaning weight in Herefords calves. Robinson (1996) also reported estimates of -0.52, -073 and -0.70 for weaning, yearling and eighteen-month weights in Angus calves. Conversely, positive direct-maternal genetic correlations have been reported in the literature for different performance traits in beef cattle (Brown & Galvez, 1969; Thompson, 1976; Wright *et al.*, 1987; Meyer, 1992; Kars *et al.*, 1994; Van der Westhuisen, 1997).

The magnitude and direction of the genetic correlation between direct and maternal effects therefore appear to be inconclusive. Tawah *et al.* (1993) attributed the highly negative direct-maternal genetic correlations in Gudali and Wakwa to a form of adaptive mechanism towards the harsh tropical environment. Females which are inherently small as calves have an adaptive genetic advantage by the fact that they grow up to be small dams utilising effectively the suboptimal tropical production environment for their maintenance and for the growth of their calves than would be larger dams. Other scientists have offered various alternative explanations to the apparently highly negative direct-maternal genetic correlation, which could be a serious impediment to selection progress. Robinson (1996) attributed the high negative direct-maternal genetic correlation to negative dam-offspring covariances effects or additional sire variations or sire x year variations not accounted for in the estimation models. Meyer (1997) attributed it to sources of variations such as paddocks or management groups not accounted for in the analyses. Tassel (personal communication) and Lee and Pollak (1997a & b) attributed it to selective reporting, sire x year interaction and to potential heterogeneity of the correlation by gender not taken into account in the estimations of genetic parameters. The problem of heterogeneous variances has also been reported by Thrift *et al.* (1981) and Garrick *et al.* (1989). Neser *et al.* (1996) attributed the high negative direct-maternal genetic correlation to herd-year-season x sex interactions. According to Van Vleck *et al.* (1977), the practical implication of the high negative direct-maternal genetic correlation is the possible reduction in expected response to selection. These authors have, therefore, suggested that selection of males for direct and females for maternal genetic values be implemented in the cases where the correlation was highly negative. This will result in greater selection response in progeny after the first generation than would be, if selection of dams was based on direct genetic estimates. Considering the various explanations from different authors, the direct-maternal genetic correlation may therefore be negative not because of genetic antagonism between direct and maternal effects but because of certain variations which might not have been taken into account in the estimation of genetic parameters. It is, therefore, possible that effects such as sire x year interaction, herd-year x sex interactions and management groups amongst others not included in the model might have attributed to the highly negative direct-maternal genetic correlations obtained in the present study. It might therefore be necessary to consider them for future estimates.

Conclusion

The estimates of genetic parameters in Gudali and Wakwa are indicative that there are possibilities of improving pre-weaning and/or post-weaning growth performance in both breeds through selection. Direct heritability estimates in the Gudali were moderate for birth weight (0.37), pre-weaning gain (0.24) and weaning weight (0.28) and highly heritable at twelve months weight (0.51). Estimates for maternal heritability (0.200), permanent maternal environmental variance (0.09) and total heritability (0.22) were highest at yearling. Considering the high negative genetic correlation between direct and maternal genetic effects, it may be recommended that direct selection be effective at yearling to optimise genetic gain. Conversely in the Wakwa direct heritability was high for birth weight (0.55) but moderately heritable for pre-weaning gain (0.26) and weaning weight (0.28). The maternal (0.23) and total (0.18) heritabilities were highest at birth. However, due to high incidence of dystocia resulting from higher birth weights, selection for optimum genetic response in the Wakwa could be more effective at weaning weight.

The role of permanent maternal environmental effect is not significant at birth in both breeds. It however, becomes progressively important from weaning to eighteen months. Hence, attempting separation of the permanent maternal environmental and maternal genetic effects during estimation of genetic parameters in these breeds is warranted.

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