GENETIC IMPROVEMENT OF BEEF CATTLE IN A TROPICAL ENVIRONMENT WITH SPECIAL REFERENCE TO THE GUDALI AND WAKWA BREEDS IN CAMEROON

BY

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PHILOSOPHIAE DOCTOR

PROMOTER: **PROFESSOR G.J. ERASMUS**

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DECLARATION STATEMENT

I, Achenduh Lot Ebangi declare that the thesis hereby submitted by me for the award of the **Philosophiae Doctor** Degree at the University of the Orange Free State is my own independent work and has not previously been submitted by me at another University/Faculty. I further more cede copyright of this thesis in favour of the University of the Orange Free State.

Signature.................................... Date 3/3/2000

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PREFACE

It is my wish that this thesis will serve as a source of useful breeding information for the design of improvement strategies for beef cattle in Cameroon and other tropical environments. The thesis is presented in the form of scientific publications (submitted) from chapter three to six. These chapters are preceded by chapter one, a general introduction, that focuses on beef cattle improvement in Cameroon during the pre- and post-independent period and chapter two, a literature search, that concentrates on factors affecting growth traits, genetic parameter estimates and genetic trends in beef cattle breeds in the tropical and temperate environments. The last portion of the work, chapter seven, constitutes the general conclusions and recommendations. This chapter gives an overall assessment of results obtained in this study in view of designing possible improvement strategies for beef cattle through selective breeding.

I was able to accomplish this work thanks to the National Research Foundation (NRF) of the Republic of South Africa and the central research fund of UOFS that supplied the funds. It is my wish to see this assistance extend into a research collaboration between the Institute of Agricultural Research for Development (IARD) of Cameroon and the Department of Animal Science, Faculty of Agriculture, University of the Orange Free State (UOFS). It was a wonderful experience studying at the beautiful University of the Orange Free State. The personnel and authorities of the University, especially those of the Department of Animal Science, Faculty of Agriculture were really accomodative and kind. I had a very condusive environment for my studies. I remain grateful for all the assistance and promise to carry this good message to any one who has the aspiration of taking up studies in UOFS.

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Today, I am satisfied for achieving my dream. Only the Lord alone knew the plans He had for me, plans to bring me prosperity and not disaster, plans to bring about the future I had hoped for. THANK YOU LORD JESUS.

DEDICATION

I would like to dedicate this thesis to the following:

My Late Dad, Ebangi Andoba, for giving me all the blessings and hope before dying,

My Late Mum, Ebangi Tabitha, for her tender care and motherly love,

My Late Brother, Ebangi Andrew, for all the assistance towards my education,

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CHAPTER ONE

GENERAL INTRODUCTION

A review of beef cattle improvement in Cameroon

Cameroon has a surface area of about 480,000 km^2 and a human population of about 14 million. It is situated between the 2^{nd} and 3^{rd} parallels above the equator in the Central African sub-region. The agro-ecology of the country is quite diverse and covers the major ecological zones, namely, the humid equatorial forest, sub-humid tropical highlands, Sudano-Guinean savannah, Sudan savannah and Sudano-sahelian. The climate and vegetation vary as a result of the different agro-ecological zones. The pastures are natural and normally very nutritive. The protein and mineral constitutions have been determined (Ndikum Moffor *et al.*, 1994). The DM biomass production of annual pasture has been estimated at 4.6 tons per hectare and the different legumes and grasses cultivated for livestock production and their annual biomass production estimated at about 10 tons per hectare (Piot & Rippstein, 1975).

Cattle predominate the livestock sector in Cameroon. They account for about 16% of the total agricultural production and 30% of the total income of the rural masses (Teuscher *et al.*, 1992). Cattle population was estimated at about 4,361,500 heads between 1986 and 1987 (Teuscher *et al.*, 1992; Maikano *et al.*, 1992). Although cattle are found in all agro-ecological zones of the country, they are concentrated in the Sudano-sahelian (38%) and the Sudan savannah zones (36.4%) (Teuscher *et al.*, 1992; Maikano *et al.*, 1992). The zebu (*Bos indicus*) is the predominant cattle type in Cameroon, accounting for about 99.8% of the national figures (ILCA, 1992), while the humpless *Bos taurus* constitutes only about 0.2%. The principal *Bos indicus* breeds include the *Red Fulani* (28.8%), *White Fulani* (25%), *Sahel Zebu* (21.4%), *Ngaoundere Gudali* or *Zebu Fulbe* (15.3%), *Arab Shuwa* (5%) and *Banyo Gudali* (3.6%) (Teuscher *et al.*, 1992; Maikaino *et al.*, 1992).

The mean annual meat production in Cameroon is roughly 105,052 tons with, about 61.3% coming from cattle (Teuscher *et al.*, 1992). This production is lower than the demand which is estimated at about 161,000 tons (Tanya *et al.*, unpublished). Offtakes are usually low and have been estimated at 10% (Mbah *et al.*, 1988). It is therefore evident that Cameroon has to import beef in order to meet with the internal demands. The reasons for the low beef production have been attributed to many factors that include, amongst others, modest fertility, slow growth and high mortalities (about five to 10% for adult cattle and 20% for calves). The high mortalities are largely due to the high incidence of trypanosomiasis, as most of the available pastures in Cameroon are infested with tsetse flies (Tanya *et al.*, unpublished). Although different control strategies have been adopted during the last two decades (Achukwi *et al.*, 1997) with proven efficacy, there are persistent re-infestations of tsetse-cleared pastures in the Adamawa (major production area) plateau of Cameroon. Such areas have increased from 90,000 hectares in 1989 to 400,000 hectres in 1990 (Cuisance, 1990). Diseases, such as foot and mouth disease (FMD), dermatophylosis, cowdriosis, rinderpest, and various forms of ecto- and endo-parasites are also common. Other factors that affect productivity include degradation of rangelands as a result of overgrazing, climatic hazards, water scarcity, absence of systematic improvement strategies, poor health facilities and socio-economic factors. There is also a deficiency in phosphorus year-round and low levels of crude protein in the dry season (Ndikum Moffor *et al.* 1994).

In recognition of the important role of cattle production in the economy of Cameroon, the government has spared little effort in bringing about improvement in this sector. Livestock policies have been defined to include increased cattle productivity, use of price incentives, construction of cattle market outlets and modern slaughterhouses and encouragement of milk production and transformation activities in Adamawa (SOGELAIT in Ngaoundere) and North West (SOTRAMILK and Tadu Diary in Bamenda and Bui, respectively) Provinces. These policies are aimed to stimulate and enhance cattle production. Also efforts have been made to enhance animal health, management and genetic improvement of the livestock. Genetic improvement has embraced selection, establishment of herdbooks, progeny and performance testing, distribution of improved stock to local farmers and crossbreeding of local breeds with highly performing exotic breeds.

The first attempt at genetic improvement of cattle in Cameroon involved the *Montbeliard operation*. This operation involved the importation of Monbeliard cattle from France in the 1930s for an on-the-spot production of purebreds and the progressive upgrading of the local zebu through crossbreeding (Mandon, 1957; Mbah, 1992; Tawah *et al.*, 1996). The project, however, failed because of problems of genotype x environmental interaction and non-acceptability of the crossbred *Bos indicus* (local zebu) X *Bos taurus* (Montbeliard) by the local breeders. This crossbreed also remained less tolerant to nutritional and heat stresses and was highly susceptible to infections (Mbah, 1982a & b; Tanya & Salah, 1985). Further attempts at improving the local Gudali resulted in the *Wakwa operation* of 1952. This operation was aimed at using the American Brahman breed as a paternal line and the local zebu as the dam line. Crossing the high yielding exotic breed (American Brahman) to the local zebu (Gudali) of lower production, but well adapted to the unfavourable tropical conditions in the region has led to the exploitation of both additive and non-additive genetic effects resulting from complementarity and heterosis. The choice of zebu Brahma, *a priori,* was based on its resistance to higher temperatures and climatic stresses. It could therefore be easily accepted by the local livestock farmer. The operation began with the importation of 45 Brahman bulls from the USA between 1952 and 1958 (Mandon, 1957). The Brahman bulls were crossed to the local Gudali females to produce the first filial generation (50% Brahman x 50% Gudali) which was called *Prewakwa*. Because of its relatively high susceptible to streptothricosis (dermatophilosis), it was *inter se* mated to produce the second filial generation which fortunately turned out to be more tolerant to this skin disease. This generation and subsequent ones became known as *Wakwa* (Figure 1.1). However, studies (Dumas *et al.*, 1971; Tanya & Salah, 1985) have shown that Wakwa, as their Brahman sire breed, are still more susceptible to streptothricosis than the Gudali. Because of the unsuccessful efforts to improve Gudali through breed substitution and upgrading, an alternative improvement strategy, selection, was attempted. This gave rise to the *Ngaoundere* or *Gudali* operation in 1969. The aim of this operation was to carry out a systematic selection of the local zebu Gudali with a view to enhance their beef production potential (Figure 1.2 & 1.3).

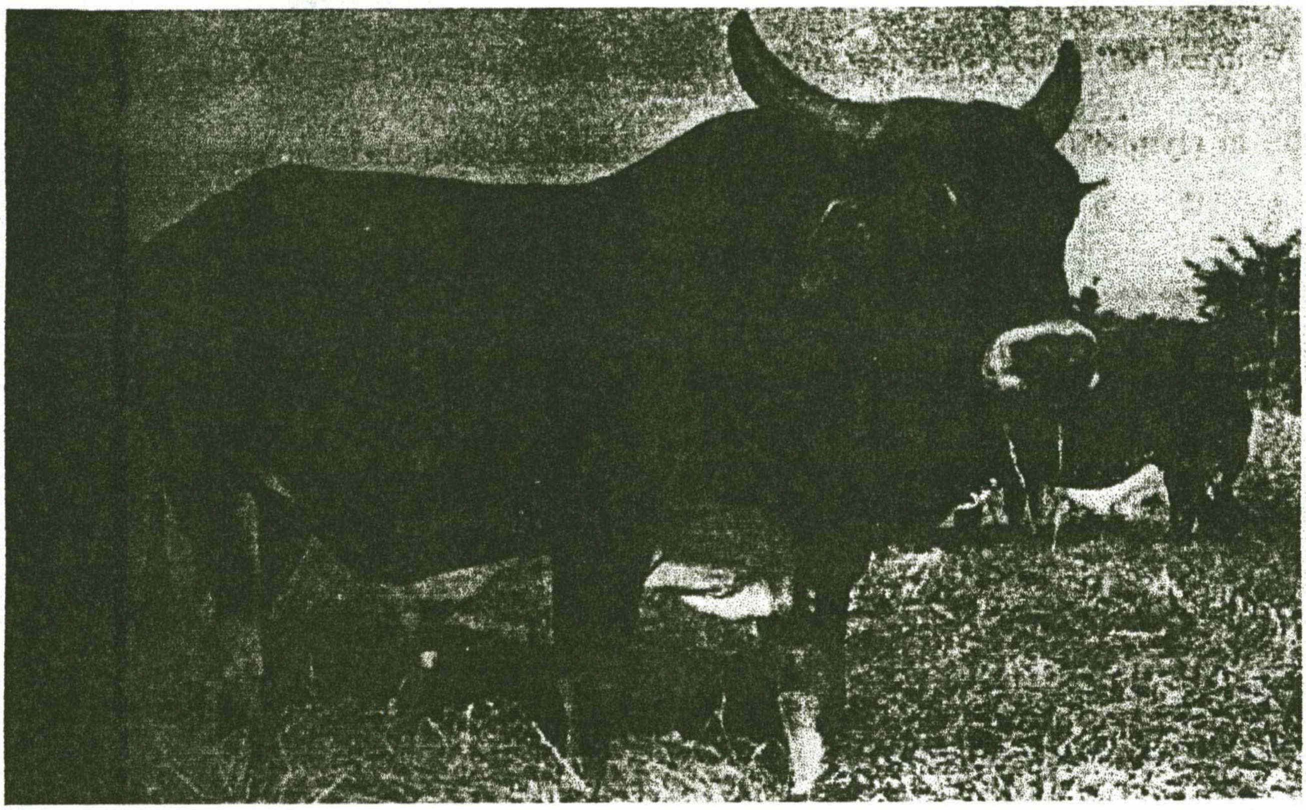

Figure 1.1 Wakwa bull

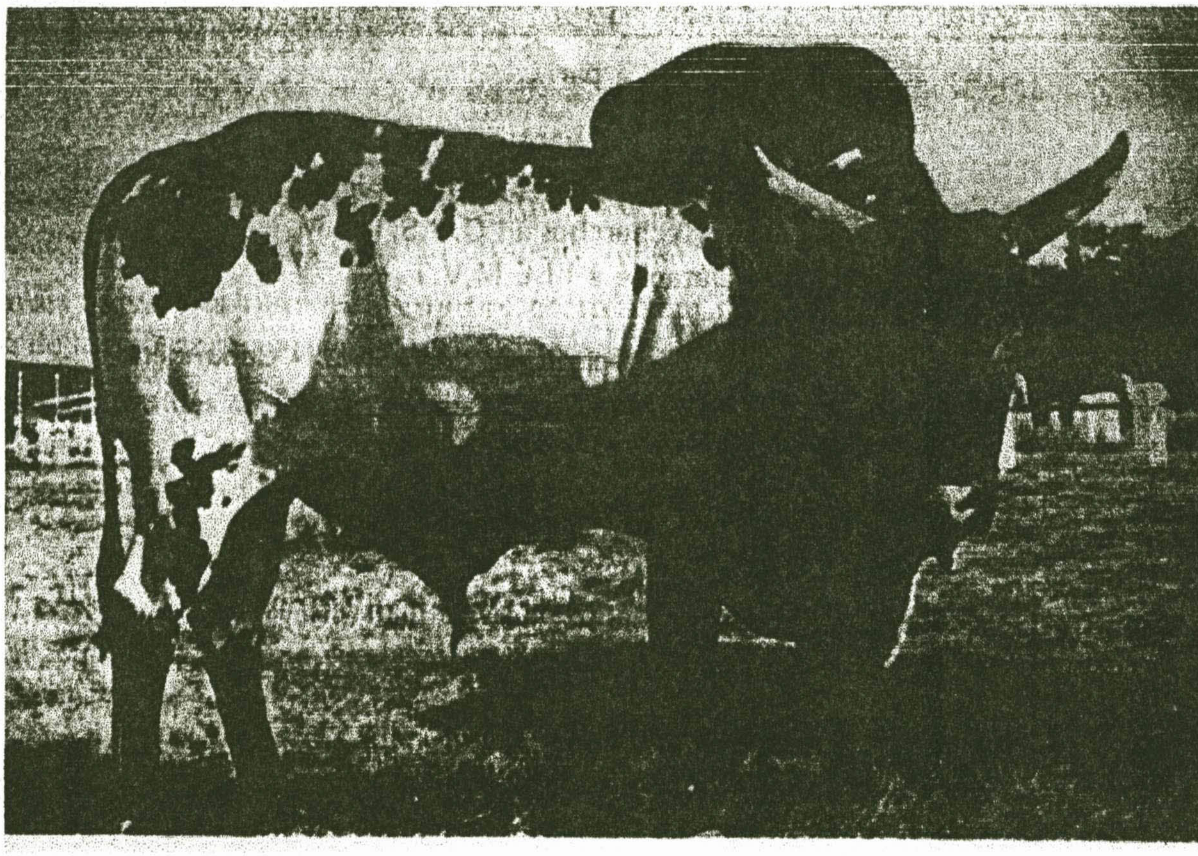

Figure 1.2 Gudali bull

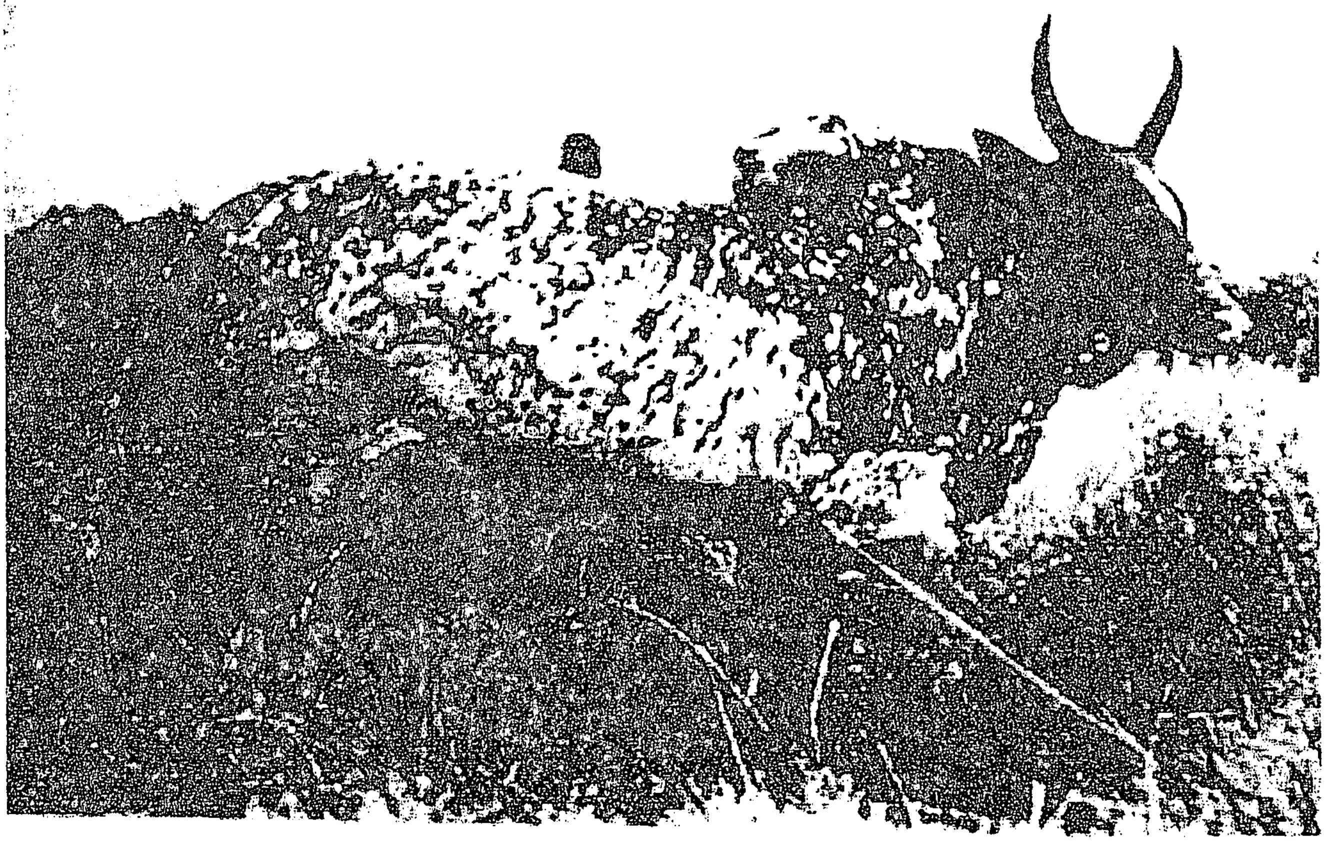

Figure 1.3 Gudali cow

These three major operations were all based in the Adamawa Province of Cameroon. Adamawa is a high plateau with an altitude varying between 900 and 1500 m. It is situated between latitude 6° and 8° N and 10° and 16° E. The surface area is about 62,000 km^2. The average rainfall is about 1600 to 1800 mm per annum with a distinct dry season of 3 to 5 months and a rainy season of 7 to 9 months, with more than 200 mm rainfall/month (IFG, 1980). Temperatures vary between 10 and 35°C. The vegetation is the Sudan savannah type with cleared or degraded forest. The natural environment and the low population density of 6.8 inhabitants/km^2 are factors that favour cattle production in the area as reflected by the highest cattle density of 19.4 cattle/km^2 and a cattle population representing 27.6% of the national average. Adamawa produces about 60% of beef cattle in Cameroon (Mbah, 1992). Cattle rearing, however, is predominantly extensive and traditional with limited inputs. The nutrition is poor and disease and parasite infestations are quite high while growth rate is slow, fertility modest and adult cattle and calf mortalities are quite high. Consequently, the level of production is low.

Over the years the *Wakwa* and *Gudali* (Ngaoundere) operations have accumulated a reasonable amount of data which have unfortunately not been comprehensively exploited. Abassa *et al.* (1993) quantified factors affecting birth and weaning weights of Gudali and Wakwa. Tawah *et al.* (1993 & 1994) estimated genetic parameters and trends for these same traits. Reliable estimates of genetic parameters of not only birth and weaning traits but also of post-weaning traits are important for sound breeding decisions. Furthermore, the study of genetic trends is an important means of tracking the progress from selection. Although improvements through selection are slow and expensive, the effects are cumulative once achieved and are transmitted with little cost from generation to generation even when selection has stopped (Dempfle, 1992). The objectives of the study were to quantify factors that affect growth performance, estimate (co)variance components and determine the direct and maternal genetic trends for pre- and post-weaning traits in the Gudali and Wakwa breeds. It was also aimed at predicting genetic merits for maternal performance in the breeds. Unfortunately, due to the small data size on preweaning weight measurements for the Wakwa, this last part of the study only concentrated on the Gudali.

CHAPTER TWO

LITERATURE REVIEW

2.1 Factors affecting performance traits in beef cattle

The environment is an important component in the development of livestock and can also react with the genotype. Various livestock breeds, especially in tropical and sub-tropical regions, are reared in environments usually characterised by high temperatures and high humidity and marked seasonal fluctuations in rainfall. Consequently, various breeds rank differently for different attributes and, therefore, respond differently to different stresses and different environments (Vercoe & Frisch, 1987). Thus, in order to improve the productivity of livestock breed, it will be necessary to have sound knowledge of both the genetic and environmental factors likely to influence their productivity. Hence the use of mixed model methodology (Henderson, 1973; Henderson & Quaas, 1976; Quaas & Pollak, 1980; Wright *et al.*, 1987) which can simultaneously adjust for the environmental factors (BLUE) and predict genetic values (BLUP). However, only limited studies have used mixed model methodology to quantify the factors that affect the growth of zebu beef cattle in the tropics. In Cameroon, some studies (Lhoste, 1968; Saint-Martin *et al.*, 1988; Tawah & Mbah, 1989) have attempted to investigate environmental factors affecting growth traits. Using least squares methodology, Abassa *et al.* (1993) reported significant effects ($p<0.01$) of breed, sire and sex on birth weights of Gudali and Wakwa beef cattle. Breed, sex and season of calving and weight at birth equally affected weaning weight ($p<0.05$) in the two breeds. The effect of sire and parity were, however, not statistically significant. Studies conducted elsewhere by Rust and Van der Westhuizen (1994) identified month and year of birth, management system and weight of dam at birth as factors affecting birth and weaning weights of Simmental cattle. Kars *et al.* (1994) also reported that sire, year of birth, sex of calf and age of dam significantly ($p<0.001$) affected growth traits in Nguni cattle. Singh *et al.* (1970) indicated that sex significantly affected birth weight, preweaning gain and weaning weight ($p<0.01$) of Hereford calves. Also, bull calves were reportedly heavier at birth than heifer calves. The same authors also reported that steers gained more weight than heifers and that age of calf at weaning affected its weaning weight ($p<0.01$). Month of calving was, however, not significant though year of calving significantly affected all three traits ($p<0.01$). Age of dam did not significantly affect birth weight but affected preweaning gain and weaning weight ($p<0.01$). Ahunu & Makarechian (1987) also reported significant year, season, sex, breed group and age of dam effects on preweaning gain ($p< 0.05$) for three groups of beef calves. Male calves were reported to be significantly ($p<0.001$) heavier than female calves. Mangus & Brinks (1971), studying the preweaning weight of Hereford calves, reported a significant ($p<0.05$) age of dam effect. They concluded that improving weaning weight of beef cattle depended on increasing the preweaning growth rate of calves and the maternal ability of cows. The effect of dam age on preweaning growth results from the variable levels of milk production of dams depending on their age. It will be necessary, therefore to quantify fixed factors that affect various performance traits at specified age-correlated weights so that reliable estimates for the traits could be obtained for a better assessment of any individual animal genetic potential.

2.2 Genetic parameter estimates for tropical zebu beef cattle

The effectiveness of any genetic improvement through selection in any trait depends on the magnitude of genetic parameter estimates for the trait, especially as selection is largely dependent on the amount of available additive variation. Though many governments in Africa have invested a great deal of resources and manpower in livestock improvement, there are still few studies in the literature on genetic parameters estimates for tropical beef cattle. This is clearly not the case for genetic parameter estimates in temperate beef cattle abound in the literature. Nevertheless, few estimates on genetic parameters for growth traits in tropical zebu cattle do exist in the literature as indicated in Table 2.1.

Table 2.1 Some estimates of genetic parameters in tropical beef cattle

Breed	Country	h^2_A	h^2_M	h^2_T	r_{AM}	Reference
Birth weight						
Gudali	Cameroon	0.39	0.06	0.22	-0.86	Tawah *et al.* (1993)
Wakwa	Cameroon	0.65	0.22	0.23	-0.93	Tawah *et al.* (1993)
Nguni	S/Africa	0.41	0.16	0.44	-0.49	Kars *et al.* (1994)
Boran	Ethiopia	0.24	0.09	0.17	-0.55	Haile-Mariam & Kassa-Mersha (1995)
Boran	Ethiopia	0.11	0.02			Arnason & Kassa-Mersha (1987)
Gobra	Senegal	0.07	0.04	0.08	-0.17	Diop & Van Vleck (1998)
Gudali	Nigeria	0.28				Iloeje (1986)
Devon	Nigeria	0.26				Iloeje (1986)
Weaning weight						
Gudali	Cameroon	0.27	0.20	0.13	-0.68	Tawah *et al.* (1993)
Wakwa	Cameroon	0.29	0.27	0.26	-0.39	Tawah *et al.* (1993)
Nguni	S/Africa	0.29	0.20	0.40	-0.39	Kars *et al.* (1994)

Continuation of Table 2.1

Boran	Ethiopia	0.29	0.06	0.21	-0.57	Haile-Mariam & Kassa-Mersha (1995)
Boran	Ethiopia	0.22	0.11			Arnason & Kassa-Mersha (1987)
Gobra	Senegal	0.20	0.12	0.21	-0.61	Diop & Van Vleck (1998)
Gudali	Nigeria	0.31				Iloeje (1986)
South Devon	Nigeria	0.21				Iloeje (1986)
Bonsmara	S/Africa	0.28	0.17		-0.53	Neser *et al.* (1996)
Mashona	Zimbabwe	0.28	0.11	0.25	-0.27	Khombe *et al.* (1995)
Average preweaning daily gain						
Boran	Ethiopia	0.22	0.14			Arnason & Kassa-Mersha (1987)
Gudali	Nigeria	0.30				Iloeje (1986)
South Devon	Nigeria	0.29				Iloeje (1986)
Yearling weight						
Nguni	S/Africa	0.26	0.08	0.34	-0.08	Kars *et al.* (1994)
Boran	Ethiopia	0.34	0.05	0.34	-0.68	Haile-Mariam & Kassa-Mersha (1995)
Gobra	Senegal	0.24	0.21	0.18	-0.50	Diop & Van Vleck (1998)
Gudali	Nigeria	0.37				Iloeje (1986)
South Devon	Nigeria	0.33				Iloeje (1986)
Eighteen-months weight						
Nguni	S/Africa	0.19	0.003	0.29	0.97	Kars *et al.* 91994)
Gobra	Senegal	0.14	0.16	0.15	-0.29	Diop & Van Vleck (1998)
Gudali	Nigeria	0.31				Iloeje (1986)
South Devon	Nigeria	0.26				Iloeje (1986)

The estimates cited in Table 2.1, appear different from breed to breed. This might be due to differences in analytical methods, sample sizes and production and management environment. The common trend for most of the studies, however, is the negative nature of the direct-maternal genetic correlations.

Genetic estimates on crossbreeds in the tropics are equally few in the literature. Mackinnon *et al.* (1991) reported 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 weight, weaning weight, yearling and eighteen months weight in zebu-crosses of Africander (50%), Hereford (25%) and Shorthorn (25%), and Africander (50%) x Brahman (50%). Direct-maternal genetic correlation was zero for these traits. Deese & Koger (1967), studying crossbred Brahman x Shorthorn, reported estimates of 0.40, 0.46 and 0.17 for direct, maternal and total heritability for weaning weight. Genetic correlation between additive and maternal genetic effects was negative. These studies show higher estimates for direct heritability for the crosses than for the purebred zebu cattle in the tropics. Direct-maternal genetic correlation appears to be inconclusive in the crossbreeds.

2.3 Genetic parameters estimates for some temperate beef cattle

Several studies appear in the literature on genetic parameter estimates in temperate beef cattle breeds. For the sake of a more complete literature review, some of the reported estimates are supplied in Table 2.2 below.

Table 2.2 Some estimates of genetic parameters in temperate beef cattle

Breed	h^2_a	h^2_m	h^2_T	r_{am}	Reference
Birth weight					
Angus	0.42	0.22		-0.12	Johnson *et al.* (1992)
Angus	0.19				Wilson *et al.* (1986)
Angus	0.36	0.07		0.28	Thompson (1976)
Angus	0.70				Susana *et al.* (1984)
Angus	0.14	0.25	0.17	-0.37	Brown and Galvez (1969)
Angus	0.36	0.07	0.46	0.29	Meyer (1992)
Angus	0.35	0.08		-0.61	Robinson (1996)
Hereford	0.56	0.30	0.36	-0.58	Brown and Galvez (1969)
Hereford	0.41				Wison *et al.* (1986)
Hereford	0.58	0.20		-0.13	Johnson *et al.* (1992)
Hereford	0.27	0.63	0.05	-1.05	Cantet *et al.* (1988)
Hereford	0.41	0.08	0.46	0.08	Meyer (1992)
Hereford	0.41	0.08		0.22	Thompson (1976)
Hereford	0.18	0.21		-1.05	Cantet *et al.* (1988)
Simmental	0.21	0.10		-0.24	Burfening *et al.* (1981)
Simmental	0.44	0.12		-0.38	Garrick *et al.* (1989)
Limousin	0.35	0.08	0.26	-0.40	Shi *et al.* (1993)
Shorthorn	0.21				Fahmy & Lalande (1973)
Charolias	0.25				Johnston *et al.* (1992)
BNS	0.35				Barlow (1978)
BNS	0.36	0.82		-0.51	Nelsen *et al.* (1984)
BNS	0.43				Koch *et al.* (1982)
BNS	0.31	0.14			Koots *et al.* (1994)
BNS	0.30	0.10		-0.35	Mohiudden (1993)
BNS	0.25	0.16		-0.48	Van der Westhuisen (1997)

Continuation Table 2.2

Preweaning gain					
Angus	0.39	0.21		-0.45	Trus and Wilton (1988)
Angus	0.57	0.15		-0.46	Johnson *et al.* (1992)
Hereford	0.30	0.27		-0.42	Trus and Wilton (1988)
Hereford	0.58	0.39		-0.06	Johnson *et al.* (1992)
Charolais	0.39	0.26		-0.14	Trus and Wilton (1988)
Simmental	0.27	0.16		-0.26	Trus and Wilton (1988)
Simmental	0.26	0.01		-0.28	Garrick *et al.* (1989)
Shorthorn	0.43	0.20		-0.45	Trus and Wilton (1988)
Limousin	0.25	0.13	0.25	-0.25	Shi *et al.* (1993)
BNS	0.23	0.16		-0.39	Van der Westhuisen (1997)
BNS	0.07				Koch *et al.* (1982)
BNS	0.27				Barlow (1978)
Weaning weight					
Angus	0.68	0.16		0.36	Johnson *et al.* (1992)
Angus	0.20	0.14		0.48	Thompson (1976)
Angus	0.16				Wilson *et al.* (1986)
Angus	0.46				Susana *et al.* (1984)
Angus	0.20	0.14	0.32	0.22	Meyer (1992)
Angus	0.20	0.09		-0.52	Robinson (1996)
Hereford	0.23	0.34	0.25	-0.28	Hohenboken & Brinks (1971)
Hereford	0.27	0.40	0.26	-0.79	Hohenboken & Brinks (1971)
Hereford	0.66	0.43		-0.08	Johnson *et al.* (1992)
Hereford	0.14	0.13		-0.78	Thompson (1976)
Hereford	0.32	0.67	0.20	-0.79	Cantet *et al.* (1988)
Hereford	0.14	0.13	0.09	-0.59	Meyer (1992)
Hereford	0.32	0.27		-0.57	Cantet *et al.* (1988)
Hereford	0.13				Wilson *et al.* (1986)
Charolais	0.09				Johnston *et al.* (1992)
Simmental	0.12	0.09		0.21	Wright *et al.* (1987)

Continuation Table 2.2

Simmental	0.36	0.19		-0.32	Garrick *et al.* (1989)
Shorthorn	0.32				Fahmy & Lalande (1973)
Limousin	0.26	0.13	0.26	-0.24	Shi *et al.* (1993)
Senepol	0.21	0.47		0.57	Wright *et al.* (1991)
Zebu cross	0.58	0.36		-0.48	Thompson (1976)
	0.30				Barlow (1978)
BNS	0.24	0.13			Koots *et al.* (1994)
BNS	0.22	0.13		-0.15	Mohiudden (1993)
BNS	0.23	0.19		-0.26	Van der Westhuisen (1997)
Yearling weight					
Angus	0.33	0.04			Thompson (1976)
Angus	0.33	0.04	0.43	0.49	Meyer (1992)
Angus	0.49				Susana *et al.* (1984)
Angus	0.24	0.06		-0.73	Robinson (1996)
Hereford	0.16	0.11	0.12	-0.48	Meyer (1992)
Hereford	0.16	0.11			Thompson (1976)
Charolais	0.16				Johnston *et al.* (1992)
Zebu cross	0.25	0.14	0.21	-0.39	Meyer (1992)
Zebu cross	0.25	0.14			Thompson (1976)
BNS	0.33	0.11			Koots *et al.* (1994)
BNS	0.33	0.11		0.26	Mohiudden (1993)
BNS	0.25	0.10		-0.18	Van der Westhuisen (1997)
Eighteen months					
Angus	0.25	0.04		-0.70	Robinson (1996)
Angus	0.46	0.03			Thompson (1976)
Hereford	0.22				Thompson (1976)
Zebu cross	0.24	0.01			Thompson (1976)
BNS	0.14	0.01		1.00	Van der Westhuisen (1997)

BNS = breed not specified

The genetic parameters for most of the breeds vary with country, production systems and methods of analysis. The genetic correlations between direct and maternal effects were highly negative in most cases as was found for tropical beef cattle. This genetic antagonism between direct and maternal effects could be indicative of the importance of maternal effects on the growth performance of young beef cattle. Koch (1969) reported that the maternal genetic and permanent environmental variances and direct-maternal covariance accounted for 15-20% of the total variance of birth weight. The maternal variance alone accounted for 10-15% of the total variance. Maternal related variance accounts for 29-35% of total variance and maternal heritability was estimated at 0.30 to 0.36 for preweaning gain. He was, however, inconclusive about direct-maternal genetic correlations for preweaning traits. The negative correlation between direct and maternal genetic effects is therefore a serious impediment for selection progress, especially when the value is high. Various researchers have tried to explain the reasons for the high negative direct-maternal genetic correlation. Robinson (1996) attributed high negative genetic correlations between direct and maternal effects to negative dam-offspring covariances or additional sire or sire x year interaction not accounted for in estimation models. Meyer (1997) attributed them to sources of variation such as paddocks or management groups not accounted for in the analyses. Tassel (personal communication) and Lee and Pollak (1997a & b) attributed them to selective reporting, sire x year and to potential heterogeneity of correlation by gender not accounted for in present day models of analyses. Neser *et al.* (1996) have also shown the importance of herd-year-season x sex interaction in the determination of the magnitude of the negative direct-maternal genetic correlation. The problem of heterogeneous variances has also been reported by Thrift *et* *al.* (1981) and Garrick *et al.* (1989) to account for this high negative covariance. Van Vleck *et al.* (1977) showed that the practical implication of the high negative direct-maternal genetic correlation was a reduction in expected response to selection. They, therefore, suggested selection of males for direct and females for maternal breeding values in cases where correlation was highly negative. This would give greater selection response after the first generation than if selection of dams were to be based on direct breeding values.

2.4 GENETIC TRENDS

Many governments in Africa continue to spend huge sums of money on beef breeding programmes. The evaluation of a breeding programme or selection experiment in the form of an assessment of genetic progress attained is imperative to identify problems and handicaps to be expected for necessary remedial actions. It is, however, rare to find studies in the literature on genetic and environmental trends for tropical beef cattle. Tawah *et al.* (1993) reported estimated annual changes in sire's transmitting ability and dam breeding values for weaning weight of 0.67 and -0.03, and 1.13 and -0.24 kg/year for the Gudali and Wakwa, respectively. The corresponding values for birth weight were 0.09 and -0.001 and -0.14, and -0.01 kg/year for Gudali and Wakwa breeds.

Kennedy & Henderson (1977) reported positive annual genetic trends of 1.74 and 0.27; 0.0084 and 0.0012; 2.60 and 0.64 and 0.0065 and 0.0044 kg/year for sire and dam trends for weaning weight, preweaning gain, yearling weight and post-weaning gain in Hereford and Aberdeen Angus calves. Elzo *et al.* (1987) reported negative trends for birth weight and positive trends for weaning and yearling weights for sire direct effects in Simmental cattle. Zollinger & Nielsen (1984a, b) reported respective positive contributions averaging 0.51 and 0.34 units/year for sires and dams, representing an overall annual genetic gain of 1.8 kg in weaning weight of Angus cattle. They observed that sire trends were generally larger than dam trends and attributed this to the negative genetic correlation between direct and maternal genetic effects. Positive annual genetic trends of 0.14 and 1.17 kg/year for birth and weaning weights of Shorthorn cattle have also been reported by Fahmy & Lalande (1973). Nwakalor *et al.* (1976) reported annual genetic trends of 1.17 and 2.09 kg/year for weaning weight in inbred and crossbred Hereford populations. Johnson *et al.* (1992) reported estimates of 0.30 and -0.58; 0.026 and -0.0059; 5.78 and -1.74 for direct and maternal genetic trends in Angus. Corresponding figures of 0.47 and 0.01; 0.0132 and 0.0083 and 3.44 and 1.91 were reported in Hereford, respectively, for birth, preweaning gain and 205-d weight, respectively. These estimates of genetic trends are supportive of the genetic antagonism between direct and maternal effects on preweaning growth, suggesting a loss in maternal performance due to intense selection for direct individual growth. This is of great concern to producers in their selection programmes.

2.5 MILKING AND NURSING ABILITY

Milk production is an essential component of selection objectives in beef cattle improvement schemes. Because direct measurements for milk production are not normally available for beef cattle, weaning weights are often used as indicators of the milk production of the dams (Diaz *et al.*, 1992). Hence the use of expected progeny difference (EPD) for weaning weight in the estimation of milking and nursing ability of beef cattle.

Diaz *et al.* (1992) obtained significant positive effects of birth weight on milk production and attributed this to the increased calf demand for milk that stimulated lactation. Marston *et al.* (1992) equally obtained a positive relationship between milk expected progeny difference, actual milk production and calf weaning weights and concluded that milk expected progeny difference (EPD) could be used to enhance the milk production potential in beef cattle. Rutledge *et al.* (1971), in a study on milk yield and its influence on 205-day weight of beef calves, found that dams nursing female calves produced significantly ($P<0.05$) more milk than those nursing male calves. Milk production was affected by the age of dam, which unfortunately did not affect 205-day weight and it could be due to the fact that effects due to age of dam might be expressed primarily through differential milk production. In a study carried out by Yokoi *et al.* (1997) on predicting merit for milking and nursing ability in beef cattle, they found that direct heritabilities were highest at birth and lowest at one month of age but increased in subsequent preweaning ages. In addition, estimates of maternal heritability were highest around two months of age but decreased in later stages. The estimates of the variance for non-additive maternal effects as a proportion of the phenotypic variance were highest at one and two months of age. The maternal heritability for cumulative daily weight gain was equally highest at two months. They concluded that the 'best' measure for predicting genetic merit for milking and nursing ability in beef cattle could be weight at two months of age.

CHAPTER THREE

FACTORS AFFECTING GROWTH PERFORMANCE

3.1 INTRODUCTION

The potential of beef cattle production in Cameroon is high and cattle are found in all the ecological regions of the country (Tanya *et al.*, unpublished). The cattle population has been put at 4,361,500 heads, representing about 61.3% of the total meat production of the country (Teuscher *et al.* 1992; Maikano *et al.*, 1992). Unfortunately, about 60% of the national herd is kept under a husbandry system which is high risk, rural, extensive, nomadic and subsistent, and where diseases and parasites abound (Tanya *et al.*, unpublished). The cattle growth rate is low and fertility modest but calf and adult mortalities are high. The latter have been associated with the high incidence of trypanosomiasis (Achukwi *et al.*, 1997). Factors that affect beef productivity amongst others include degradation of rangelands caused by overgrazing, climatic hazards caused by the variability, severity and length of the rainy and dry seasons, water scarcity, poor health facilities and socio-economic problems. The role of the environment in the determination of beef cattle production and productivity in this area is therefore of great importance.

Despite the important role of the environment in beef cattle production in Cameroon, studies on non-genetic factors that affect growth performance are rare in the literature. Lhoste (1968) investigated factors that affect the growth performance of Gudali and Wakwa breeds using simply the raw means of the performance traits. Abassa *et al.* (1993) and Tawah *et al.* (1993) examined factors affecting preweaning growth performance of both breeds using the least squares approach. However, these authors used only a portion of the data from the two breeds.

Besides, their models included neither herd nor herd x year x season interaction effects. There has, however, been no attempts to extensively quantify environmental factors affecting pre-weaning and post-weaning performance traits for the overall selection data from the two breeds. Genetic improvement of any breed within a given environment will depend on identifying the major environmental constraints to performance, devising means of alleviating or controlling them and then evaluating the breed for its adaptability to cope with constraints that can not be readily controlled. Knowledge of these constraints will be useful in the modification of improvement strategies and/or adjustment of animal records for reliable genetic evaluation of their performance. The aim of the present study was to use mixed model methodology to investigate and quantify factors which may affect pre-weaning and post-weaning growth traits in Gudali and Wakwa beef cattle within the tropical highlands of Cameroon.

3.2 MATERIALS AND METHODS

The data used included weights at birth (BWT), weaning (WWT), yearling (YWT) and eighteen months (EWT), collected between 1968 and 1988 and compiled from the various herdbooks of Adamawa, maintained at the Wakwa Veterinary Research Centre. Weaning, yearling and eighteen months weights were selected from monthly weights at roughly eight, twelve and eighteen months, respectively. The data were obtained from two selection experiments involving a local purebred zebu beef cattle, the Gudali, and a two-breed synthetic beef cattle, the Wakwa. The Gudali is also popularly known as Peulh Fulbe because of its predominance and importance to the Peulh pastoralists in the Adamawa Province of Cameroon (Tawah & Rege, 1996). It is a short-horned zebu characterised by a large dewlap, a navel shealth in the females, a pendulous preputial shealth in the males, erect ears, a well developed cervico-thoracic hump and a variable coat colour with a predominant brownish-white. The breed is fairly large with an average adult male and female weight of about 552 and 307 kg, respectively. The height-at-withers, heart girth and scapulo-ischial length average about 123, 187 and 128 cm, respectively, at adult age (Mandon, 1957). On the other hand, the Wakwa is a two-breed synthetic derived from *inter se* matings of American Brahman x Gudali F1 animals (Prewakwa). A detailed description of the Wakwa is in Mandon (1957), Lhoste (1969), Lhoste and Pierson (1975), Tawah & Mbah (1989) and Tawah *et al.* (1993). Briefly, the Wakwa is characterised by a variety of coat colours. It has a broad but slightly convex face, long but drooping ears, short but broad-based horns, an oval hump and a straight but broad back. At about 30 months, males and females weigh averagely 512 and 426 kg and the height-at-wither, heart girth and scapulo-ishial length average about 133, 140 and 147 cm, respectively (Mandon, 1957).

The animals were maintained at the Wakwa Station for Animal Production of the Ministry of Livestock, Fisheries and Animal Industry and at the Wakwa Research Station of the Institute of Agricultural Research for Development of the Ministry of Scientific Research. The Wakwa Animal Production and Research Stations are located on the Adamawa highlands of Cameroon at an altitude of about 1100 m above sea level. The management system, pastures and climatic conditions are well documented by Dumas and Lhoste (1966); Lhoste (1968 & 1977); Lhoste & Pierson (1973); Piot & Rippstein (1975); Pamo & Yokeu (1987); Tawah & Mbah (1989) and Tawah *et al.* (1996).

Data were edited for valid pedigree information and consistency checks were made on dates, sex, herds, seasons, ages at weaning, yearling and eighteen months and weight ranges. Consequently, the years 1985 to 1987 and 1986, for preweaning traits in Gudali and Wakwa and 1985 to 1988 for postweaning traits in both breeds, were omitted because weight measurements for these years were not available. The valid data were then classified according to sire, sex, herd, season, calf birth year (CBY), cow age group (CAG) and exact ages at weighing at roughly eight months (WAGE), twelve months (YAGE) and eighteen months (EAGE). Seasons were defined as reported by Tawah *et al.* (1993): a five months dry season from November to March and a seven months rainy season from April to October. WAGE, YAGE and EAGE were calculated as the difference between a calf's birth date and its corresponding dates at weaning, yearling and eighteen months, respectively. The cow age group (CAG) was defined as the deviation of dam's year of birth from the calf birth year (CBY). Three categories of CAG were defined: CAG1 for cow age group less than 8 years, CAG2 for cow age group greater than 7 but less than 11 and CAG3 for cow age group greater than 10 years.

Statistical Model and Analytical Techniques

The data were analysed using a mixed linear model, with sire fitted as a random effect and sex, herd (H), season (S), calf birth year (C), HxSxC interaction and cow age group fitted as fixed effects and ages at weaning, yearling and eighteen month fitted as linear covariates on weaning, yearling and eighteen months weights, respectively. Analyses were carried out for each breed separately. The model used for each trait was presented as follows:

$$y_{ijklmno} = \mu + P_i + G_j + S_k + H_l + D_m + C_n + (HxSxC)_{lkn} + b(x_{ijklmno} - \overline{X}) + e_{jklmno},$$

where $y_{ijklmno}$ = growth trait (BWT, ADG, WWT, YWT and EWT) for the o^{th} calf of sex j, from the i^{th} sire, born by cow of the m^{th} group in the k^{th} season and within the n^{th} year and reared in the k^{th} herd,

μ = overall mean,

Pi = random effect of i^{th} sire,

G_j = fixed effect of the j^{th} sex (j = 1, 2),

S_k = fixed effect of the k^{th} season of calving (k = 1, 2),

H_l = fixed effect of the l^{th} herd (l= 1,2...14 for Gudali

and l = 1,2...7 for Wakwa),

D_m = fixed effect of the m^{th} cow age group (m = 1, 2, 3),

C_n = fixed effect of the n^{th} calf birth year (n = 68, 67...88),

$(HxSxC)_{lkn}$ = herd x season x calf birth year interaction,

b = linear regression of calf weight (WWT, YWT or EWT) on age at weaning, yearling and eighteen months, respectively,

$x_{ijklmno}$ = exact age of o^{th} calf (days) at weaning, yearling or eighteen months,

$\overline{X}$ = mean age at weaning, yearling or eighteen months and

$e_{ijklmno}$ = random error, assumed to be normally and independently distributed with a zero mean and variance of $ó^2$.

The data were analysed with the SAS computer program (1991) using the General Linear Model procedure (GLM). Effects included in the final analysis were those found to be significant from a preliminary analysis carried out. The program adjusted for significant fixed effects. The least square means (LSM) and standard errors (se) for each growth trait were computed. The edited data structure on number of progeny records per performance trait per breed and number of sires contributing to the progeny records, trait means (kg), standard deviations (SD) and coefficients of variation (CV) is presented in Table 3.1.

Table 3.1 Summary data structure on fixed effects

BREED	TRAIT	RECORDS	MEAN	SD	CV	No. of SIRES
Gudali	BWT	2886	24.09	2.73	11.34	93
	ADG	2732	0.52	0.12	23.14	93
	WWT	2899	149.79	28.49	9.15	93
	YWT	2098	159.12	28.04	17.64	82
	EWT	1957	197.77	36.50	18.45	79
Wakwa	BWT	1793	24.90	3.14	12.62	60
	ADG	1656	0.57	0.12	21.11	60
	WWT	1838	161.65	29.54	18.27	60
	YWT	1372	170.70	27.71	16.23	53
	EWT	1328	213.65	37.38	17.50	53

There were more records at weaning than at birth. This was simply due to the fact that some calves were not weighed at birth due to the failure of some herdsmen to report the calvings within 24 hours. Consequently, not all calf birth weights needed for computation of preweaning gain were available.

3.3 RESULTS AND DISCUSSIONS

The fixed effects and covariables used in the models for the estimation of the least squares means (LSM) and standard errors (SE) for pre-weaning and post-weaning growth traits in Gudali and Wakwa breeds are presented in Tables 3.2 and 3.3 and 3.4 and 3.5, respectively.

Table 3.2 Least squares means (standard errors) for preweaning growth traits in Gudali cattle

Effects	no	BWT	no	ADG	no	WWT
SEX	***		***		***	
Male	1412	24.42 (0.10)	1345	0.57 (0.004)	1435	160.79 (0.97)
Female	1474	23.57 (0.10)	1387	0.53 (0.004)	1464	150.15 (0.97)
SEASON (S)		***		***		***
Dry	397	23.73 (0.14)	368	0.59 (0.006)	405	164.26 (1.41)
Rainy	2489	24.25 (0.07)	2664	0.51 (0.003)	2494	146.69 (0.69)
HERD (H)		***		***		***
1	252	24.53 (0.18)	245	0.53 (0.007)	259	149.71 (1.74)
2	249	23.83 (0.18)	220	0.53 (0.008)	226	151.02 (1.87)
3	237	24.03 (0.18)	220	0.56 (0.008)	231	158.23 (1.79)
4	293	23.95 (0.17)	288	0.56 (0.007)	306	158.21 (1.62)
5	243	23.71 (0.18)	226	0.54 (0.008)	235	153.89 (1.78)
6	219	24.37 (0.19)	209	0.55 (0.008)	231	156.59 (1.83)
7	241	24.05 (0.18)	232	0.53 (0.008)	251	152.72 (1.78)
8	213	23.79 (0.19)	196	0.52 (0.008)	221	150.85 (1.92)
9	207	23.94 (0.20)	184	0.53 (0.009)	195	151.81 (1.99)
10	209	24.21 (0.19)	208	0.58 (0.008)	222	162.87 (1.86)
11	122	23.72 (0.25)	118	0.55 (0.011)	128	155.01 (1.36)
12	216	23.70 (0.19)	202	0.56 (0.008)	209	158.73 (1.88)
13	151	23.13 (0.23)	141	0.57 (0.010)	147	158.58 (2.30)
14	43	24.92 (0.42)	43	0.58 (0.018)	48	159.03 (2.92)
CBY (C)		***		***		***
68	135	23.72 (0.24)	135	0.54 (0.010)	136	155.90 (2.38)
69	180	24.62 (0.21)	180	0.53 (0.009)	196	152.69 (2.04)
70	226	24.25 (0.20)	220	0.49 (0.008)	222	141.15 (1.96)
71	178	24.66 (0.21)	175	0.53 (0.009)	177	152.18 (2.12)
72	250	24.92 (0.20)	248	0.55 (0.008)	253	155.38 (1.81)
73	199	24.68 (0.24)	133	0.54 (0.010)	138	153.66 (2.33)
74	133	23.31 (0.21)	128	0.53 (0.010)	131	149.57 (2.35)
75	162	23.53 (0.21)	162	0.57 (0.009)	168	159.10 (2.05)
76	165	23.39 (0.20)	156	0.60 (0.009)	165	165.36 (2.07)
77	199	22.90 (0.21)	186	0.61 (0.009)	189	170.30 (2.04)
78	187	23.07 (0.21)	180	0.54 (0.009)	184	150.83 (2.06)
79	176	23.71 (0.21)	164	0.55 (0.009)	173	155.83 (2.12)
80	154	24.20 (0.22)	151	0.52 (0.010)	152	148.78 (2.22)
81	152	24.51 (0.23)	152	0.55 (0.010)	152	149.68 (2.28)

Continuation Table 3.2

82	128	23.80 (0.25)	115	0.52 (0.011)	115	148.47 (2.56)
83	164	24.10 (0.22)	155	0.55 (0.009)	159	155.55 (2.15)
84	98	24.60 (0.27)	92	0.63 (0.012)	125	173.06 (2.40)
88					64	161.03 (3.40)
CAG		ns		ns		***
1	1570	23.82 (0.09)	1487	0.56(0.004)	1579	156.12 (0.89)
2	998	23.98 (0.10)	939	0.55(0.004)	997	155.85 (1.01)
3	318	24.17 (0.17)	306	0.54(0.007)	323	154.45 (1.62)
SIRE		***		***		***
HxSxC		***		***		***
WAGE						***

BWT = birth weight (kg), no = number of records, ADG = preweaning weight gain (kg), WWT = weaning weight (kg), WAGE = weaning age (days), CBY = calf birth year, CAG = cow age group, *** =$p<0.001$, ** = $p<0.01$, * $p<0.05$, ns = non-significance.

Table 3.3 Least squares means (standard errors) for yearling and eighteen-months weights in Gudali cattle

Effects	no	YWT	no	EWT
SEX		***		***
Male	969	170.18 (1.13)	888	211.39 (0.97)
Female	1129	155.87 (1.08)	1069	196.12 (0.97)
SEASON (S)		**		***
Dry	292	165.38 (1.60)	283	209.97 (1.41)
Rainy	1806	160.67 (0.79)	1674	197.54 (0.69)
HERD (H)		***		***
1	162	155.57 (2.01)	148	196.41 (1.74)
2	180	159.34 (1.95)	171	198.52 (1.87)
3	179	165.00 (1.91)	169	208.83 (1.79)
4	227	167.51 (1.80)	213	210.84 (1.62)
5	172	160.09 (1.96)	153	203.15 (1.78)
6	157	159.55 (2.10)	157	197.50 (1.83)
7	149	162.06 (2.16)	142	207.12 (1.78)
8	147	161.71 (2.15)	138	203.87 (1.92)
9	156	156.61 (2.12)	149	200.25 (1.99)
10	154	167.74 (2.83)	141	207.37 (1.86)
11	77	164.02 (2.83)	63	204.04 (1.36)
12	150	167.18 (2.08)	135	206.51 (1.88)

Continuation Table 3.3

13	128	167.16 (2.32)	122	205.79 (2.30)
14	60	168.84 (3.30)	56	202.38 (2.92)
CBY (C)		***		***
68	133	159.38 (2.25)	127	198.18 (2.38)
69	173	142.72 (2.04)	174	185.55 (2.04)
70	210	146.27 (1.92)	195	187.59 (1.96)
71	125	158.09 (2.32)	105	189.10 (2.12)
72	208	159.57 (1.86)	191	193.18 (1.81)
73	130	152.78 (2.26)	113	182.98 (2.33)
74	81	153.04 (2.75)	79	201.38 (2.35)
75	164	172.79 (1.94)	165	210.50 (2.05)
76	123	177.11 (2.20)	135	245.53 (2.07)
77	165	168.57 (2.04)	159	192.67 (2.04)
78	131	152.42 (2.27)	110	186.89 (2.06)
79	112	160.04 (2.40)	105	201.26 (2.12)
80	60	172.38 (3.20)	55	225.01 (2.22)
81	22	169.51 (5.17)	22	206.79 (2.28)
82	67	156.58 (3.06)	71	204.93 (2.56)
83	122	175.03 (2.30)	92	221.97 (2.15)
84	72	195.19 (2.94)	59	230.33 (2.40)
CAG		ns		**
1	1152	164.36 (1.02)	1091	207.36 (0.89)
2	736	163.55 (1.13)	687	204.46 (1.01)
3	210	161.17 (1.85)	179	199.44 (1.62)
SIRE		*		ns
HxSxC		*		ns
YAGE		***		
EAGE				ns

YWT = yearling weight (kg), EWT = eighteen months weight (kg), YAGE = yearling age (days), EAGE = eighteen month age (day), no = number of records, CBY = calf birth year, CAG = cow age group, *** =p<0.001, ** = p<0.01, * = p<0.05, ns = non-significance.

Table 3.4 Least squares means (standard errors) for preweaning growth traits in Wakwa cattle

Effects	no	BWT	no	ADG	no	WWT
SEX		***		***		***
Male	903	25.13 (0.15)	845	0.63 (0.006)	953	174.36 (3.67)
Female	890	24.22 (0.15)	811	0.58 (0.006)	885	160.58 (3.63)
SEASON (S)		***		***		***
Dry	175	24.49 (0.23)	160	0.65 (0.009)	211	176.57 (3.91)
Rainy	1618	24.85 (0.11)	1496	0.56 (0.005)	1627	158.38 (3.57)
HERD (H)		***		***		***
15	310	24.75 (0.21)	296	0.60 (0.009)	317	169.28 (2.00)
16	257	24.39 (0.21)	236	0.61 (0.009)	269	168.85 (2.00)
17	305	25.05 (0.20)	288	0.63 (0.008)	317	175.58 (1.82)
18	251	23.48 (0.21)	227	0.60 (0.009)	256	166.58 (2.01)
19	305	24.98 (0.20)	281	0.60 (0.008)	320	168.75 (1.85)
20	259	25.51 (0.21)	232	0.59 (0.009)	247	167.72 (2.04)
21	106	24.53 (0.30)	96	0.61 (0.013)	112	168.73 (2.86)
CBY (C)		***		***		***
68	146	25.34 (0.27)	146	0.56 (0.011)	151	157.60 (4.24)
69	154	26.34 (0.26)	154	0.59 (0.011)	167	164.49 (4.17)
70	158	25.38 (0.27)	155	0.57 (0.011)	163	158.70 (4.23)
71	56	26.51 (0.33)	83	0.60 (0.014)	87	168.05 (4.65)
72	128	25.95 (0.27)	119	0.61 (0.011)	126	168.20 (4.28)
73	147	25.66 (0.27)	89	0.62 (0.013)	94	168.17 (4.56)
74	101	24.32 (0.30)	86	0.59 (0.013)	94	161.41 (4.51)
75	77	24.43 (0.34)	77	0.58 (0.014)	86	162.31 (4.60)
76	109	24.91 (0.28)	102	0.63 (0.011)	113	173.42 (4.32)
77	119	23.22 (0.29)	112	0.62 (0.012)	115	168.52 (4.37)
78	113	22.09 (0.29)	102	0.59 (0.012)	110	162.93 (4.40)
79	96	23.32 (0.31)	91	0.60 (0.013)	97	164.33 (4.51)
80	112	24.66 (0.30)	110	0.59 (0.012)	112	163.95 (4.42)
81	92	24.56 (0.31)	89	0.60 (0.013)	92	161.01 (4.59)
82	59	24.73 (0.38)	53	0.60 (0.016)	58	161.03 (5.01)
83	53	24.28 (0.41)	50	0.63 (0.017)	51	171.91 (5.20)
84	35	24.68 (0.48)	30	0.63 (0.021)	35	173.08 (5.76)
85	8	23.84 (1.01)	8	0.69 (0.040)	8	182.62 (10.3)
87					52	187.25 (4.81)
88					27	170.47 (6.45)
CAG		ns		ns		***

Continuation Table 3.4

1	270	25.02 (0.20)	252	0.62 (0.008)	288	171.27 (3.86)
2	1258	24.49 (0.13)	1162	0.61 (0.005)	1291	169.07 (3.56)
3	265	24.51 (0.21)	242	0.58 (0.009)	259	162.07 (3.91)
SIRE		ns		ns		ns
HxSxC		ns		ns		ns
WAGE						***

BWT = birth weight (kg), no = number of records, ADG = preweaning weight gain (kg), WWT = weaning weight (kg), WAGE = weaning age (days), CBY = calf birth year, CAG = cow age group, *** =p<0.001, ** = p<0.01, * p<0.05, ns = non-significance.

Table 3.5 Least squares means (standard errors) for yearling and eighteen-months weights in Wakwa cattle

Effects	no	YWT	no	EWT
SEX		***		***
Male	709	180.98 (1.54)	652	227.39 (2.07)
Female	663	165.94 (1.53)	676	215.58 (1.95)
SEASON (S)		***		***
Dry	125	176.84 (2.42)	130	230.34 (3.15)
Rainy	1247	170.08 (0.96)	1194	212.63 (1.27)
HERD (H)		***		***
15	273	171.04 (2.02)	264	213.70 (2.69)
16	256	173.75 (1.93)	242	221.31 (2.63)
17	168	181.33 (2.27)	164	231.80 (3.00)
18	174	165.03 (2.22)	166	218.31 (3.00)
19	234	170.79 (2.03)	222	215.67 (2.75)
20	209	174.16 (2.09)	206	222.47 (2.76)
21	58	178.14 (3.55)	64	227.13 (4.55)
CBY (C)		***		***
68	141	173.87 (2.58)	142	222.95 (3.44)
69	150	162.38 (2.45)	148	215.24 (3.29)
70	156	172.74 (2.47)	147	227.57 (3.33)
71	67	178.37 (3.33)	65	206.00 (4.53)
72	109	176.75 (2.63)	105	217.86 (3.56)
73	87	163.44 (2.95)	79	201.03 (4.09)

Continuation Table 3.5

74	66	157.48 (3.25)	63	213.88 (4.43)
75	86	180.88 (2.91)	88	228.25 (3.83)
76	89	192.02 (2.69)	92	259.08 (3.55)
77	107	179.35 (2.72)	101	201.97 (3.71)
78	63	167.04 (3.41)	60	212.58 (4.65)
79	58	163.10 (3.53)	53	217.49 (4.87)
80	73	177.07 (3.23)	46	223.33 (5.19)
81	42	174.23 (3.97)	58	227.81 (4.54)
82	26	161.11 (5.03)	32	212.39 (6.06)
83	36	187.36 (4.27)	28	237.03 (6.43)
84	16	181.69 (6.25)	21	240.79 (7.33)
CAG		ns		*
1	656	174.44 (1.47)	639	223.92 (1.93)
2	534	174.93 (1.60)	511	223.59 (2.12)
3	182	171.02 (2.22)	178	216.94 (2.94)
SIRE		ns		ns
HxSxC		ns		ns
YAGE		***		
EAGE				***

YWT = yearling weight (kg), EWT = eighteen-months weight (kg), YAGE = yearling age (days), EAGE = eighteen-months age (day), no = number of records, CBY = calf birth year, CAG = cow age group, *** = p<0.001, ** = p<0.01, * = p<0.05, ns = non-significance.

The Wakwa calves (Tables 3.4 and 3.5) outperformed the Gudali (Tables 3.2 and 3.3) in all the traits studied. This observation is in agreement with studies by Lhoste (1969), Tawah (1992), Tawah *et al.* (1993) and Abassa *et al.* (1993) that reported significant (p<0.05) higher pre-weaning weights in favour of Wakwa. This comparative advantage could be attributed to heterosis and complementarity genes from the parental breeds: Brahman and Gudali.

Sex was a highly significant (p<0.001) source of variation for weights at birth (BWT), weaning (WWT), yearling (YWT), eighteen months (EWT) and preweaning daily gain (ADG) in the

Gudali and Wakwa breeds. Similar results were also reported by Lhoste (1969), Tawah *et al.* (1993), and Abassa *et al.* (1993) for the preweaning growth traits in both breeds. On the average, male calves were 0.85 and 0.91 kg; 10.64 and 13.78 kg; 14.31 and 15.04 kg and 15.87 and 11.81 kg heavier than the female calves at birth, weaning, yearling and eighteen months and grew faster by 0.04 and 0.05 kg/d from birth to weaning in the Gudali and Wakwa breeds, respectively. The differences agree with those reported by Tawah *et al.* (1993) but were much greater than those reported by Abassa *et al.* (1993). This difference may be attributed to the small sample size (428 calves) used in the latter study. The results in the present study agree with those reported elsewhere for preweaning weights for different beef cattle breeds (Singh *et al.*, 1970; Reynolds *et al.*, 1982; Kassa-Mersha & Arnason, 1986; Ahunu & Makarechian, 1987; Kars *et al.*, 1994). The reported effects of sex on postweaning traits are sparse in the literature for any objective comparative studies. The higher weights for male calves obtained in the present study may be attributed to hormonal differences in their endocrinological and physiological functions and to selection pressure that was more intense on males than female calves.

The effect of season on BWT, ADG, WWT, YWT and EWT was highly significant ($p<0.01$ or $p<0.001$) in both breeds. Even though calves born in the dry season had lower birth weights than those born in the rainy season, the tendency was reversed for ADG, WWT, YWT and EWT. The dry season calves outperformed the rainy season calves by 17.57 and 18.19 kg; 4.71 and 6.76 kg and 12.43 and 17.71 kg in weight at weaning, yearling and eighteen months weights and grew faster by 0.08 and 0.09 kg/d from birth to weaning in Gudali and Wakwa breeds, respectively. The significant heavier weaning weights and faster growth from birth to weaning for dry season calves compared to the rainy season calves, obtained in this study agree with the results obtained by Tawah (1992) for the same breeds. The highly significant season effect on birth weight was constrasted with the results of Abassa *et al.* (1993) for the same breeds. The authors, however, obtained similar results for weaning weight. The significant season effect on preweaning traits obtained in the present study is also in agreement with reports by Kahi *et al.* (1995) in crosses of Ayrshire, Brown Swiss and Sahiwal cattle in the lowlands of tropical Kenya and by Kassa-Mersha & Arnason (1986) in Ethiopian Boran cattle. The highly significant effect of season could be attributed to seasonal variations in the total physical environment due to changes in the weather which affect feed availability and incidence of diseases. About 84 % of the dry season calvings occurred between February and April, with about 69% of the calvings occurring within the month of April alone (last month of the dry season). By implication, most of the dams that calved in the dry season, conceived either in the earlier part of the dry season of the previous year or in the later part of the rainy season. During this period, the pastures are usually mature and less nutritious, resulting in weight losses and poor body conditions of pregnant dams. This has the consequence of impairing development in the young calf, thereby causing a developmental handicap, which can have genetic effects on the calf. This nutrition-induced developmental stress is then reflected in the calf by a lower weight at birth in the dry season. This late dry season calves and their dams are, however, exposed to the earlier part of the rainy season, characterised by lush nutritious pastures, favourable for better body condition for the dam and higher milk production for her calf. The consequence is a higher calf growth leading to a higher weaning weight. On the other hand, most of the rainy season calvings (73%) occurred between April and June. By implication, most of the dams that calved in the rainy season conceived either in the latter part of the dry season or earlier part of the rainy season of the previous year. The pregnant dams, therefore, benefited from better nutrition that resulted in better body conditions and higher weights. This comparative advantage is passed on to the calf during the prenatal development. The inherent advantage is subsequently reflected in a higher birth weight during the rainy season. However, according to Deese & Koger (1967) and Hohenboken & Brinks (1971), a higher nutritional environment conducive for early rapid growth in the dam usually results in a poor maternal performance, which is reflected in the progeny weaning weight. This poor maternal performance may, therefore, be responsible for the lower weights at weaning, yearling and eighteen months obtained for rainy season calvings.

Calf birth year (CBY) was found to be a highly significant ($p<0.001$) source of variation for birth weight, average preweaning daily gain and weights at weaning, yearling and eighteen months. There was, however, no consistent trend over time for maximal average weights. The heaviest mean weights for calves of 24.92 and 26.51 kg and 173.06 and 187.25 kg for birth and weaning were obtained in 1972 and 1971 and 1984 and 1987 in the Gudali and Wakwa breeds, respectively. High average weights for calves of 195.19 and 192.02 kg and 230.33 and 259.08 kg at yearling and eighteen months were obtained in 1984 and 1976, respectively, in both breeds. This inconsistency in performance from year to year probably resulted from the fact that environmental conditions encountered, especially in Africa, in a specific year will seldom, if ever, be repeated. The highly significant ($p<0.001$) herd x year x season interaction which also accounts for management differences from year to year might have contributed to this inconsistency. The significant ($p<0.001$) year effect obtained in the present study is in agreement with reports by Rust & Van der Westhuizen (1994) for Simmental calves, Kars *et al.* (1994) for Nguni calves, Kahi *et al.* (1995) for crosses of Ayrshire and Brown Swiss calves, Ahunu & Makarechian (1987) for Hereford, Beef synthetic (Angus, Charolais and Galloway) and crossbred (Hereford x Beef synthetic) calves and Kassa-Mersha & Arnason (1986) for Boran calves. The significant effect of year on preweaning and postweaning growth traits may be explained in terms of the pattern of rainfall in Wakwa. There were fluctuations in annual rainfall which generally affected the quality and quantity of forage available for the cow-calf pair. The quality and quantity of forage usually influence the quality and quantity of milk produced by the dam, an essential component for calf growth. Non-systematic annual fluctuations could equally be responsible for differences in growth. The non-systematic factors may induce the application of supplementary feeding in the form of cotton-seed cake and rice bran in the dry season, in some years. Improvement in pastures and improvement in herd management as a result of improvement in herdsmen skills over the years could equally attribute to the significant year effect. Possible changes in the genetic make-up of the animals during the selection period (1968-1988) could equally be responsible for differences in growth as will be discussed in chapter five on genetic trends.

Herd also significantly ($p<0.001$) affected all weight traits in both breeds. As was in the case with CBY, the effect of herd was also slightly inconsistent as the highest weight averages in BWT, WWT, YWT and EWT were obtained in herds 14 and 20; 10 and 17; 14 and 17 and three and 17 for the Gudali and Wakwa breeds, respectively. Each herd was however, managed by a different herdsman and attributed a permanent grazing area. There were two principal zones within which the herds were located:young basaltic (Vina zone) and ancient basaltic (plateau zone). The Vina zone is a swampy and woody area and the grazing areas located there were not fenced, thereby limiting grazing space for the animals. Though this zone with its swampy and woody nature and thick forest provided the animals with forage all year round, it was at the same time a natural habitat and breeding ground for tsetse flies (glossina spp), principal vectors for trypanosomiasis. In contrast, grazing areas found in the ancient basalt (plateau zone) were not fenced and as a result, the animals here were exposed to more grazing land. Although the zone was unable to provide forage to the animals all year round, the difference was partly compensated for by annual preparation of hay supplementation during the dry season. But for herd 20 located within the Vina zone, herds three, 10, 14 and 17 with heaviest average weights were located in the plateau zone (hilltop). Suggesting that the plateau environment was more favourable for calf growth. The non-heterogenous nature of the two principal zones within which the herds were distributed therefore played a significant role in herd performance. Consiquently, the significant herd effect could be attributed to variation in herd location, variation in degradation levels of grazing areas, stocking density, variation in soil composition and pastures, variation in tsetse fly infestation and overall differences in herd management and herdsman skill across seasons and years as indicated by the highly significant ($p<0.001$) level of herd x season x calf birth year.

The effect of cow age group was not significant on BWT, ADG and YWT. It was however, found to significantly ($p<0.01$ or $p<0.001$) affect weaning and eighteen months weights in both breeds. This was in disagreement with the findings of Abassa *et al.* (1993) with respect to the same breeds. Though cow age group was not significant at birth, Gudali calves born from group one cows (CAG1) had lower birth weights but grew faster and attained higher weights at weaning and post weaning ages (Tables 3.2 and 3.3) compared to those from group two and three cows (CAG2, CAG3) . On the contrary, Wakwa calves from group one cows were heavier than those from group two and three cow at birth, an average which they maintained from birth to eighteen months. The report by Mbah *et al.* (1991) that the lightest calves came from primiparous cows agrees with present observations. The findings in the present study agree with those of by Singh *et al.* (1970), Kassa-Mersha & Arnason (1986) and Kars *et al.* (1994) but differ from those of Ahunu & Makarechian (1987) and Mangus & Brinks (1971). The relatively faster growth rate of calves from CAG1 cows compared to CAG2 and CAG3 cows might be largely attributed to differences in milk production. The majority of cows in CAG1 are within the age range in which their milk production is at the peak. The calves, therefore, benefited from this high milk production and translated it into rapid growth and higher weight gain.

Sire effect was also a significant ($p<0.05$ or $p<0.001$) source of variation on ADG, BWT, WWT and YWT in Gudali breed. Surprisingly, the effect of sire on the EWT in Gudali and preweaning and postweaning growth traits in Wakwa was not significant. Abassa *et al.* (1993), however, obtained a non-significant sire effect on weaning weight in both breeds. The effect of herd x season x calf birth year (HxSxC) significantly ($p<0.05$ or $p<0.001$) affected ADG, BWT, WWT and YWT in Gudali. It howver, showed no significant influence for EWT in Gudali and the preweaning and postweaning growth of Wakwa. The significant effect of HxSxC could be attributed to seasonal variations and management differences across the years. WAGE and YAGE showed higher significant associations (p<0.001) with WWT and YWT, respectively, in both Gudali and Wakwa breeds.

3.4 CONCLUSION

Sex, herd, season of calving, calf birth year and herd x year x season interaction were found to be significant sources of variation for preweaning and postweaning growth traits in both Gudali and Wakwa cattle in Cameroon. The effect of cow age group was only significant for weaning and yearling weights in both breeds. These significant effects should therefore be taken into consideration in the estimation of genetic parameters and evaluation of the genetic merit of an individual animal during selection.

The calves born in the dry season though lighter than wet season calves at birth, had the advantage that they grew faster and attained heavier weights at weaning, yearling and eighteen months. It may, therefore, be necessary that under low husbandry regime, a breeding programme for cows be designed so that they calve towards the end of the dry season. The late dry season calving will reduce incidences of dystocia because of the low birth weight. The cows, also, will benefit from earlier rainy season nutritious pastures, favourable for higher milk production and optimum profitability as a result of rapid growth and heavier calf weights at weaning, yearling and eighteen months.

Ages at weaning, yearling and eighteen months were also significant sources of variation for weights at weaning, yearling and eighteen months. It will be necessary therefore to consider them as covariates in models for estimation of genetic parameters and breeding values of calves.

CHAPTER FOUR

GENETIC PARAMETER ESTIMATES FOR GROWTH TRAITS

4.1 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.*, unpublished). 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 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 relatively 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 and permanent maternal environmental effects were not important. Though genetic parameters for growth traits of various breeds of beef cattle exist in the literature, it is important that such estimates be obtained under the specific management and production environment of the breeds.

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 parameters. It is therefore necessary to obtain reliable information on genetic parameters of not only birth and weaning weights but also post-weaning traits. The objective of the study was therefore to estimate preweaning and postweaning genetic parameters for growth traits in Gudali and Wakwa beef cattle in the tropical highlands of Cameroon.

4.2 MATERIALS AND METHODS

4.2.1 Foundation animals

The foundation population for the Wakwa project was composed of 45 purebred Brahman bulls imported from the USA between 1952 and 1958 and six herds each consisting of 40 females in 1965, and in 1969, 12 herds each consisting of 40 breeding females (Tawah, 1992), all of the purebred Gudali. Purebred foundation bulls 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).

4.2.2 Breed description

The Gudali and Wakwa breeds have been described by Lhoste (1969) and Tawah and Mbah (1989). 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 of Cameroon (Tawah *et al.*,1996). 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).

4.2.3 Management

Breeding animals 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 minimized. At birth, calves were ear-tagged and weighed and their sires and dams recorded. Records of breed, sex, date, month and year of birth were also maintained. Calves were weighed within 24 hours of birth and monthly thereafter. At weaning, 12, 24 and 36 months the animals were subjected to a selection scheme which was based on individual and progeny performance Lhoste, 1977; Tawah *et al.*, 1994).

From 1968 to 1988, 14 Gudali and seven Wakwa herds were in operation. The herds were managed at the Wakwa Research Station (2000 ha) of the Institute of Agricultural Research for Development and at the Breeding Station (4000 ha) of the Ministry of Livestock, Fisheries and Animal Industry. Grazing and management were essentially extensive on natural pastures growing on granitic and basaltic soils. The pastures were composed mainly of *Hyparrhenia* spp, *Panicum maximum, Andropogon guyanensis* and *Pennisetum purpurreum* (Piot & Rippstein, 1975). There was some supplementation with rice bran and cotton-seed cake during the dry season. The management system and production conditions for these animals have already been well described (Lhoste, 1968 & 1977; Pamo & Yonkeu, 1987; Tawah & Mbah, 1989). Health management involved routine dipping against ticks, vaccinations against pasteurellosis, brucellosis, anthrax and rinderpest, and deworming. Water was available all year round in the paddocks.

4.2.4 Data collection and editing

Data on calves born from 1968 to 1988 were compiled from the various Adamawa herdbooks 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 weights at weaning (WWT), yearling (YWT) and eighteen months (EWT) selected from monthly weights for dates closest to eight, twelve and eighteen months, respectively. Weaning age (WAGE), yearling age (YAGE), eighteen-month age (EAGE), (precised ages nearest eight, twelve and eighteen months, respectively), cow age group (CAG) and preweaning daily gain (ADG) were derived from the data set.

WAGE, YAGE and EAGE were calculated as the difference between an individual calf's birth date and its weaning, yearling and eighteen month date, respectively. CAG was calculated as the deviation of the dam's year of birth from her corresponding calf's birth year (CBY). Three cow age categories were defined as: CAGl was attributed to cow age group less than 8; CAG2 to cow age group greater than 7 but less than 11 and CAG3 to cow age group greater than 10. The ADG was calculated as (WWT-BWT)/WAGE. 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 weights less than 120 kg were omitted. The resulting summary data structures for the two breeds are presented in Tables 4.1 and 4.2.

Table 4.1 Data summary structure for trait means and variation in Gudali beef cattle

ITEMS	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 = preweaning average daily 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), IC = inbreeding coefficient, SD = standard deviation, CV (%) = coeficient of variation

Table 4.2 **Data summary structure for trait means and variation for Wákwa beef cattle**

ITEM	BWT	ADG	WWT	YWT	EWT	WAGE	YAGE	EAGE
No. record	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 = preweaning average daily 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), IC = inbreeding coefficient, SD = standard deviation, CV (%) = coeficient of variation

4.2.5 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 additive direct animal effect, maternal direct effect correlated to the animal effect, non-additive maternal permanent environmental effect, uncorrelated to direct and maternal effects and environmental effect, associated with the animal, 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 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 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, 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 additive direct, additive maternal direct and non-additive maternal permanent environmental effects to y;

$\underline{a}$ and $\underline{m}$, nonobservable correlated random vectors for direct and maternal effects;

$\underline{c}$, nonobservable uncorrelated random vector associated with the non-additive maternal permanent environmental effect and $\underline{e}$, random vector associated with residual effect of error. The vectors $\underline{a}$, $\underline{m}$, $\underline{c}$ and $\underline{e}$ 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:

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

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

4.3 RESULTS AND DISCUSSION

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

The estimates of (co)variance components for the growth traits in Gudali and Wakwa are presented in Tables 4.3 and 4.4, respectively.

Table 4.3 (Co)variance estimates for pre-weaning and post-weaning growth traits in Gudali cattle

Trait	$\acute{O}^{2}_{A}$	$\acute{O}^{2}_{M}$	$\acute{O}_{AM}$	$\acute{O}^{2}_{PE}$	$\acute{O}^{2}_{e}$	$\acute{O}^{2}_{P}$
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

$\acute{O}^{2}_{A}$ = direct additive genetic variance, $\acute{O}^{2}_{M}$ = maternal additive variance, $\acute{O}_{AM}$ = direct-maternal covariance, $\acute{O}^{2}_{PE}$ = permanent maternal environmental variance, $\acute{O}^{2}_{e}$ = residual variance, $\acute{O}^{2}_{P}$ = phenotypic variance

Table 4.4 (Co)variance estimates for pre-weaning and post-weaning growth traits in Wakwa cattle

Trait	$\acute{O}^{2}_{A}$	$\acute{O}^{2}_{M}$	$\acute{O}_{AM}$	$\acute{O}^{2}_{PE}$	$\acute{O}^{2}_{e}$	$\acute{O}^{2}_{P}$
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

$\acute{O}^{2}_{A}$ = direct additive genetic variance, $\acute{O}^{2}_{M}$ = maternal additive variance, $\acute{O}_{AM}$ = direct-maternal covariance, $\acute{O}^{2}_{PE}$ = permanent maternal environmental variance, $\acute{O}^{2}_{e}$ = residual variance, $\acute{O}^{2}_{P}$ = phenotypic variance

In both tables, estimates of direct additive genetic variances were higher than corresponding maternal additive 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 additive, maternal additive, residual and phenotypic variances decreased at yearling (YWT) and increased at eighteen 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 YWT and EWT. The additive estimates in the Wakwa breed were higher than corresponding values 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 values in the Wakwa. The higher direct and maternal variance components corresponded to the higher direct and maternal heritabilities (see Tables 4.3, 4.4, 4.5 & 4.6). The differences between direct and maternal genetic variances are in agreement with those of Trus and Wilton (1988) in birth and average preweaning daily gain in Angus, Hereford, Charolais, Simmental and Shorthorn calves; Burfening *et al.* (1981) in birth weight of Simmental calves; and Bertrand & Benyshek (1987) in birth and weaning weights of Limousin and Brangus calves. Kars *et al.* (1994), Haile-Mariam & Kassa-Mersha (1995) and Meyer (1992) also reported higher estimates for direct additive variance components of preweaning and postweaning growth traits in Nguni, Boran and Australian Hereford, 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 4.5 and 4.6, respectively.

Table 4.5 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 $\acute{O}^2_A + 1/2\acute{O}^2_M + 3/2\acute{O}_{AM}$ (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 4.6 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.

Apart from EWT in both breeds and YWT in Wakwa, all the other traits were moderately to highly heritable. Lower estimates for total heritability were obtained for traits with negative direct-maternal genetic correlations. The estimates for direct heritabilities (h^2_A) were higher than those for maternal heritabilities (h^2_M) for all the performance traits. Similar patterns have been reported by some researchers (Burfening *ct al.*, 1981; Bertrand & Benyshek, 1987; Arnason & Kassa-Mersha, 1987; Trus and Wilton, 1988; Meyer, 1992; Shi *et al.*, 1993; Kars *et al.*, 1994; Koots *et al.*, 1994; Khombe *et al.*, 1995; Haile-Mariam & 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; Nelsen *et al.*, 1984; Cantet *et al.*, 1988; Hohenboken & Brinks, 1971). In Tables 4.5 and 4.6, 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 additive genetic effect associated with the genotype of the Gudali and Wakwa calves, respectively. The contribution of the maternal effects to total phenotypic variation increased from average preweaning daily gain (24%) to yearling weight (51%) in the Gudali. In the Wakwa, it declined from birth (55%) to eighteen months (14%). Accordingly, the proportionate contributions of the maternal related (co)variances to total phenotypic variances were between 17% and 54%; 41 and 19%; 41 and 36%; 54 and 12%, and 14 and 6% in BWT, ADG, WWT, YWT and EWT in Gudali and Wakwa, respectively (Table 4.5 & 4. 6). The proportionate contributions of maternal related variances to total phenotypic variances were 5 and 23%; 17 and 7%; 19 and 9%; 20 and 20% and 2 and 6% for BWT, ADG, WWT, YWT and EWT in Gudali and Wakwa, respectively. The proportionate contributions of the maternal variance to total phenotypic variation were higher than corresponding contributions from permanent maternal environmental variances for all performance traits in Gudali, and for average preweaning daily gain, birth and eighteen-months weights in Wakwa (Tables 4.5 & 4.6). The proportionate contributions from direct-maternal covariances towards the total phenotypic variance ranged from 12 to 25% in Gudali, and 0 to 32% in Wakwa.

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 genetic correlation between direct and maternal effect was zero, the direct-maternal genetic correlations for the rest of the traits included in this study were high and negative. These correlations ranged from -0.88 to -0.77 in Gudali and -0.98 to -0.76, 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 in the present study. With the exception of the high yearling weight direct heritability (0.51), direct heritabilities reported for birth weight, average preweaning daily gain, weaning and eighteen-month weights for Gudali in the present study were within range of estimates reported on some other tropical zebu cattle (Iloeje, 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 preweaning daily gain and weaning weight in the present study are equally within range of reported estimates in 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 the literature review estimates (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 heritability for weaning weight in crossbred Brahman x Shorthorn registered by Deese & Koger (1967) are different from those of the present study. The variation in the genetic estimates of the crossbreeds 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 preweaning and postweaning traits in tropical beef cattle are negative and high, those obtained in the present study were much higher. The estimates for preweaning weights were higher than those reported by Koch (1972). These high 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 Hereford and Angus calves, respectively. Hohenboken & 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

Hereford 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 high 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 high negative direct-maternal genetic correlation, which could be a serious impediment to selection progress. Robinson (1996) attributed high negative direct-maternal genetic correlation to negative dam-offspring covariance 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 & 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 estimation of genetic parameters. The problem of heterogeneous variances has also been reported by Thrift *et al.* (1981) and Garrick *et al.* (1989) to account for the high negative direct-maternal genetic correlation. 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 correlation was highly negative. This will result in greater selection response in progeny after the first generation than would be, if selection of dams were based on direct genetic values. Considering the various explanations from different authors, direct-maternal genetic correlation may therefore be negative not because of genetic antagonisms 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 high negative direct-maternal genetic correlations obtained in the present study. It might therefore be necessary to consider them in future estimates.

4.4 CONCLUSION

The estimates of genetic parameters of growth traits in Gudali and Wakwa indicate that selection can be effective in improving these traits in both breeds. Heritability estimates obtained in the Gudali suggest that BWT (0.37), ADG (0.24) and WWT (0.28) are moderately heritable, while YWT (0.51) is highly heritable. Estimates for maternal heritability, permanent maternal environmental effects and total heritability were highest for yearling weight. As previously stated, it is possible to improve growth in the Gudali through selection. However, considering the high negative genetic correlation between direct and maternal genetic effects, it may be recommended that selection be carried out at yearling in order to achieve a much greater genetic gain.

In the Wakwa breed, there are more possibilities of improving preweaning growth through selection as the preweaning traits are more moderately to highly heritable than the postweaning traits. Birth weight direct heritability (0.55) is high and its maternal heritability (0.23) is moderately high. In addition, the direct heritability estimates for average daily gain (0.28) and weaning weight (0.28) are moderately high. Therefore, it is possible to obtain improved growth in the Wakwa by selecting for WWT. However, WWT is favourably genetically correlated with BWT, implying that BWT is likely to increase growth as well. As a result, there is the likelihood of a high incidence of dystocia in the population. This situation can be overcome by recommending the use of restricted selection index with more emphasis on weaning than birth weight.

The role of permanent maternal environmental effect is not significant at birth in both breeds. It however, becomes progressively important from weaning to yearling in the Gudali and from weaning to eighteen months in the Wakwa. Hence, the necessity to separate the permanent maternal environmental from maternal genetic effects in models for estimation of genetic parameters for these traits in both breeds.

CHAPTER FIVE

DIRECT AND MATERNAL GENETIC TRENDS FOR GROWTH TRAITS

5.1 INTRODUCTION

Cattle production in Cameroon is essentially under a traditional small-scale husbandry management system. The resultant effects are high inbreeding, low fertility, high mortalities of about five to 10% in adult cattle and about 20% in calves (Tanya *et al.*, unpublished). In an effort to improve the situation, the government has put in place a number of programmes for beef cattle production. In 1952 a programme code-named "Wakwa" was initiated (Mandon, 1957), with the goal to develop a highly productive two-breed synthetic beef breed, the Wakwa from mating the American Brahman to the Gudali and then interse mating the first filial generation and selection for growth and reproduction (Tawah & Mbah, 1989). In 1969 the "Gudali" (Ngaoundere) programme, geared towards the systematic improvement of the indigenous Gudali through selection alone was initiated (Lhoste, 1977).. Much data on growth traits have accumulated over the years since the inception of the two programmes. An evaluation of these data, in the form of an assessment of genetic progress attained, is imperative in an effort to identify problems to be expected for possible remedial actions. Hence the need to investigate the genetic accomplishments in both programmes.

Improvement in beef cattle through selective breeding presupposes the ability to recognize and mate animals with superior genotypes for economically important traits. Initial evaluation of bulls in the two programmes have, however, simply been based on within-group comparisons. Research findings have shown that mass selection on own performance can lead to bias (Hagrove & Legates, 1971; Kemp *et al.*, 1984) as a result of the misranking of bulls and the non-adjustment of group averages for genetic changes that have taken place (Zollinger & Nielsen, 1984a & b). Tawah *et al.* (1994), in an effort to improve on this methodological bias, used the Best Linear Unbiased Prediction (BLUP) approach developed by Henderson (1973 & 1975) to estimate genetic trends for birth and weaning traits in the Gudali and the Wakwa breeds. However, no attempt has been made to include post growth in the genetic evaluation of the performance of these two breeds. Hence the purpose of this study.

Henderson's (1973 & 1975) mixed model methodology (MMM) is now the method of choice world-wide for the evaluation of Best Linear Unbiased Prediction (BLUP) for direct and maternal breeding values because of its desirable properties that include the maximum utilization of information from relatives (Quaas, 1976; Quaas & Pollak, 1980; Wright *et al.*,1987; Crump *et al.*, 1997), leading to more precise inferences about genetic values. Other desirable properties include correction of biases due to ignoring many relationships (Gianola, 1999), effectiveness in separating genetic effects from environmental effects (Blair & Pollak, 1984; Crump *et al.*, 1997) and across-herd and across-year evaluations, provided there is genetic connectedness among herds and years (Henderson, 1973; Henderson & Quaas, 1976). Consequently, BLUP evaluation can substantially improve genetic progress in beef cattle as it results in higher accuracy, increased selection intensity and early identification of young animals of higher genetic merits as a result of comparing estimated breeding values (EBV) across herds and years. The objective of the study was to utilize mixed model methodology to estimate comparable genetic trends for direct and maternal effects for preweaning and postweaning growth traits in the Gudali and Wakwa breeds of Cameroon.

5.2 MATERIALS AND METHODS

Comprehensive description of the data used to estimate breeding values for growth traits in the Gudali and Wakwa breeds has already been done by Ebangi *et al.* (1999b). Records were obtained from a selection experiment initiated to evaluate the genetic response to selection in the Gudali and a two-breed synthetic the Wakwa beef breeds. The experiment was conducted at the Wakwa Animal Production and Research Station from 1968 and 1988 (Lhoste, 1977). The management system and production conditions for these animals have been well documented (Lhoste 1968 & 1977; Pamo & Yonkeu, 1987; Tawah & Mbah, 1989).

In beef cattle, selection experiments are normally based on what is regarded as important, viz., increased growth rate. In the Gudali and Wakwa selection experiment, a weight ratio at weaning, 12, 24 and 36 months of age, was used for individual selection. The ratio was calculated on a within age-sex-breed group basis. Individual animals were selected on a weight index calculated as a ratio of an individual's weight at weaning, yearling, twenty four and thirty six months to its corresponding age-sex-breed contemporary group average weight. The selection truncation point varied with numbers available, influenced by reproductive rate, deaths, sales, emergency slaughters and replacement requirements. According to Tawah *et al.* (1994), conformation and physical or structural soundness were additional criteria used for sires and heifers that had already been subjected to individual weaning weight screening for final selection. The test bulls were then randomly mated to about 30 to 40 breeding females for progeny testing. The testing procedure has been fully described by Tawah *et al.* (1994). Heifers were usually mated at three to four years or at 250 kg body weight and a proportionately 0.05 to 0.10 cows were regularly culled together with their progeny for poor calf weaning weight or poor individual performance (age, conformation, agalactia, hardiness, disease resistance, maternal instinct and temperament) and failure to conceive after two successive matings (Tawah *et al.*, 1994).

Statistical model and analytical techniques

Best Linear Unbiased Prediction (BLUP) for direct and maternal breeding values were obtained for each animal using a single-trait animal model. The model included a direct effect, maternal effect correlated to the direct effect, non-additive maternal permanent environmental effect, uncorrelated to the direct and maternal effects and environmental effect, associated with each animal, 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 eighteen month weights, respectively, as described by Ebangi *et al.* (1999a). The estimated breeding value (EBV) for each animal was obtained with the MTDFREML programme (Boldman *et al.*, 1995) together with estimates of variances and covariances for the different performance traits as described by Ebangi *et al.* (1999b). Annual genetic values for direct and maternal effects were obtained as the average estimated breeding values (EBV) per year of calving. Direct and maternal genetic trends and standard errors, regression fit (R^2) and level of significance for each breed-trait combination were estimated by regressing BLUP-derived annual mean EBVs on year of calving using General Linear Regression (SAS, 1991). The total direct and maternal trends were obtained by multiplying the annual trend for each breed-trait combination (regression coefficient) by the number of years of selection. The overall genetic trend for each breed-trait combination was obtained by adding corresponding direct and maternal genetic trends. Due to difficulties in obtaining true cumulative selection differentials as proposed by James (1966) for mixed model analyses, an approximation of the "realized heritability" (h^2_R) for each trait was calculated using the formula $h^2_R = R/i\acute{O}_P$, (Falconer & Mackay, 1996), where R was the overall genetic trend (TTD), i the unweighted means selection intensities for males and females obtained from appendix A of Falconer & Mackay (1996) and $\acute{O}_P$ the phenotypic standard deviation calculated from phenotypic variances reported by Ebangi *et al.* (1999b). It was assumed that the selection intensity was the same in the two breeds and that 0.30 and 0.10 of the bulls and heifers, respectively, were culled as reported by Tawah *et al.* (1994).

5.3 RESULTS AND DISCUSSIONS

The direct genetic trends (DTD), maternal genetic trends (MTD), total genetic trend (TTD), regression fit (R^2), "realized heritability" (h^2_R), standard errors and level of significance for the traits evaluated are presented in Tables 5.1 & 5.2, respectively for Gudali and Wakwa.

Table 5.1 Direct and maternal genetic trends (standard errors) for pre-weaning and post-weaning traits in Gudali cattle from 1968 to 1988

TRAIT	DTD	TDT	R^2	MTD	TMT	R^2	TTD	h^2_R
BWT	0.022***	0.418	0.60	-0.007***	-0.133	0.60	0.285	0.33
	(0.004)			(0.001)				
ADG	0.0005*	0.0095	0.18	-0.0001 ns	-0.0019	-0.03	0.008	0.23
	(0.0001)			(0.0001)				
WWT	0.228***	4.351	0.49	-0.103*	-1.957	0.24	2.394	0.29
	(0.053)			(0.030)				
YWT	0.326***	5.542	0.65	-0.145***	-2.465	0.58	3.077	0.39
	(0.06)			(0.03)				
EWT	0.245***	4.165	0.47	-0.013*	-0.221	0.21	3.944	0.37
	(0.06)			(0.006)				

DTD = direct trend (kg/year), TDT = total direct trend, MTD = maternal trend (kg/year), TMT = total maternal trend, R^2 = regression fit, h^2_R = realized heritability, TTD = total genetic trend (TDT + TMT), *** = $p<0.001$, ** = $p<0.01$, * = $p<0.05$, ns = non-significance.

Table 5.2 Direct and maternal genetic trends (standard error) for pre-weaning and post-weaning traits in Wakwa cattle from 1968 to 1988

TRAIT	DTD	TDT	R^2	MTD	TMT	R^2	TTD	h^2_R
BWT	0.027* (0.01)	0.540	0.16	-0.017* (0.007)	-0.340	0.20	0.200	0.21
ADG	0.0008* (0.0003)	0.016	0.23	-0.0003* (0.0001)	-0.006	0.20	0.010	0.03
WWT	0.199* (0.08)	3.983	0.28	-0.064* (0.03)	-1.088	0.15	2.895	0.32
YWT	0.238*** (0.06)	4.046	0.53	-0.001*** (0.0002)	-0.017	0.53	4.029	0.50
EWT	0.243*** (0.036)	4.131	0.61	0.044 ns (0.02)	0.748	0.12	4.879	0.46

DTD = direct trend (kg/year), TDT = total direct trend, MTD = maternal trend (kg/year), TMT = total maternal trend, R^2 = regression fit, h^2_R = realized heritability, TTD = total genetic trend (TDT + TMT), *** = p<0.001, ** = p<0.01, * = p<0.05, ns = non-significant.

The mean annual direct genetic trends in the Gudali were positive and significantly (p<0.05 or p<0.001) different from zero. There was an upward trend from average daily gain (0.0005 kg/year) to yearling weight (0.33 kg/year). Corresponding mean annual maternal trends (MTD) though negative, were also significantly (p<0.05 or p<0.001) different from zero but for average preweaning daily gain trends. There was a decline in maternal trends from ADG (-0.0001 kg/year) to YWT (-0.15 kg/year). In the Wakwa breed, the mean annual DTD were also positive and significantly (p<0.05 or p<0.001) different from zero. There was an upward trend from average preweaning daily gain (0.0008 kg/year) to eighteen month weight (0.24 kg/year) (Table 5.2). Mean maternal trends in the Wakwa breed were also negative and significantly ($p<0.05$ or $p<0.001$) different from zero but for eighteen month weight trends. There was a decline from average preweaning daily gain (-0.000 kg/year) to weaning weight (-0.06 kg/year). An upward trend was, however, noticeable from yearling (-0.001 kg/year) to eighteen month (0.04 kg/year) weights. But for annual direct trends for birth weight and average daily gain, direct trends in the Gudali were higher than corresponding trends in the Wakwa. Conversely, maternal trends in the Wakwa were negative but greater than corresponding trends in the Gudali but for WWT and YWT trends. The regression fits (R^2) were low to high and ranged from 18 to 65% and -3 to 60% in the Gudali and from 16 to 61% and 12 to 53% in the Wakwa for direct and maternal trends, respectively. The estimates for "realized heritability" ranged from 0.23 to 0.39 in the Gudali and 0.03 to 0.50 in the Wakwa.

The total genetic trends (TTD), a reflection of the overall genetic changes in the population as a result of selection for both direct and maternal effects, were lower than TDT but for EWT trends in the Wakwa. This was because the positive trends for the direct breeding values were offset by the negative trends for the maternal breeding values. The TTD were 0.29 and 0.20 kg; 0.01 and 0.01 kg; 2.39 and 2.90 kg; 3.08 and 4.03 kg and 3.94 and 4.88 kg, respectively for BWT, ADG, WWT and EWT in Gudali and Wakwa. Estimated annual breeding values (EBV) for the direct and maternal genetic effects are presented graphically in Figures 5.1 to 5.10.

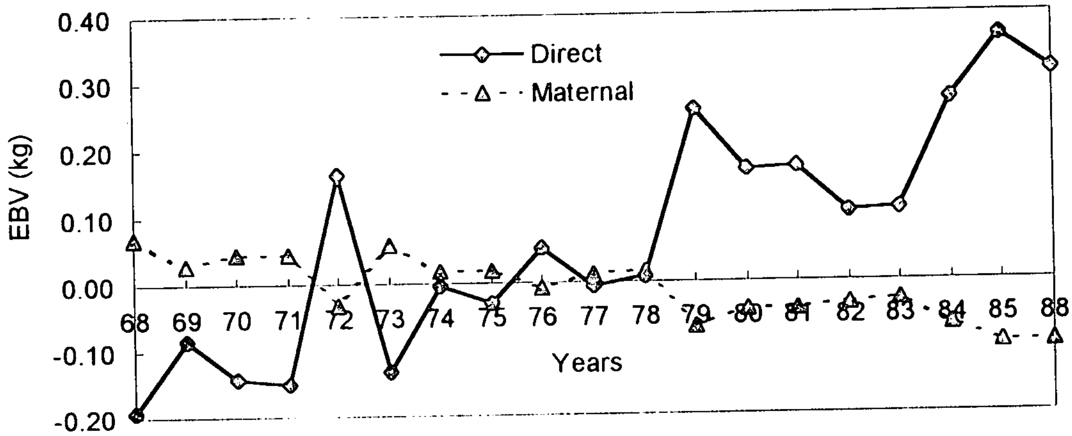

Figure 5.1 Direct and maternal genetic trends for BWT in Gudali beef cattle

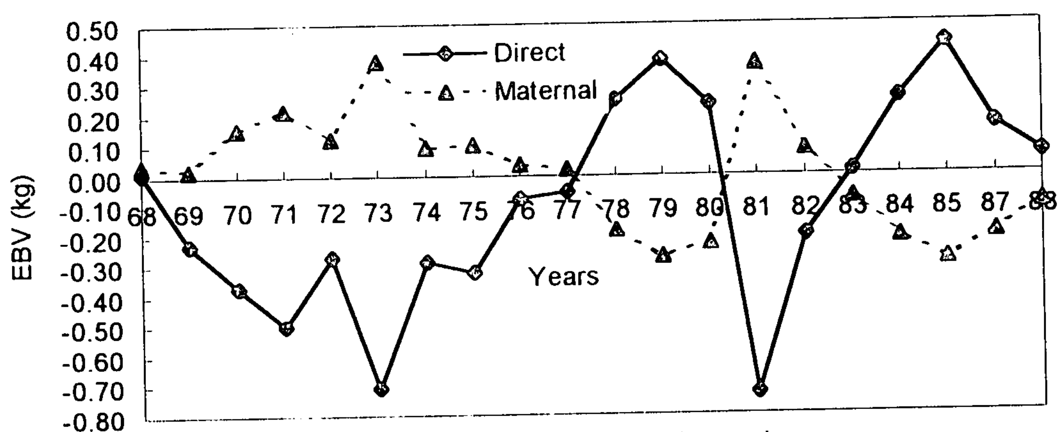

Figure 5. 2 Direct and maternal genetic trends for BWT in Wakwa beef cattle

With the exception of the EBVs for direct genetic effect for birth weight (Figure 5.1) in the Gudali, two patterns were evident for figures 2 to 10: an earlier downward trend in EBVs followed by an upward trend. The BWT in the Gudali experienced an upward trend from 1968 (-0.19 kg/year) to 1972 (0.16 kg/year) and then dropped in 1973 (-0.13 kg/year).

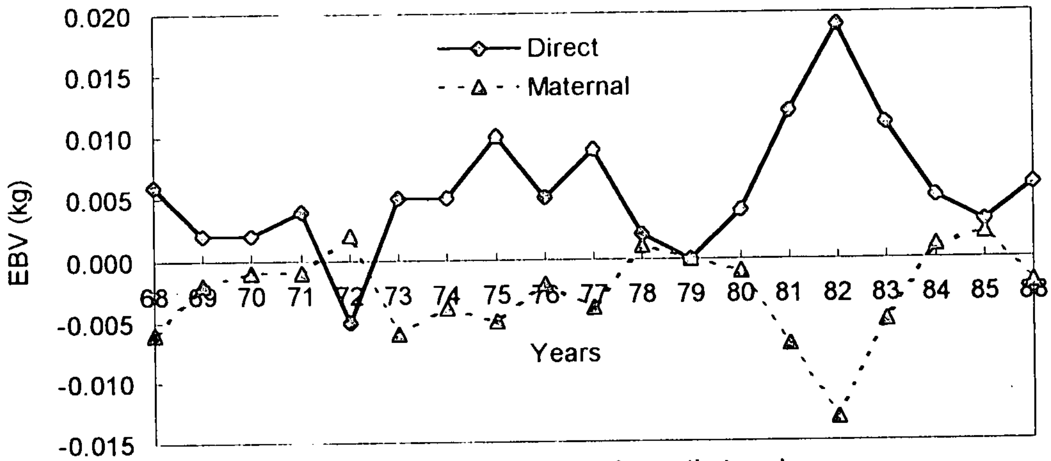

Figure 5.3 Direct and maternal genetic trends for ADG for Gudali beef cattle

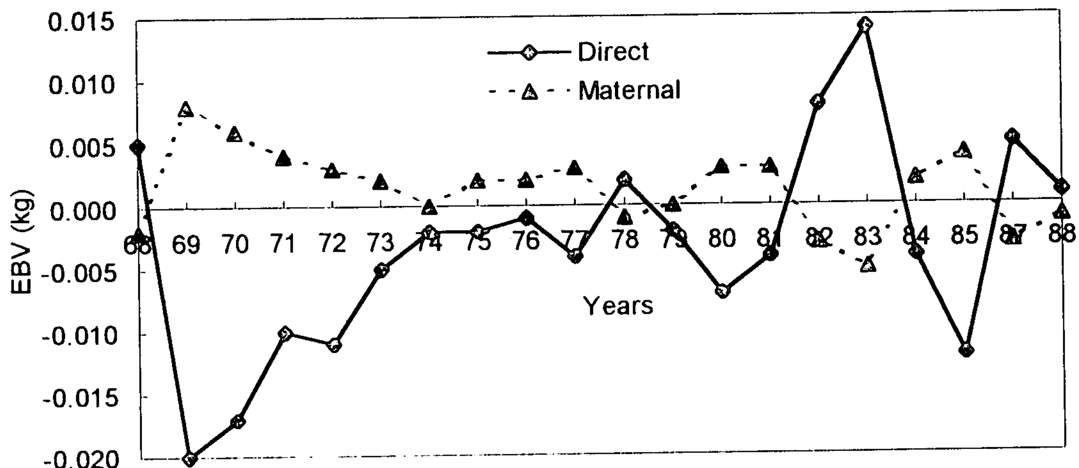

Figure 5. 4 Direct and maternal genetic trends for ADG in Wakwa beef cattle

It then experienced an upward trend thereafter and attained an annual maximum trend of 0.37 kg/year in 1985. In the Wakwa, the direct genetic trend for birth weight followed a decline from 1968 (0.01 kg/year) to 1973 (-0.71 kg/year) and was followed thereafter by an upward trend to attain a maximum annual genetic response of 0.44 kg/year in 1985.

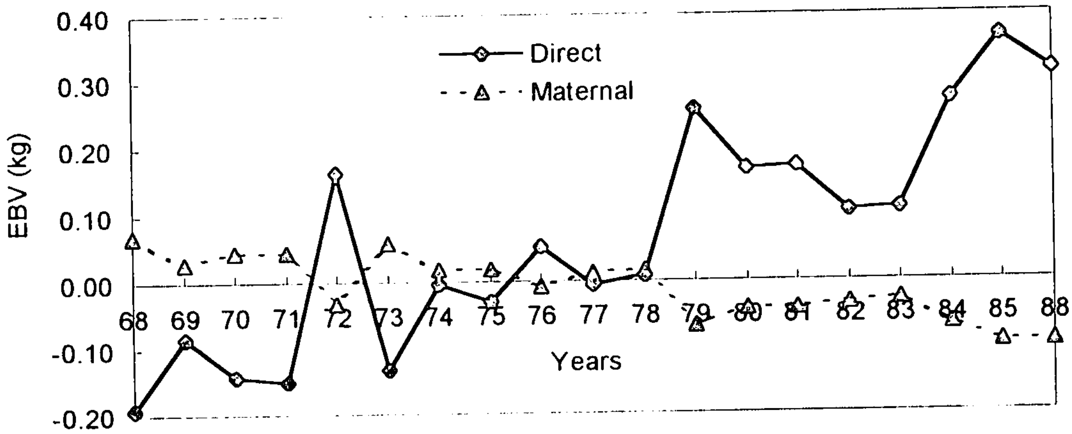

Figure 5.1 Direct and maternal genetic trends for BWT in Gudali beef cattle

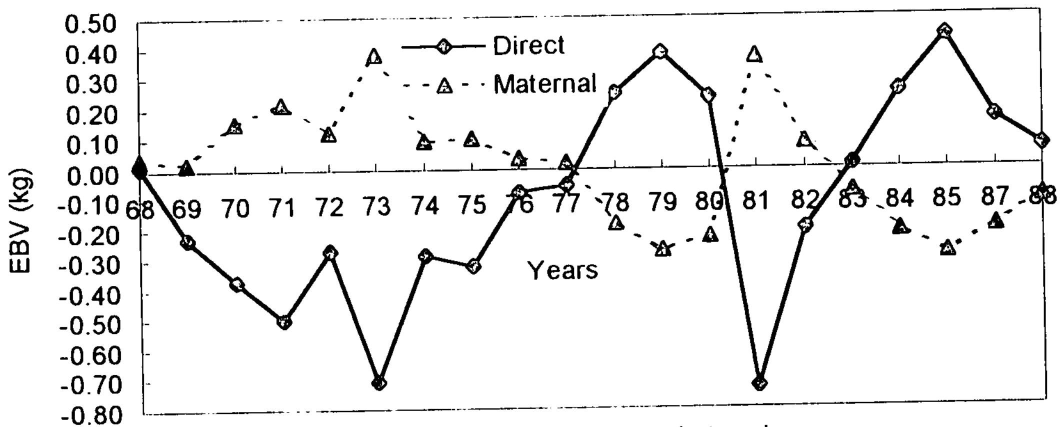

Figure 5. 2 Direct and maternal genetic trends for BWT in Wakwa beef cattle

With the exception of the EBVs for direct genetic effect for birth weight (Figure 5.1) in the Gudali, two patterns were evident for figures 2 to 10: an earlier downward trend in EBVs followed by an upward trend. The BWT in the Gudali experienced an upward trend from 1968 (-0.19 kg/year) to 1972 (0.16 kg/year) and then dropped in 1973 (-0.13 kg/year).

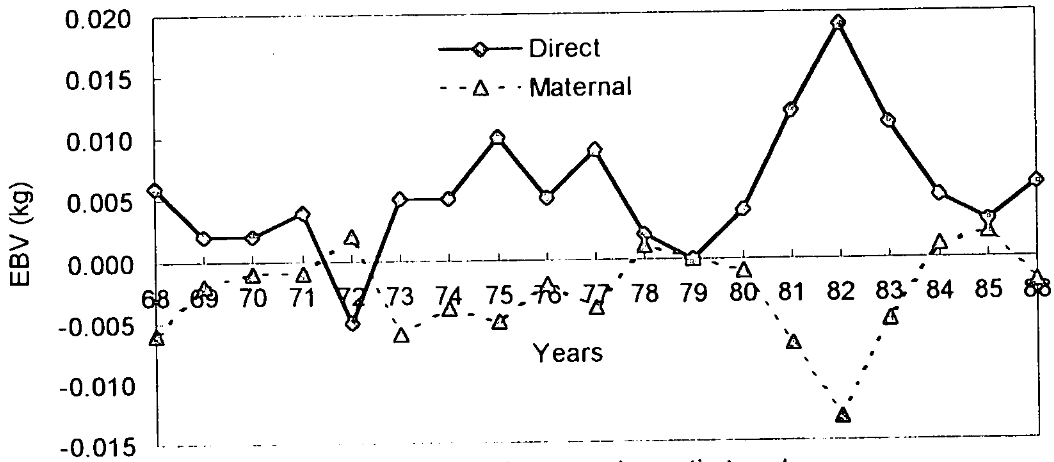

Figure 5.3 Direct and maternal genetic trends for ADG for Gudali beef cattle

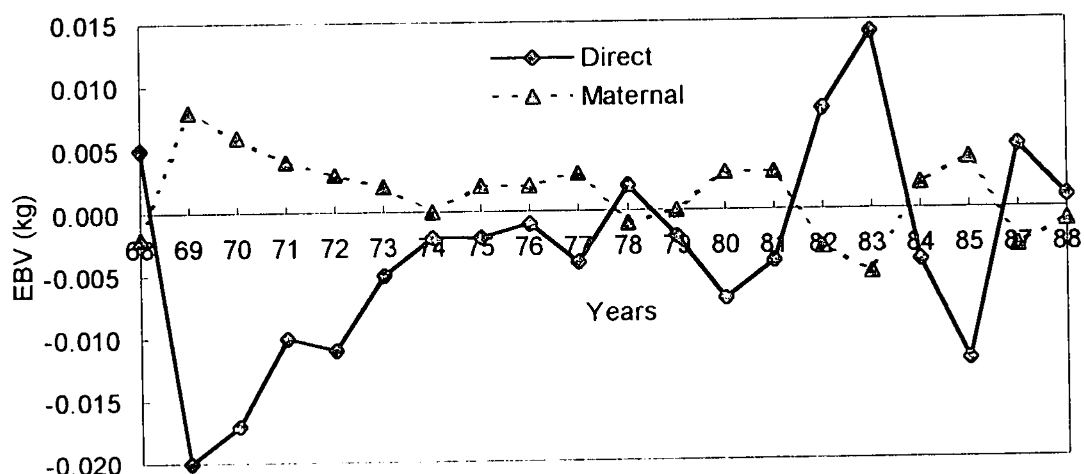

Figure 5. 4 Direct and maternal genetic trends for ADG in Wakwa beef cattle

It then experienced an upward trend thereafter and attained an annual maximum trend of 0.37 kg/year in 1985. In the Wakwa, the direct genetic trend for birth weight followed a decline from 1968 (0.01 kg/year) to 1973 (-0.71 kg/year) and was followed thereafter by an upward trend to attain a maximum annual genetic response of 0.44 kg/year in 1985.

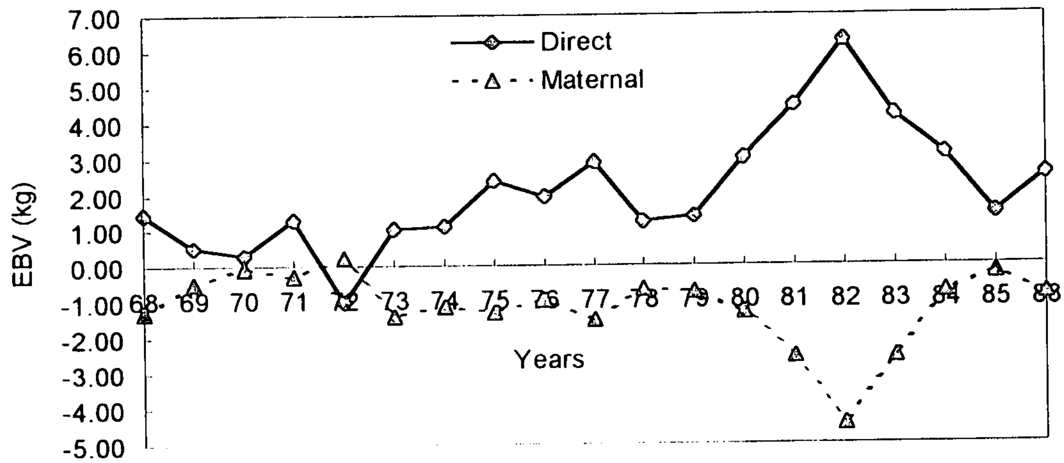

Figure 5.5 Direct and maternal genetic trends
for WWT in Gudali beef cattle

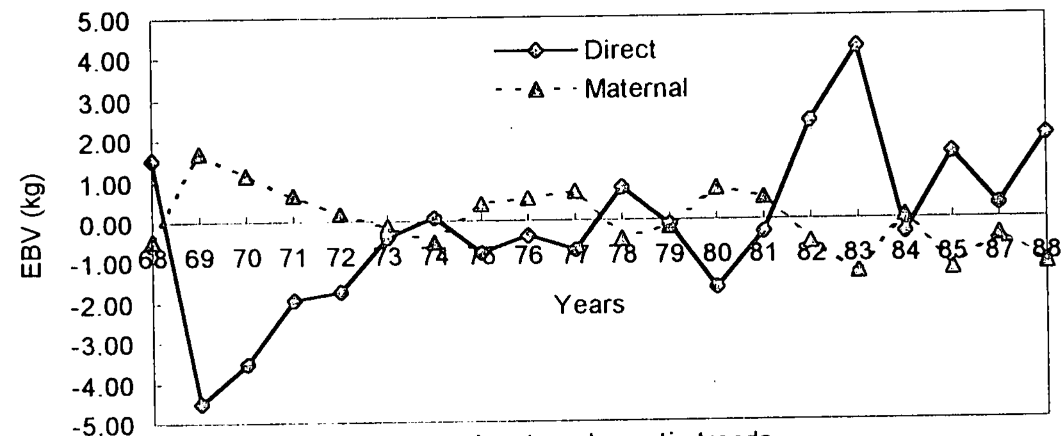

Figure 5.6 Direct and maternal genetic trends
for WWT in Wakwa beef cattle

The downward trend experienced by the EBVs for ADG and WWT, and YWT and EWT direct genetic effects in the Gudali was from 1968 to 1972 and 1968 to 1970, respectively. It was followed thereafter by an upward trend, attaining annual maximum genetic responses of 20 g/day, 6.3, 6.3 and 4.0 kg/year for ADG, WWT, YWT and EWT, respectively, in 1982 (Figures 5.3, 5.5, 5.7 & 5.9). The pattern for EBVs of the maternal genetic effects was the reverse of that for direct trends but for EWT where it was virtually zero.

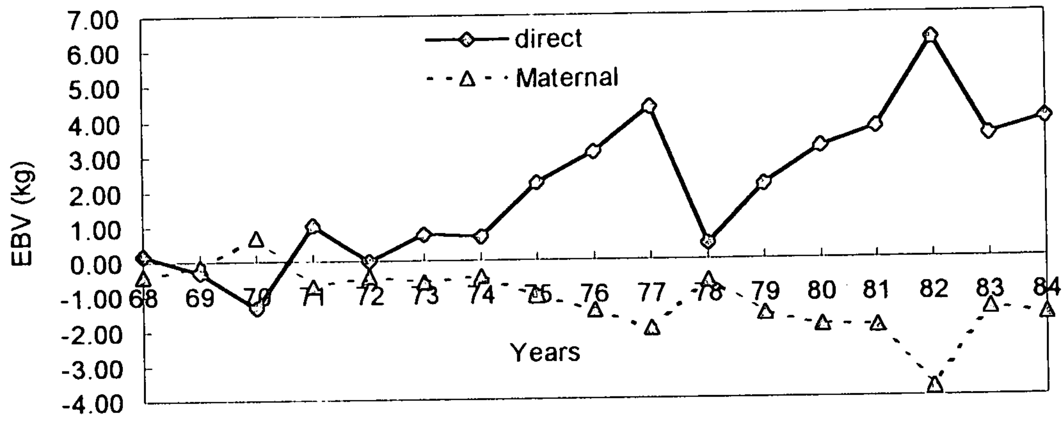

Figure 5.7 Direct and maternal genetic trends for YWT in Gudali beef cattle

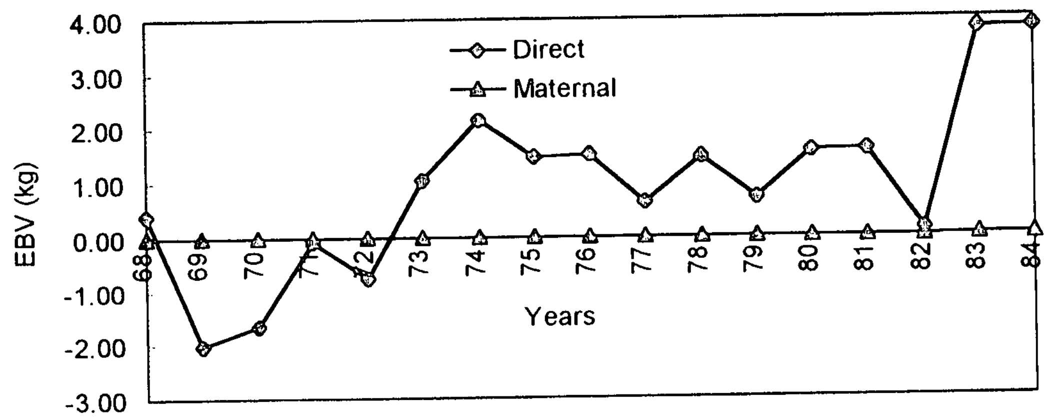

Figure 5. 8 Direct and maternal genetic trends for YWT in Wakwa beef cattle

On the other hand, the downward trend for EBVs for direct genetic effects for ADG, WWT, YWT and EWT in the Wakwa occurred between 1968 and 1969. This was followed by an upward trend, attaining maximum annual genetic responses of 10 g/day, 4.2, 3.8 and 5.4 kg/year in 1983 for ADG, WWT, YWT and EWT, respectively (Figures 5.4, 5.6, 5.8 & 5.10). As was the case with the Gudali, the direction of the maternal trends was the reverse of that of the direct trends but for EWT.

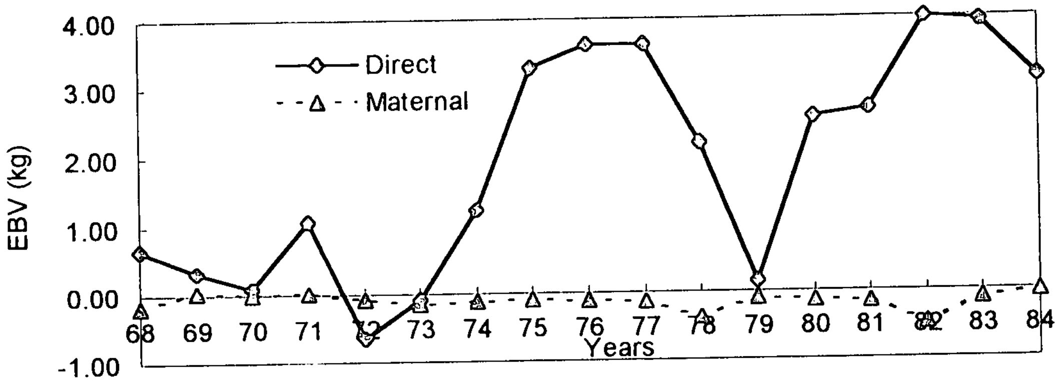

Figure 5.9 Direct and maternal genetic trends for EWT in Gudali beef cattle

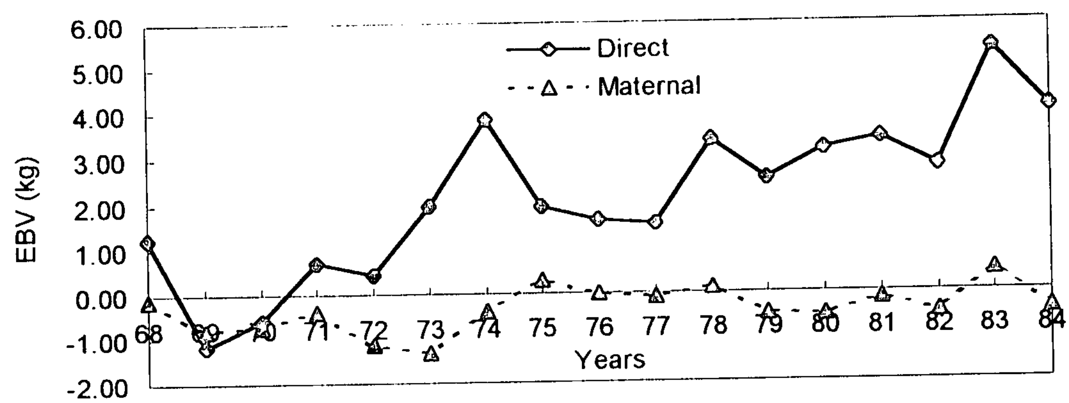

Figure 5.10 Direct and maternal genetic trends for EWT in Wakwa beef cattle

Considerable fluctuations in the EBVs for direct and maternal genetic effects are observed in figures 5.1 to 5.10 as reflected by the predominant peaks. This is probably an indication that estimates of annual genetic trends tended to hide substantial variations across years and herds. With the exception of the EWT trait in the Wakwa, the general tendency was that, as the EBVs for direct effects increased, corresponding maternal EBVs decreased. This observation is in agreement with findings by Johnson *et al.* (1992) for birth weight, preweaning daily gain and 205-d weight in Angus and birth weight in Hereford. The initial downward trends can be attributed to the limited number of animals in the population during the earlier phase of the experiment which resulted in a reduction in genetic variability and selection intensity. Culling of animals at this stage was therefore relaxed and consequently genetically inferior animals were allowed to reproduce in order to increase the herd size. The positive trend could be attributed to an increase in selection intensity as a result of improved methodology and increase in the population size resulting in greater genetic variability. In the later part of the selection programme, most of the calves born in the herds had become proven sires and dams. The positive and negative swings in EBVs might be attributed to fluctuations in selection differentials, possibly as a result of alterations in selection objectives and management policies. Replenishment of stock, especially in the Gudali, by later introductions, could equally have contributed to the fluctuations in EBVs. The early increase in EBVs in the Wakwa breed might be attributed to the fact that the selection programme in the breed started during the early stage of breed formation when there was larger variation in the growth traits. Consequently, there was a higher response of the traits to selection in the Wakwa than was the case in the Gudali breed which was gradually being constituted along the selection period. Tawah *et al.* (1994) also predicted a decline in trends in the Wakwa due to a reduction in herd size as a result of continuous distribution of animals to farmers, high mortalities due to dermatophilosis and lack of a clear breed selection policy. Consequently, while selection differentials were on the rise in the Gudali, as a result of an increase in population size and genetic variability, it was the opposite in the Wakwa.

The low overall genetic responses might most likely also be attributed to the genetic antagonism found between direct and maternal genetic effects as a result of the high negative genetic correlations between direct and maternal effects in both breeds (Ebangi *et* *al.*, 1999b). As a result of this genetic antagonism, the estimates of the overall genetic trends were lower because the positive estimated breeding values obtained for direct genetic effects were offset by corresponding negative contributions from the maternal genetic effects. Further explanation could also be attributed to the fact that maternal contribution measures one-half of the trend for direct effects plus the full trend in the maternal environment due to genetic and non-genetic effects. Accordingly, a negative trend in maternal genetic effects and (or) non-genetic effects such as heifer rearing practices would certainly bring about the lower (negative) maternal trend as indicated in studies by Deese & Roger (1967) and Hohenboken & Brinks (1971). On the other hand, the present trends obtained are merely results from retrospective analyses over a period when the contemporary group comparison method was used in ranking bulls. However, as stated earlier, contemporary comparison has been shown to produce bias results (Hagrove and Legates, 1971; Kemp *et al.*, 1984) and not to adjust for group averages in situations where genetic changes have taken place (Zollinger & Nielsen, 1984 a & b). Consequently, it could be possible that inferior bulls were maintained in the herds. Also, selection for single traits in the Gudali and Wakwa beef cattle were seldom practised. Apart from selecting for growth, selection usually involved, amongst others, functional and structural soundness of udders, feet, legs, eyes and fertility, viability and disposition. Other factors likely to lower the genetic trends include, high mortality rates (Lhoste & Pierson, 1973) for less than two-year old calves, low parturition rate (Tawah & Mbah, 1989), prolonged mating of heifers as a result of poor growth, long generation intervals (7.1 years in Gudali and 8.7 years in Wakwa, Tawah *et al.*, 1994), preference placed on certain sires leading to the fact that they were maintained for an extended period of time in the herds and use of dubious young bulls.

The observed trends are lower than theoretically attainable trends. Tawah *et al.* (1994) reported higher sire estimated transmitting ability (ETA) and dam estimated breeding values (EBV) for birth and weaning weights in the Gudali. The authors also reported higher dam EBV and sire ETA for birth and weaning weights, respectively, in the Wakwa. The sire ETA and dam EBV reported for birth, and weaning weights in the Wakwa were however, lower than reported estimates in this study. The differences in the trends are most likely due to differences in models and analytical procedures and sample size. The direct trends for weaning weight in the Gudali were higher than the direct trends reported for weaning weight of Mashona cattle breed of Zimbabwe by Khombe *et al.* (1995). The overall genetic trends (TTD) were also higher than the trends of 0.003, -0.013, 0.097 and 0.097 kg/year, reported by Diop and Van Vleck (1998), in the Gobra breed for birth, weaning, yearling and final weights, respectively. However, present estimates were low compared to those obtained for temperate beef cattle breeds by some researchers (Koch *et al.*, 1974a & b; Nwakalor *et al.*, 1976; Nadarajah *et al.*, 1987; Mrode, 1988; Wilton, 1988; Crump *et al.*, 1997). On the other hand, the overall annual genetic trends (TTD) obtained in the present study for preweaning daily gain (ADG) in the Gudali (0.5 g/day) and Wakwa (0.8 g/day), were higher than the estimate of -0.8 g/day reported by Wilton (1988) in the Limousin breed.

"Realized heritability" essentially describes selection response and might not provide valid information of real heritability (Falconer & Mackay, 1996). The estimates obtained in the present study were moderate to high but for that for average preweaning daily gain in the Wakwa. These moderate to high estimates might therefore be indicators of higher responses to selection when management and husbandry practises are improved, assuming the selection intensity remains constant.

5.4 CONCLUSION

The significant positive direct trends reported for average preweaning daily gain, and weaning and yearling weights in both the Gudali and Wakwa are indications that selection was effective. The significant positive trends reported for birth and eighteen month weights are also indications that direct selection for weaning and yearling weights could bring about positive correlated responses in these traits. The direct genetic trends were generally higher than the corresponding maternal components, indicating that the emphasis placed on direct performance was not successful in increasing maternal performance. Consequently, selecting mainly for direct performance could result in maternal breeding values contributing very little or even negatively to the overall genetic gain. While the direct genetic trend contributes positively to the overall genetic gain, corresponding maternal component contributes negatively to it. Intense selection for individual growth, when the antagonism between direct and maternal genetic effects is pronounced, could therefore, result in a substantial loss in maternal performance. This aspect, seemingly a paradox, requires further investigation.

CHAPTER SIX

GENETIC PARAMETER ESTIMATES FOR PREWEANING GROWTH TRAITS

6.1 INTRODUCTION

The preweaning development of the calf is greatly influenced by the maternal genetic and environmental variations. This becomes more evident, especially, when the calf suckles its dam at will from birth to weaning. The rate of liveweight gain of the calf, therefore, will be partly determined by the dam's potential for milk production and any other related maternal behaviour. Willham (1972) defined maternal effect as the phenotypic value of the dam measurable only as a component part of her offspring's phenotypic value. According to Yokoi *et al.* (1997), maternal effect is thought to be mainly a function of milking and nursing ability. Roy Beeby (1985) described the maternal role as more than milk production reflected in weaning weight but as all the factors that make-up motherhood in a cow such as regular reproduction, gestation length, trouble-free calving, mothering ability, survival of progeny, foraging ability, maximum intake of forage, adaptation to adversity and weaning a desirable calf without heavy supplementation. Tassel (personal communication) however, suggested that maternal effect was equally responsible for temperament and immunity of the calf. Koch (1972) reported that maternal genetic and permanent environmental variations and direct-maternal covariation accounted for 15-20% of the total variation of birth weight and that maternal variation alone accounted for 10-15%. The total maternal variation and covariation accounted for 29-38% of the phenotypic variation in gain from birth to weaning weight. The author was, however, inconclusive about direct-maternal genetic correlation for preweaning traits. Rutledge *et al.* (1971) reported that about 60% of variance for 205-day weight was attributable to the direct influence of the dam's milk yield. Meyer *et al.* (1994) reported that milk production was the main determinant of maternal effects on the growth of beef calves. Rutledge *et al.* (1971) and Shimada *et al.* (1988) reported that the highest milk production of cows occurred at the earlier stages of lactation and declined thereafter. In a related situation, Deese & Koger (1967) and Hohenboken and Brinks (1971) reported a phenomenon of a negative environmental covariation between the dam's own preweaning growth and that of her subsequent maternal ability in US cattle. Diaz *et al.* (1992) and Marston *et al.* (1992) in separate studies, recommended that expected progeny difference (EPD) at weaning be used as indicators of milk production in dams. The Gudali cows have been shown to produce more milk at the earlier stages of lactation and to dry off at about six months after giving birth (Tawah & Mbah, 1989). Therefore, weaning weight might not be the best indicator of milking and nursing ability in the cow. The objective of this study was to estimate variances and covariances for direct and maternal related effects for calf preweaning weight traits in the Gudali cattle. The findings will be used to suggest appropriate preweaning trait(s) for optimisation of genetic improvement in maternal performance.

6.2 MATERIALS AND METHODS

Data originated from a selection experiment carried out at the Animal Production and Agricultural Research Stations of Wakwa, in the Adamawa Province of Cameroon. The management system, pastures and climatic conditions have been documented by various researchers (Dumas & Lhoste, 1966; Lhoste, 1968; Lhoste, 1977; Lhoste & Pierson, 1975; Piot & Rippstein, 1975; Pamo & Yokeu, 1987; Tawah & Mbah, 1989 and Tawah *et al.*, 1996). Records consisted of birth weight (BWT) and adjusted weights at one (OMWT), two (TMWT), three (THMWT), four (FMWT), five (FIMWT), six (SMWT) and seven (SEMWT) months of age. Cumulative average daily weight gains were calculated from the various age adjusted weights as follows:

ADG1 = (OMWT - BWT)/30;

ADG2 = (TMWT - BWT)/60;

ADG3 = (THMWT - BWT)/90;

ADG4 = (FMWT - BWT)/120;

ADG5 = (FIMWT - BWT)/150;

ADG6 = (SMWT - BWT)/180 and

ADG7 = (SEMWT - BWT)/210.

Data were included for all calves subject to the restriction that the calf must have survived to seven months of age and has been nursed by its natural mother and should have had weight measurements for all age categories. However, calves with negative cumulative preweaning daily gains were excluded from the data set. The records were classified according to sire, dam, sex, season, herd and calf birth year. The final data set consisted of 1787 calf records (10 inbred with average inbreeding coefficient of 0.109) from 76 sires and 878 dams. The means, standard deviations (SD) and coefficients of variation (CV) for preweaning weight and preweaning cumulative daily gains are presented in Table 6.1.

Table 6.1 Means, standard deviation (SD) and coefficient of variation (CV) of adjusted pre-weaning growth traits in Gudali cattle

Trait	Mean (kg)	SD (kg)	CV (%)
Birth weight (BWT)	24.09	12.73	11.34
One month weight (OMWT)	52.65	10.30	19.56
Two months weight (TMWT)	73.33	13.52	18.44
Three months weight (THMWT)	92.04	6.04	17.43
Four months weight (FMWT)	109.42	17.85	16.31
Five months weight (FIMWT)	125.86	21.50	17.08
Six months weight (SMWT)	138.75	23.98	17.28
Seven months weight (SEMWT)	148.61	26.32	17.71
ADG1	0.80	0.09	11.94
ADG2	0.82	0.22	26.94
ADG3	0.76	0.18	23.58
ADG4	0.71	0.15	20.82
ADG5	0.68	0.14	21.08
ADG6	0.64	0.13	20.93
ADG7	0.59	0.12	21.00

ADG1 - ADG7 = cumulative average daily gain (days) for one to seven months weight

Statistical model and analytical techniques

A single-trait animal model was used with the additive direct effect, maternal direct effect correlated to the direct effect, non-additive maternal permanent environmental effect, uncorrelated to direct and maternal effects and environmental effect associated with the animal fitted as random effects. Sex of calf, calving season, herd and calf birth year were fitted as fixed effects. The MTDFREML software (Boldman *et el., 1995*) was used for the analyses. 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 until the variance was less than 10E-9. Where the search strategy did not converge to a global maximum the program was re-started until twice the logarithms changed no more than 0.00 to 0.02.

The model in matrix notation can be presented as:

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

$\underline{y}$ = observation vector for preweaning performance records;

X = known incidence matrix relating observations to the fixed effects;

$\underline{b}$ = vector of fixed (sex, season, herd and calf birth year effects);

Z_1, Z_2 and Z_3 = known incidence matrices relating elements of additive direct, additive maternal direct and maternal permanent environmental effects to y;

$\underline{a}$ and $\underline{m}$ = nonobservable correlated random vectors for direct and maternal effects;

$\underline{c}$ = nonobservable uncorrelated random vector associated with the maternal permanent environment, and

$\underline{e}$ = random vector associated with residual effects. The vectors $\underline{a}$, $\underline{m}$, $\underline{c}$ and $\underline{e}$ 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 can be 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 σ^2_a is the direct additive genetic variance, σ^2_m additive maternal genetic variance, σ_{am} covariance for additive direct-maternal genetic effects, σ^2_c uncorrelated non-additive maternal permanent environmental effect, A the numerator relationship matrix, I an identity matrix and σ^2_e error random variable for the trait.

6.3 RESULTS AND DISCUSSIONS

The coefficient of variation for preweaning weight traits was relatively constant with the exception of that for birth weight. The CV for culmulative average daily gain traits varied (11-26%) with age category from birth to three months (ADG1-ADG3) and thereafter, it remained relatively constant (Table, 6.1).

The estimates of the variance and (co)variances for the preweaning weight and preweaning cumulative average daily gain traits are presented in Table 6.2.

Table 6.2 (Co)variance estimates for pre-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	4.633	1.976	- 2.725	0.340E-05	4.612	8.496
OMWT	7.553	12.177	-7.800	0.809E-04	83.723	95.654
TMWT	38.629	35.450	-30.156	7.806	94.286	146.015
THMWT	39.391	28.030	-25.237	25.132	134.511	201.827
FMWT	54.368	40.501	-36.327	41.150	152.829	252.521
FIMWT	95.007	51.111	-49.097	48.513	213.252	358.787
SMWT	134.548	39.163	-68.732	86.869	267.662	459.511
SEMWT	180.929	50.878	-84.419	92.686	309.794	549.867
ADG1	0.007	0.003	0.000	0.56E-04	0.101	0.111
ADG2	0.011	0.008	-0.008	0.18E-02	0.027	0.040
ADG3	0.003	0.0002	-0.0003	0.33E-02	0.018	0.025
ADG4	0.002	0.000	-0.00004	0.34E-02	0.012	0.017
ADG5	0.002	0.002	0.0001	0.31E-03	0.011	0.016
ADG6	0.002	0.001	0.0005	0.99E-05	0.010	0.014
ADG7	0.003	0.000	0.000	0.18E-02	0.008	0.012

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

There was a steady increase in the additive direct, non-additive maternal permanent environmental, residual and phenotypic variance components from birth (BWT) to seven months (SEMWT). While the maternal variance component increased from birth to two months (TMWT), the direct-maternal covariance was on the decrease. The changes in the maternal and direct-maternal (co)variance became inconsistent in relative value after TMWT. The direct and maternal variance components for preweaning cumulative average daily gain increased from birth to two months then dropped thereafter to remain relatively constant. There was a steady increase in the non-additive maternal permanent environmental variance for cumulative average daily gain from one month (ADG1) to three months (ADG3) and thereafter, it remained relatively constant. The residual and phenotypic variations decreased steadily from ADG1 to ADG7 but the change in direct-maternal covariation was inconsistent. Estimates for genetic parameters are presented in Table 6.3.

Table 6.3 Estimates of genetic parameters for pre-weaning growth traits in Gudali cattle

Traits	h^2_A	h^2_M	C^2	C_{AM}	r_{AM}
BWT	0.37	0.05	0.28E-06	-0.32	-0.88
OMWT	0.09	0.13	0.85E-06	-0.08	-0.81
TMWT	0.26	0.24	0.53E-01	-0.21	-0.81
THMWT	0.20	0.14	0.12	-0.13	-0.76
FMWT	0.22	0.16	0.16	-0.14	-0.77
FIMWT	0.26	0.14	0.14	-0.14	-0.70
SMWT	0.29	0.09	0.19	-0.15	-0.95
SEMWT	0.33	0.09	0.17	-0.15	-0.88
ADG1	0.06	0.02	0.51E-03	0.00	0.00
ADG2	0.28	0.19	0.46E-01	-0.19	-0.85
ADG3	0.11	0.01	0.13	-0.01	-0.04
ADG4	0.09	0.00	0.20	-0.001	-0.30
ADG5	0.11	0.14	0.20	-0.004	0.04
ADG6	0.11	0.11	0.71E-03	-0.04	0.33
ADG7	0.20	0.00	0.14	0.00	0.00

h^2_A = direct heritability, h^2_M = maternal heritability, 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.

The highest direct heritability (h^2_A) for weight traits was obtained for birth weight (0.37) and the lowest for one month weight (0.09). It then increased for TMWT (0.26), dropped slightly for THMWT (0.20) and followed thereafter by a consistent increase. The lowest estimate (0.05) for maternal heritability (h^2_M) was obtained for birth weight and the highest (0.24) for two-months weight. The estimate decreased thereafter for subsequent weights. Whereas the proportionate contribution of the maternal environmental variation (C^2) to total phenotypic variation increased steadily from birth to SEMWT, that for direct-maternal covariation (C_{AM}) varied with preweaning weight trait and ranged from -0.32 to 0.00. Estimates for the direct-maternal genetic correlations (r_{AM}) were highly negative and ranged between -0.95 and -0.70.

On the other hand, highest estimates for direct (0.28) and maternal (0.19) heritabilities, were obtained for cumulative average daily gain at two months. The estimates decreased for subsequent cumulative average daily gain traits. The proportionate contribution of maternal permanent environmental variation to total phenotypic variation increased for cumulative average daily gain from one month (ADG1) to two months (ADG2) and thereafter, it became relatively constant while that for the direct-maternal covariation was inconsistent and varied from -0.19 to 0.00.

Estimates for monthly weights from birth to weaning in tropical cattle are sparse in the literature. However, estimates obtained for direct and maternal heritability for birth and one month weight in the current study were lower than those reported by Yokoi *et al.* (1997) in Japanese Black cattle. While direct heritability estimates for monthly weight traits from two to six months in current study were higher, corresponding maternal heritability estimates were comparable with those reported by Yokoi *et al.* (1997). However, estimates for direct and maternal heritabilities for cumulative average daily gains for one to six months by the same authors were higher than those reported in the present study. The differences in estimates might be attributed to breed differences.

From the results presented in Table 6.3, it is evident that while the direct heritability increased from birth to weaning, the reverse was true of the maternal. It was therefore obvious that the impact of the maternal effect tended to reduce as the calf approached weaning age. Given the high negative genetic correlation between direct and maternal effects in preweaning weight traits as reported in the current study, it is obvious that one Gudali beef cow herd will be unable to produce sires of high genetic merit and functionally efficient maternal females if selection was to be based solely on direct performance. An intense breeding for size will certainly create problems in maternal trait selection. As previously stated, Roy Beeby (1985) described the role of an effective maternal selection as being multipurpose. Therefore, as suggested by Van Vleck *et al.* (1977), It is necessary to establish different selection objectives for sire and dam lines.

The selection of animals for ages where maternal effects are not important will be unnecessary and wasteful since large numbers of animals have to be kept for prolonged periods before selection decisions are taken. Considering, estimates reported in this study, we realised that maternal heritability was highest for two months weight (0.24) and decreased thereafter. The maternal heritability was equally highest for cumulative average gain at two months (0.19). The contribution of the non-additive maternal permanent environmental variances to preweaning weight and cumulative average daily gain traits as a proportion of the total phenotypic variation increased from birth to two months and became relatively constant thereafter. While the direct heritability for preweaning weights consistently increased three to seven months age, corresponding maternal heritabilities were on the decrease. This trend in maternal heritability is consistent with the peak milk production at the earlier stages of lactation (between one and two months), followed by a decline, reported by Shimada *et al.* (1988), and Rutledge *et al.* (1971) in Japanese Black and Hereford beef cows, respectively. Based on these assessments, therefore, it could be deduced that while direct effects tended to increase with increased age of calf from birth to weaning, the maternal effects tended to decrease. Consequently, preweaning weight measurement at two months when the impact of maternal effect was optimized (h^2_M = 0.24) might be a better proxy trait for the prediction of maternal merits in the Gudali breed. Yokoi *et al.* (1997) obtained the highest maternal heritability estimate (0.34) for cumulative average daily gain at two months as against a lower estimate (0.20) for two-months weight. As a result, the authors recommended that the average daily gain from birth to two months be used as a suitable indicator of maternal trait for the Japanese Black cattle. A similar performance was observed in the present study, thereby suggesting that we can use either weight at two months or average daily gain from birth to two months as proxy traits for maternal performance.

6.4 CONCLUSION

Whereas the direct maternal genetic effect on Gudali calves tended to decrease as the calves attain weaning age, the direct genetic effect tended to increase. The relationship between direct and maternal genetic effects for preweaning traits was highly negative. An intense breeding for direct performance only, may therefore, be detrimental to maternal traits. Consequently, for an effective optimisation of breeding strategies in the Gudali maternal line it may be necessary to carry out selection toward maxima for maternal females on two months calf weight when maternal heritability is maximised and moderately heritable and the contribution from maternal permanent environmental variation as proportion of the total phenotypic variation is favourable.

CHAPTER SEVEN

GENERAL CONCLUSIONS AND RECOMMENDATIONS

The tropical environment in Cameroon is characterised by high temperatures and humidities and marked seasonal and annual variations in rainfall. The resultant effect is seasonality of parasite burdens, diseases and their vectors and large fluctuations in the quantity and quality of available feed for grazing animals. Also, beef cattle production in this environment is essentially under a traditional husbandry management system, plagued with problems which include, amongst others, high inbreeding, low fertility, slow growth, high mortalities, incidences of trypanosomiaisis, overgrazing, poor health facilities, socio-economic problems and absence of effective programmes for breed improvement. An attempt at genetic improvement of beef cattle in this environment, therefore, should consider the identification of some of the major environmental constraints to performance and devise means of alleviating or controlling them before evaluating the breed for its ability to cope with those other constraints that could not be readily identified and controlled.

The present study, identified inherent non-genetic effects such as sex, sire, cow age group, ages at weaning, yearling and eighteen-months as significant ($p<0.05$) sources of variation for performance traits in the Gudali and Wakwa beef breeds of Cameroon. Also, environmental factors such as season of calving (S), calf birth year (C), herd (H), HxSxC interaction were also significant ($p<0.01$) sources of variation for performance traits in both breeds. Therefore, considering these factors, in the estimation of genetic parameters and evaluation of the genetic merits of animals could be more effective for selection decisions.

The results indicated that Gudali and Wakwa calves born in the dry season were, respectively, 0.53 and 0.36 kg lighter ($p<0.001$) at birth but were 17.57 and 18.19 kg, 4.71 and 6.76 kg and 12.43 and 17.71 kg heavier at weaning, yearling and eighteen months, and had 80 and 90 g/day faster growth from birth to weaning than those born in the rainy season. Consequently, under a low input husbandry regime, as was the case in the present study, it may be necessary that a breeding programme under similar seasonal and management conditions, be designed so that the cows calve towards the end of the dry season. The late dry season calvings will result in reduced incidences of dystocia due to light birth weights. At the same time, the cows will benefit from the early rainy season nutritious pastures, favourable for higher milk production and more rapid growth and higher calf weights at weaning, yearling and eighteen months.

Although estimates of genetic parameters for beef cattle breeds in the tropical environment are sparse in the literature, the estimates reported so far including those from the present study, are indicative that there exists possibilities of improving growth traits through selection. The direct heritability estimates obtained in the Gudali were moderate for BWT (0.37), ADG (0.24) and WWT (0.27) and high for YWT (0.51). The maternal heritability estimates in the Gudali were low for BWT (0.05) and moderate for YWT (0.24). On the other hand, direct heritability estimates in the Wakwa were high for BWT (0.55) and moderate for ADG (0.26) and WWT (0.28). The estimates for maternal heritability were zero for YWT and moderate for BWT (0.23). The general trend of the results was that there was an increase in the direct genetic effect and a decrease in maternal direct effect as the calves attained weaning age. The results also showed that the direct-maternal genetic correlation estimates were highly negative in both preweaning and postweaning traits and ranged from -0.98 to -0.70 in both breeds, illustrating a genetic antagonism between direct and maternal ability. This antagonism was responsible for the substantial reduction in the overall genetic gain as reflected in the estimates of total heritability (0.07 to 0.22) which were lower than corresponding direct heritabilities in both breeds. Given the highly negative genetic correlation between the direct and maternal genetic effects, intense selection for direct performance may not only be detrimental to maternal traits on the long run, but could result in a substantial loss in the overall genetic performance of an individual. Consequently, an attempt to optimise improvement in both direct and maternal traits through selection, may necessitate the creation of separate herds for terminal sires and maternal females. The sire herd could be used for performance testing, effective at yearling ($h^2_A = 0.51$) in the Gudali breed and at weaning ($h^2_A = 0.28$) in the Wakwa breed. On the other hand, in the Gudali, the female herd could be effective for selection towards maxima for maternal traits, effective at two months calf weight, when the maternal heritability estimate (0.24), though moderate, was optimised. The negative genetic correlation between direct and maternal effects generally reported and also found in the present study, poses a very awkward problem. Since it presents a potential restriction on selection improvement for growth traits in all environments, it requires urgent specific attention in research programmes. Finding or establishing a suitable set of data for this purpose, will probably be the biggest problem.

An assessment of the genetic progress from 1968 to 1988 indicated that the annual direct trends for average preweaning gain (0.0005 kg/year), birth (0.02 kg/year), weaning (0.23 kg/year), yearling (0.33 kg/year) and eighteen months (0.25 kg/year) weights in the Gudali were all positive and significantly ($p<0.01$ or $p<0.001$) different from zero. Corresponding annual trends of 0.0005, 0.03, 0.20, 0.24 and 0.24 kg/year obtained for the Wakwa were also significantly ($p<0.05$ or $p<0.001$) different from zero. With the exception of trends for average preweaning daily gain in the Gudali and eighteen months in the Wakwa, annual maternal trends were negative and significantly ($p<0.05$ or $p<0.001$) different from zero. Consequently, selecting mainly for direct performance could result in maternal breeding values contributing very little or even negatively to the overall genetic response. This resulted in a lower than expected overall genetic gains of 0.010 and 0.010 kg, 0.29 and 0.200 kg, 2.39 and 2.90 kg, 3.08 and 4.03 and 3.94 and 4.88 kg for average preweaning daily gain and weights at birth, weaning, yearling and eighteen months in the Gudali and Wakwa, respectively. To optimise genetic response, therefore, it might be necessary to create separate herds for direct and maternal traits as discussed above.

The environment within which the selection experiment was conducted was rudimentary in terms of infrastructure, harsh as a result of high temperatures and humidities and fluctuating due to seasonal and annual variations in rainfall. The selection intensity was minimised and selection decisions constantly altered. It is, therefore, likely that with an improvement in the management conditions, increased selection intensity, well define selection objectives and breed policies, a better response to selection could be obtained. There was no significant difference between corresponding direct responses in the Gudali and Wakwa. In separate studies conducted by Dumas *et al.* (1971) and Tanya & Salah

(1985), it was shown that the Wakwa was more susceptible to streptothricosis and less tolerant to the tropical environment than the Gudali. It may, therefore, be economically more advantageous improving the Gudali breed than resorting to crossbreeding. The advantage is that the indigenous Gudali breed is more resistant and well adapted to the Cameroonian tropical environment, characterised by a low input regime husbandry management system. Selecting the Gudali for increased productivity will raise the breed potential for productive traits without any serious detrimental effects to its adaptational qualities. On the other hand, resorting to crossbreeding poses the problem of genotype-environment interaction and danger of extinction. Although the improvement of the Gudali breed could be slow and expensive, the selection effects would be cumulative once achieved and would be transmitted with little cost from generation to generation even when selection would have stopped. Emphasis on the improvement of the Gudali breed will not only result in retaining genetic biodiversity and conservation but will contribute substantially in improving the Cameroon economy in future.

However, the present study might not have been exhaustive as much still remains to be done in the genetic evaluation of the breeds. It might be necessary to improve in the model used in the analyses to include sire x year, sire x season x year and herd-year-season x sex interactions, amongst others. This will be useful in determining the impact of these effects on the magnitude and direction of the direct-maternal genetic correlation, which was of great concern in the study. Further studies are also necessary for the genetic evaluation of traits such as postweaning gains and fertility as well determine the genetic relationship between traits at different ages.

ABSTRACT

In an attempt to genetically improve Gudali beef cattle in Cameroon, two selection experiments were conducted between 1968 and 1988 at the Animal Production and Research Stations of Wakwa, Ngaoundere. The one experiment involved a two-breed synthetic beef breed, the Wakwa, obtained from *inter se* matings of the first filial generation of American Brahman (50%) x Gudali (50%) crosses. The other experiment involved recurrent selection of the indigenous purebred Gudali in an effort to enhance its beef production without any serious detrimental effects to its adaptational qualities.

In order to assess the genetic progress of the two experiments, a study using mixed model methodology was carried out. The objectives were to quantify factors affecting growth traits, estimate (co)variance components, predict genetic merit (breeding values) for direct and maternal performance and determine genetic progress by examining direct and maternal genetic trends for all animals. A total of 2886 records for birth weight (BWT), 2732 for average preweaning daily gain (ADG), 2899 for weaning weight (WWT), 2098 for yearling weight (YWT) and 1957 for eighteen months weight (EWT) of Gudali cattle were used in the study. Corresponding number of records for the Wakwa were 1793, 1656, 1838, 1372 and 1328.

The results indicated that sire, sex, season (S), calf birth year (C), herd (H), HxSxC interaction, cow age group and ages at weaning (WAGE), yearling (YAGE) and eighteen months (EAGE), as well as covariates for weaning, yearling and eighteen month weights, were significant ($p<0.05$) sources of variation for these traits. Therefore, for reliable

genetic parameter estimations and evaluation of genetic merit of individual candidate animals for selection, these sources of variation should be taken into consideration. Hence the inclusion of these factors in the mixed model for the estimation of genetic parameters and prediction of breeding values.

Estimates obtained for direct, maternal and total heritabilities were 0.37, 0.05 and 0.21 for BWT; 0.24, 0.17 and 0.07 for ADG; 0.27, 0.19 and 0.11 for WWT; 0.51, 0.20 and 0.22 for YWT; and 0.18, 0.02 and 0.18 for EWT, respectively, 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. Estimates for genetic correlations between direct and maternal effects were generally highly negative and ranged from –0.76 for ADG to –0.98 for YWT in the Wakwa and from -0.77 for WWT to -0.88 for BWT in the Gudali. However, in both breeds the genetic correlation was nil for EWT.

These estimates obtained are indicative that there are distinct possibilities of improving direct preweaning and/or postweaning growth in the both breeds through selection. However, a high selection intensity for direct performance may in the long run be detrimental to maternal performance as a result of the generally strong genetic antagonism between them. Although some estimates of genetic parameters for preweaning weight from one to seven months traits were not obtained for the Wakwa breed due to limited data, estimates obtained for the Gudali indicated that the highest, although moderate, estimate for maternal heritability (0.24) was for weight at two months of age. Therefore, an attempt to optimise direct and maternal performance in the Gudali through selection could be most effective at two months and at yearling, respectively. It is suggested that the apparent genetic antagonism generally found between direct and maternal ability be specifically investigated using more suitable data.

An assessment of genetic progress indicated positive and significant ($p<0.01$) mean annual direct trends of 0.02 and 0.03 kg/year for BWT; 0.0005 and 0.0005 kg/year for ADG; 0.23 and 0.20 kg/year for WWT; 0.33 and 0.24 kg/year for YWT and 0.25 and 0.24 kg/year for EWT in the Gudali and the Wakwa, respectively. The difference between direct responses for all traits in both breeds were not significant. Corresponding trends for maternally influenced traits were -0.01 and -0.02; -0.1 and -0.3; -0.10 and -0.06; -0.15 and -0.00, -0.01 and 0.04. With the exception of ADG in the Gudali and EWT in the Wakwa, maternal trends were also significant ($p<0.05$) but negative.

Considering the fact that the Wakwa breed has been shown to be more susceptible to streptothricosis and less tolerant to the tropical environment than the Gudali, it is economically justified to improve the purebred Gudali by selection rather than crossbreeding to the American Brahman or other exotic breeds.

OPSOMMING

In 'n poging om Gudali vleisbeeste in Kameroen geneties te verbeter, is twee seleksieproewe tussen 1968 en 1988 by die Wakwa dierproduksie- en navorsingstasie te Ngaoudere uitgevoer. Die een proef het 'n sintetiese ras behels wat ontstaan het uit 'n terminale kruis tussen die Amerikaanse Brahman (50%) en die Gudali 50%. Die ander proef het herhalende seleksie van die inheemse suiwer Gudali behels in 'n poging om sy vleisproduksie te verhoog sonder benadeling van aanpasbaarheid.

Om genetiese vordering in die twee proewe vas te stel, is 'n studie, waar van gemengde model prosedures gebruik gemaak is, onderneem. Die doel was om die faktore wat groei-eienskappe beïnvloed te kwantifiseer, (ko) variansiekomponente en gevolglike direkte en maternale genetiese tendense te beraam sowel as om die genetiese meriete (teeltwaardes) van al die diere vir direkte sowel as maternale prestasie te voorspel. 'n Totaal van 2886 rekords vir geboortegewig (BWT), 2732 vir gemiddelde daaglikse toename voor speen (ADG), 2899 vir speengewig (WWT), 2098 vir jaaroudgewig (YWT) en 1957 vir gewig op 18 maande (EWT) is gebruik vir die studie met die Gudali-ras. Ooreenstemmende aantal rekords vir die Wakwa was onderskeidelik 1993, 1656, 1838, 1372 en 1328.

Die resultate verkry het aangedui dat vaar, geslag, seisoen (S), kalf geboortejaar (C), kudde (H), HxSxC interaksie, koei-ouderdomsgroep en werklike ouderdom met speen (WAGE), jaaroud (YAGE) en agtien maande (EAGE) sowel as die kovariate vir speen, jaaroud en agtien maande betekenisvolle ($p<0.05$) bronne van variasie was. Vir betroubare beraming van genetiese parameters en teeltwaardes van individuele diere, sal hierdie

bronne van variasie derhalwe in ag geneem moet word wat die geval was in hierdie studie. Beramings verkry vir direkte-, maternale- en totale oorerflikheid was onderskeidelik 0.37, 0.05 en 0.21 vir BWT; 0.24, 0.17 en 0.07 vir ADG; 0.27,0.19 en 0.11 vir WWT; 0.51, 0.20 en 0.22 vir YWT en 0.18, 0.02 en 0.18 vir EWT in die Gudali. Ooreenstemmende beramings vir die Wakwa was onderskeidelik 0.55, 0.23 en 0.18 vir BWT; 0.26, 0.07 en 0.12 vir ADG; 0.28, 0.09 en 0.15 vir WWT; 0.18, 0.00 en 0.17 vir YWT en 0.14, 0.06 en 0.17 vir EWT. eramings van genetiese korrelasies tussen direkte genetiese en maternale effekte was deurgaans hoogs negatief en het gewissel van –0.76 vir ADG en –0.98 vir YWT, albei verkry in die Wakwa ras.

Die beramings verkry dui daarop dat genetiese verbetering van direkte voorspeense en/of naspeense groei deur seleksie 'n besliste moontlikheid in albei rasse is. 'n Hoë seleksie-intensiteit vir direkte prestasie mag egter op die lange duur skadelik wees vir maternale prestasie as gevolg van die verkreë hoë genetiese antagonisme tussen die twee. Alhoewel beramings van sommige genetiese parameters vir voorspeense gewigte tussen een en sewe maande nie vir die Wakwa verkry is nie weens beperkte data, het beramings verkry vir die Gudali getoon dat die hoogste, hoewel slegs matig, beraming vir maternale oorerflikheid (0.24) vir gewig op twee maande ouderdom was. Seleksie vir gewig op twee maande ouderdom in die Gudali en op jaaroud in die Wakwa blyk derhalwe die mees effektief te mag wees om direk en maternale prestasie te optimaliseer. Dit word ernstig voorgestel dat die skynbare genetiese antagonisme wat redelik algemeen verkry word tussen direkte en maternale vermoë spesifiek ondersoek word deur gebruik te maak van meer gepaste data.

'n Beraming van genetiese vordering het betekenisvol ($p<0.05$) positiewe jaarlikse gemiddelde tendense getoon van 0.02 en 0.03 kg per jaar vir BWT, 0.0005 en 0.0005 kg/jaar vir ADG, 0.23 en 0.20 kg/jaar vir WWT, 0.33 en 0.24 kg/jaar vir XWT en 0.25 en 0.24 kg/jaar vir EWT vir onderskeidelik Gudali en Wakwa. Die verskil in tendense verkry vir die Gudali en Wakwa was nie-betekenisvol vir al die eienskappe. Ooreenstemmende tendense verkry vir die eienskappe soos maternaal beïnvloed was -0.01 en -0.02; -0.1 en -0.3; -0.10 en -0.06; -0.15 en -0.00; -0.01 en -0.04. Met die uitsondering van ADG in die Gudali en EWT in die Wakwa, was maternale tendense ook betekenisvol ($p<0.05$) maar negatief.

Siende dat dit reeds aangetoon is dat die Wakwa ras meer vatbaar vir streptothricosis en minder tolerant vir tropiese toestande as die Gudali is, kan dit ekonomies meer regverdig wees om die suiwer Gudali deur seleksie te probeer verbeter as om gebruik te maak van die halfkruis Wakwa.

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APPENDICES

Appendix 5.1 Direct and maternal genetic trends for BWT in Gudali beef cattle

Obs	year	freq	direct	maternal	STDD	STDM
1	68	184	-0.193	0.069	0.677	0.198
2	69	389	-0.083	0.028	0.551	0.161
3	70	230	-0.143	0.044	0.854	0.266
4	71	181	-0.151	0.045	0.845	0.261
5	72	258	0.164	-0.031	1.217	0.381
6	73	241	-0.132	0.059	1.004	0.309
7	74	137	-0.003	0.018	0.89	0.277
8	75	167	-0.029	0.019	0.952	0.294
9	76	178	0.053	-0.007	0.792	0.253
10	77	206	-0.005	0.013	0.806	0.251
11	78	190	0.008	0.017	0.812	0.25
12	79	202	0.258	-0.067	0.721	0.225
13	80	161	0.168	-0.041	0.695	0.214
14	81	161	0.172	-0.041	1.022	0.319
15	82	131	0.105	-0.033	0.893	0.278
16	83	184	0.109	-0.027	0.765	0.237
17	84	82	0.272	-0.066	0.833	0.257
18	85	33	0.367	-0.093	0.783	0.249
19	88	64	0.314	-0.094	0.417	0.132

Appendix 5.2 Direct and maternal genetic trends for ADG in Gudali beef cattle

Obs	year	freq	direct	maternal	STDD	STDM
1	68	184	0.006	-0.006	0.019	0.015
2	69	389	0.002	-0.002	0.018	0.017
3	70	230	0.002	-0.001	0.022	0.016
4	71	181	0.004	-0.001	0.02	0.016
5	72	258	-0.005	0.002	0.029	0.023
6	73	241	0.005	-0.006	0.021	0.019
7	74	137	0.005	-0.004	0.02	0.017
8	75	167	0.01	-0.005	0.022	0.019
9	76	178	0.005	-0.002	0.023	0.018
10	77	206	0.009	-0.004	0.022	0.018
11	78	190	0.002	0.001	0.026	0.019
12	79	202	0	0	0.023	0.015
13	80	161	0.004	-0.001	0.026	0.018
14	81	161	0.012	-0.007	0.025	0.018
15	82	131	0.019	-0.013	0.027	0.018
16	83	184	0.011	-0.005	0.028	0.02
17	84	82	0.005	0.001	0.02	0.013
18	85	33	0.003	0.002	0.021	0.012
19	88	64	0.006	-0.002	0.014	0.01

Appendix 5.3 Direct and maternal genetic trends for WWT in Gudali beef cattle

Obs	year	freq	direct	maternal	STDD	STDM
1	68	182	1.469	-1.286	4.804	3.894
2	69	390	0.549	-0.475	4.546	4.355
3	70	231	0.327	-0.05	5.384	3.856
4	71	181	1.315	-0.279	5.15	4.199
5	72	258	-1.001	0.234	7.013	5.696
6	73	241	1.065	-1.393	5.219	4.573
7	74	137	1.132	-1.14	5.328	3.839
8	75	170	2.391	-1.287	5.857	4.486
9	76	175	1.962	-0.966	6.401	4.699
10	77	206	2.895	-1.512	5.911	4.793
11	78	190	1.259	-0.647	6.34	4.432
12	79	202	1.387	-0.715	6.26	3.86
13	80	162	3.027	-1.296	7.36	4.778
14	81	160	4.465	-2.532	6.987	4.569
15	82	131	6.289	-4.455	6.407	4.44
16	83	165	4.204	-2.565	7.209	5.219
17	84	101	3.137	-0.744	7.136	4.401
18	85	34	1.447	-0.221	8.446	4.878
19	88	63	2.526	-0.795	5.487	3.267

Appendix 5.4 Direct and maternal genetic trends for YWT in Gudali beef cattle

Obs	year	freq	direct	maternal	STDD	STDM
1	68	178	0.198	-0.391	8.208	3.841
2	69	353	-0.312	-0.151	6.016	3.469
3	70	215	-1.329	0.687	9.001	3.958
4	71	124	1.056	-0.716	8.795	3.949
5	72	222	0.008	-0.448	7.209	3.894
6	73	163	0.76	-0.605	7.405	3.893
7	74	83	0.703	-0.453	9.931	4.846
8	75	164	2.221	-1.028	10.018	4.962
9	76	125	3.105	-1.436	10.522	5.096
10	77	156	4.375	-1.958	9.889	5.189
11	78	133	0.481	-0.592	9.513	5.087
12	79	137	2.143	-1.546	9.339	4.311
13	80	69	3.203	-1.9	9.267	4.472
14	81	25	3.762	-1.947	10.317	4.378
15	82	65	6.28	-3.751	11.102	5.435
16	83	122	3.526	-1.455	13.802	6.514
17	84	70	3.976	-1.643	13.569	5.991

Appendix 5.5 Direct and maternal genetic trends for EWT in Gudali beef cattle

Obs	year	freq	direct	maternal	STDD	STDM
1	68	171	0.667	-0.17	6.655	0.712
2	69	344	0.331	0.029	5.797	0.786
3	70	198	0.101	-0.005	8.301	0.702
4	71	105	1.076	0.019	8.048	0.734
5	72	193	-0.648	-0.083	5.459	0.664
6	73	156	-0.09	-0.167	5.385	0.699
7	74	80	1.225	-0.125	6.732	0.769
8	75	163	3.288	-0.104	8.427	0.814
9	76	137	3.62	-0.117	6.457	0.796
10	77	162	3.623	-0.136	6.408	0.981
11	78	113	2.177	-0.372	6.002	0.878
12	79	105	0.143	-0.095	5.298	0.613
13	80	63	2.556	-0.143	6.596	0.737
14	81	25	2.68	-0.16	7.064	0.554
15	82	69	4	-0.478	6.259	0.584
16	83	92	3.946	-0.12	7.307	0.66
17	84	58	3.121	-0.017	7.135	0.635

Appendix 5.6 Direct and maternal genetic trends for BWT in Wakwa beef cattle

Obs	year	freq	direct	maternal	STDD	STDM
1	68	153	0.01	0.034	1.21	0.72
2	69	170	-0.226	0.02	0.868	0.488
3	70	166	-0.369	0.154	1.111	0.64
4	71	105	-0.499	0.216	0.927	0.558
5	72	141	-0.267	0.124	1.17	0.638
6	73	158	-0.706	0.379	1.183	0.615
7	74	106	-0.284	0.092	1.111	0.637
8	75	91	-0.323	0.099	1.187	0.739
9	76	118	-0.079	0.036	1.359	0.862
10	77	122	-0.056	0.022	0.96	0.553
11	78	119	0.245	-0.183	0.949	0.655
12	79	111	0.379	-0.272	1.176	0.7
13	80	142	0.234	-0.229	1.143	0.702
14	81	69	-0.727	0.368	1.635	0.989
15	82	60	-0.201	0.085	1.468	0.86
16	83	60	0.011	-0.076	0.991	0.556
17	84	43	0.25	-0.209	1.351	0.723
18	85	11	0.435	-0.287	1.669	0.882
19	87	55	0.163	-0.197	0.75	0.466
20	88	28	0.064	-0.1	0.841	0.489

Appendix 5.7 Direct and maternal genetic trends for ADG in Wakwa beef cattle

Obs	year	freq	direct	maternal	STDD	STDM
1	68	153	0.005	-0.002	0.021	0.009
2	69	170	-0.02	0.008	0.027	0.013
3	70	166	-0.017	0.006	0.032	0.015
4	71	105	-0.01	0.004	0.033	0.016
5	72	141	-0.011	0.003	0.031	0.014
6	73	158	-0.005	0.002	0.026	0.011
7	74	106	-0.002	0	0.038	0.015
8	75	91	-0.002	0.002	0.021	0.01
9	76	118	-0.001	0.002	0.028	0.012
10	77	122	-0.004	0.003	0.028	0.013
11	78	119	0.002	-0.001	0.029	0.013
12	79	111	-0.002	0	0.027	0.012
13	80	142	-0.007	0.003	0.026	0.011
14	81	69	-0.004	0.003	0.027	0.011
15	82	60	0.008	-0.003	0.024	0.01
16	83	60	0.014	-0.005	0.023	0.009
17	84	43	-0.004	0.002	0.02	0.009
18	85	11	-0.012	0.004	0.026	0.01
19	87	55	0.005	-0.003	0.013	0.006
20	88	28	0.001	-0.001	0.012	0.005

Appendix 5.8 Direct and maternal genetic trends for WWT in Wakwa beef cattle

Obs	year	freq	direct	maternal	STDD	STDM
1	68	153	1.53	-0.446	5.755	2.214
2	69	170	-4.506	1.719	7.222	3.558
3	70	166	-3.534	1.168	8.456	3.955
4	71	105	-1.947	0.644	7.913	4.178
5	72	146	-1.744	0.211	7.533	3.878
6	73	153	-0.382	-0.122	6.515	3.054
7	74	106	0.094	-0.52	9.82	3.756
8	75	91	-0.777	0.441	6.15	2.875
9	76	119	-0.363	0.555	8.023	3.372
10	77	121	-0.708	0.735	7.338	3.487
11	78	119	0.822	-0.467	7.196	3.196
12	79	109	-0.093	-0.178	6.566	2.723
13	80	115	-1.665	0.789	6.51	2.919
14	81	97	-0.306	0.566	6.803	3.079
15	82	61	2.42	-0.558	6	2.551
16	83	60	4.241	-1.331	6.136	2.493
17	84	43	-0.331	0.085	5.352	2.554
18	85	11	1.648	-1.251	6.096	2.287
19	87	55	0.363	-0.405	9.208	3.747
20	88	28	2.063	-1.11	5.602	1.999

Appendix 5.9 Direct and maternal genetic trends for YWT in Wakwa beef cattle

Obs	year	freq	direct	maternal	STDD	STDM
1	68	144	0.415	0.001	4.999	0.017
2	69	153	-2.021	-0.007	5.032	0.017
3	70	159	-1.646	-0.005	5.361	0.018
4	71	85	-0.066	0	5.71	0.02
5	72	124	-0.753	-0.003	5.163	0.017
6	73	93	1.058	0.003	5.376	0.019
7	74	68	2.155	0.007	6.073	0.021
8	75	91	1.463	0.005	6.457	0.022
9	76	100	1.513	0.005	5.442	0.019
10	77	111	0.634	0.002	5.354	0.018
11	78	67	1.467	0.005	4.677	0.017
12	79	63	0.71	0.002	4.463	0.016
13	80	78	1.565	0.005	5.54	0.019
14	81	62	1.593	0.006	4.301	0.015
15	82	21	0.115	0	3.788	0.013
16	83	53	3.806	0.013	6.165	0.021
17	84	19	3.819	0.013	4.132	0.014

Appendix 5.10 Direct and maternal genetic trends for EWT in Wakwa beef cattle

Obs	year	freq	direct	maternal	STDD	STDM
1	68	144	1.23	-0.135	6.711	2.005
2	69	149	-1.18	-0.798	5.217	1.981
3	70	151	-0.579	-0.736	5.603	2.074
4	71	86	0.711	-0.395	5.822	2.618
5	72	121	0.444	-1.131	5.031	2.141
6	73	82	1.952	-1.304	5.629	2.192
7	74	66	3.866	-0.404	6.902	2.183
8	75	88	1.926	0.3	6.902	1.86
9	76	96	1.624	0.002	6.218	2.003
10	77	102	1.535	-0.084	6.078	1.896
11	78	61	3.385	0.097	6.231	2.459
12	79	54	2.53	-0.472	4.97	1.877
13	80	51	3.186	-0.499	6.173	1.675
14	81	57	3.414	-0.171	5.554	2.092
[illegible]	82	24	2.788	-0.46	5.706	1.558
16	83	39	5.414	0.465	6.087	1.984
17	84	19	4.068	-0.401	5.083	1.496