

**GENETIC PARAMETER ESTIMATES FOR WEANING TRAITS IN A
MULTIBREED BEEF CATTLE POPULATION**

by

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DECLARATION

I the undersigned, hereby declare that the work in this thesis is my own original work and that it has not, as a whole or partially, been submitted to any other university for the purpose of acquiring a degree.

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SUMMARY

GENETIC PARAMETER ESTIMATES FOR WEANING TRAITS IN A MULTIBREED BEEF CATTLE POPULATION

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The aim of this study was to estimate genetic parameters as well as to evaluate the influence of some genetic factors on preweaning growth traits in a multibreed beef cattle population. These preweaning growth traits were birth weight (BW), weaning weight (WW) and average daily gain (ADG). Three aspects were addressed in this particular study; namely the Estimation of (co)variance components and genetic parameters, the effect of sire breeds and dam genotypes and the contribution of Charolais and Angus breeding levels on weaning traits in a multibreed beef cattle herd.

Variance components and resulting genetic parameters of BW, WW and ADG in the population were estimated by Restricted Maximum Likelihood (REML) procedures. Four different unitrait and multitrait animal models were fitted ranging from a simple model with the animal direct effects as the only random effect to the model allowing for both genetic and permanent maternal environmental effects. The model that included direct

genetic and permanent maternal environmental effects generally best described the data analysed. The simple model ignoring maternal effects most likely inflated direct heritability estimates. Direct heritability estimates were 0.11, 0.19, and 0.15 for BW, WW and ADG, respectively, fitting a multitrait model that comprised of both the genetic and maternal environmental effects. Under this comprehensive model, maternal heritabilities were low under both analyses, ranging from 0.02 to 0.10. Permanent maternal environmental effects were more important than maternal additive genetic effects for WW and ADG. Direct and maternal genetic correlations range from 0.42 to 0.44 for BW, -0.22 to -0.25 for WW and -0.17 to -0.23 for ADG, while the corresponding estimates of unitrait analysis varied from 0.58 to 0.61 for BW, -0.43 to -0.53 for WW and -0.49 to -0.79 for ADG.

The effect of Charolais and Hereford sires and dam breed genotypes on BW and WW in calves of Hereford, F₁, two and three breed rotational as well as terminal crosses among the Charolais, Hereford, Angus and Bonsmara breeds were investigated. BW and WW of the Charolais sired calves were significantly ($P < 0.001$) heavier than the Hereford sired calves. Angus dams produced calves of smaller ($P < 0.05$) BW than those of purebred and crossbred dams. The majority of the crossbred dams were not significantly different in BW of calves. With regard to WW, with the exception of 3/4H1/4A, all crossbred dams were superior ($P < 0.05$) to Angus and Hereford dams. Calves of crossbred dams were on the average 8% heavier at weaning than calves of purebred dams. Crossbred dams, with intermediate Charolais contribution tend to wean heavier calves.

Data collected were also analysed to determine the optimum breeding levels of Charolais and Angus, fitting a unitrait animal model. Further, the estimated heritabilities were subsequently used to predict direct and maternal breeding values (Best linear unbiased predictions) for individual animals. Best linear unbiased estimates (BLUEs) were also calculated for the traits. BLUEs, direct and maternal breeding values per genetic group estimated were regressed on proportions of Charolais and Angus breeding, respectively. BLUEs of BW, WW and ADG increased with increasing the proportion of Charolais while they decreased with increasing Angus breeding levels. In general, maternal

breeding values increased with increasing the proportions of both breeds. Direct breeding values of Charolais increased and reached maximum values at 35, 38, and 45% proportion of Charolais for BW, WW and ADG, respectively. No optimal Angus proportion was found within these specific environmental conditions. In this herd it may be suggested that increasing the proportion of Charolais to intermediate levels would tend to improve the performances of preweaning traits.

SAMEVATTING

GENETIESE PARAMETER BERAMINGS VIR SPEENEIENSKAPPE IN 'N MEERRAS VLEISBEES POPULASIE

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Die doel van die studie was om genetiese parameters in 'n meerras vleisbeeskudde te beraam, sowel as om die invloed van sekere genetiese faktore te evalueer. Die voorspeense groei-eienskappe het geboortegewig (BW), speengewig (WW) en gemiddelde daaglikse toename (ADG) ingesluit. Drie aspekte is in dié betrokke studie ondersoek, naamlik; die beraming van (ko)variansiëkomponente en genetiese parameters, die invloed van ras van vader en moeder-genotipe en die invloed van Charolais en Angus bydrae op speeneienskappe in 'n meerras vleisbeeskudde.

Variansiëkomponente en afgeleide genetiese parameters vir BW, WW en ADG in die kudde is met behulp van die Beperkte Maksimum Waarskynlikheidsprosedure (REML) beraam. Vier verskillende enkel- en meereienskapmodelle is gepas, wat vanaf 'n eenvoudige model wat slegs die direkte effek as enigste toevallige effek, tot dié model waarin beide die genetiese en permanente materne omgewingseffekte ingesluit is. Die model wat beide die direkte en permanente materne effekte ingesluit het, het die data die beste gepas. Die eenvoudige model, wat die materne effekte nie insluit nie, het in alle waarskynlikheid die direkte oorerflikhede oorberaam. Die direkte oorerflikheidsberamings

was onderskeidlik 0.11, 0.19 en 0.15 vir BW, WW en ADG met dié meereienskapmodel wat beide genetiese en materne effekte ingesluit het. Met die omvattende model was die materne oorerflikhede laag en het van 0.02 tot 0.10 gewissel. Die permanente materne omgewingseffekte was belangriker as die direkte materne effekte vir WW en ADG. Die genetiese korrelasies tussen direkte en materne effekte het vir BW tussen 0.42 en 0.44, vir WW tussen -0.22 en -0.25 en vir ADG tussen -0.49 en -0.79 gewissel.

Die invloed van Charolais en Hereford bulle en moederrasgenotipes op BW en WW van Hereford, F₁, twee- en dieras rotasie sowel as terminale kruisings tussen die Charolais, Hereford, Angus en Bonsmara is ondersoek. BW en WW van kalwers van Charolais bulle was betekenisvol ($P < 0.001$) swaarder as kalwers van Hereford bulle. Angus koeie het kalwers met laer ($P < 0.05$) BW as die van ander suiwer en kruisraskoeie geproduseer. Kalwers van die meerderheid kruisraskoeie het egter nie in BW verskil nie. Wat WW betref, maar met die uitsondering van $\frac{3}{4}H\frac{1}{4}A$, was alle kruisraskoeie beter ($P < 0.05$) as beide Angus en Hereford koeie. Kalwers van kruisraskoeie was gemiddeld 8 % swaarder met speen as kalwers van suierraskoeie. Kruisraskoeie met intermediêre vlakke van Charolaisbydrae het geneig om die swaarste kalwers te speen.

Die data is verder ook geanaliseer om die optimum vlakke van Charolais en Angus, deur die passing van 'n enkeleienskap dieremodel, te bepaal. Die beraamde oorerflikhede is vervolgens gebruik om direkte en materne teelwaardes (Beste liniêre onsydige voospellers) vir individuele diere te voorspel. Beste liniêre onsydige beraamings (BLUE's) is ook vir elke eienskap bereken. Die regressies van BLUE's, direkte en materne teelwaardes per genetiese groep bereken, is vervolgens op proporsie Charolais en Angus bydraes onderskeidelik gepas. BLUE's vir BW, WW en ADG het met toename in Charolaisproporsie toegeneem, terwyl dit met toename in Angusbydrae afgeneem het. In die algemeen het materne teelwaardes met toename in die bydrae van beide rasse toegeneem. Direkte teelwaardes van die Charolais het toegeneem en maksimum waardes by 35, 38 en 45 % proporsie Charolais vir onderskeidelik BW, WW en ADG bereik. Vir die Angus is geen optimum proporsie in dié spesifieke omgewing gevind nie. In dié kudde word intermediêre Charolais vlakke vir die verbetering van voorspeense eienskappe aanbeveel.

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CHAPTER 1

GENERAL INTRODUCTION

A large number of breeds and crosses between these breeds constitute the national beef cattle population of the Republic of South Africa. The breeds vary considerably for a variety of economically important traits (*e.g.* fertility, growth rate and adaptability). The genetic diversity with regard to these traits provides excellent opportunities for improving cattle productivity and efficiency in varying climatic and production conditions. Increasing productivity of beef production by genetic means is based on two important procedures, namely selection within breeds to improve the desired traits, and selection among breeds and crossing of breeds to produce animals that better fit specific production environments and available resources (Long, 1980).

Crossbreeding is a standard breeding practice in many countries of the world. Although little information is available, crossbreeding is a widely used procedure in beef cattle in South Africa (Schoeman, 1999). Crossbreeding among the breeds may be carried out for these traits where the existing breeds of cattle performs unsatisfactorily in its particular production environment or production system or when the interest is to optimise simultaneously the use of both nonadditive (heterosis) and additive (breed difference) effects of genes. The cumulative effect of heterosis on traits that contribute to weight of calf weaned per cow exposed to breeding have been shown to be 23.3% for crosses among breeds of *Bos taurus* (Cundiff *et al.*, 1974a; b) and 50% or more for crosses between *Bos taurus* and *Bos indicus* breeds of cattle (Koger *et al.*, 1975). In general, according to Harwin (1989), Legates & Warwick (1990) and Bourdon (2000) crossbreeding has some basic advantages, such as:

- Generates heterosis in respect of fertility, viability, milk production, growth rate and adaptability.
- Provides an opportunity to introduce new desired genes and incorporate them into crossbred animals at a faster rate than by selection methods within breeds.

- Combines the desired economically important traits of two or more breeds to achieve more suitable combinations in crossbred animals than is available in one breed.

Increased weaning weight resulting from superior maternal abilities of the crossbred dams is undoubtedly the most important economic advantage of crossbreeding in beef cattle. Birth weight of an animal and its early growth rate, in particular from birth to weaning are influenced not only by the individual's own genetic makeup but also by the maternal environment (Koch, 1972; Bourdon, 2000). The factors, which may play an important role for these maternal effects, include the cytoplasm of the egg, the uterine environment and postnatal environment that comprise milk production and maternal abilities of the dams (Baker, 1980). The genotype of a dam therefore affects the performances of growth traits of her young offspring through a simple half of her direct additive genes for growth as well as through her genotype for maternal effects on growth (Willham, 1972; Baker, 1980; Meyer, 1992a).

Effective breed utilization requires knowledge of the relative amount of the genetic variation attributable to maternal effects and especially the sign and magnitude of the genetic correlation between direct and maternal effects of the traits are critical in designing and application of practical breeding programmes (Willham, 1980). This requires appropriate estimation of population parameters (*e.g.* heritabilities, genetic correlations, breeding values) and characterization of breeds and their combinations for growth traits in various production conditions. Genetic parameters are a characteristic of the population in which they are estimated for the traits of interest. Their estimates vary widely across authors, years, methods of estimation, breeds and production systems (Mohiuddin, 1993; Swalve, 1993; Koots *et al.*, 1994a; b; Robinson, 1996a). Therefore, when parameters for Best Linear Unbiased Predictions (BLUP) evaluations are needed no obvious set of parameters exist for a given breed (Swalve, 1993). In various beef production areas, the major problems in designing optimal breeding plans to improve the biological and economic efficiency of beef productions are lack of adequate information regarding the genetic nature of preweaning growth traits and suitable breeds and breeds combination that should be used in different feed environments and production conditions.

The development of more powerful computers and new genetic evaluation techniques has facilitated use of more complex models to increase accuracy of estimation. To date, the animal model is considered as the model of choice for parameters estimation. Numerous estimates of genetic parameters for growth traits in beef cattle can be found in the literature (Meyer, 1992a, Mohiuddin, 1993). However, only a small number are derived from animal models *e.g.* Meyer (1992a), Swalve (1993), Rust *et al.* (1998) and Schoeman & Jordaan (1999).

The primary objectives of this study therefore were to generate information regarding genetic parameters applying animal models and to evaluate the influence of some genetic factors influencing preweaning traits in a multibreed beef cattle herd.

CHAPTER 2

ESTIMATES OF (CO)VARIANCE COMPONENTS AND GENETIC PARAMETERS OF PREWEANING GROWTH TRAITS

2.1 INTRODUCTION

The potential for genetic improvement in economically important traits of beef cattle in a selection programme depends on the extent of the genetic variance and heritability of the traits considered. Effective beef cattle breeding programmes are therefore based on knowledge of the relative importance of the genetic and environmental variation of the traits in the population. Variance and covariance component estimates provide information about the genetic nature of traits and help in the design of breeding programmes (Cameron, 1997; Hofer, 1998). In addition, these (co)variance components are important to predict direct and correlated responses to selection.

Accurate genetic evaluation requires accurate estimates of genetic variances for direct and maternal effects and the correlation between them. Several estimates of maternal heritabilities and direct-maternal genetic correlations in the past have been obtained by equating variance component estimates from sire-maternal-grand-sire and sire-dam models analyses (Quaas *et al.*, 1985; Trus & Wilton, 1988; Brown *et al.*, 1990; Wright *et al.*, 1991). However, owing to the recent increased computing power available, linear models are employed in the genetic evaluation of animals separating direct, maternal genetic and maternal permanent environmental effects, using animal models (Mackinnon *et al.*, 1991; Meyer, 1992a; Swalve, 1993; Robinson, 1996b; Schoeman & Jordaan, 1999). In general, the animal model is considered as the preferred model for a wide range of applications. A number of investigations applied this methodology for unitrait analyses of early growth traits of beef cattle, but to date, limited estimates from corresponding multitrait analyses have been reported.

This paper describes both unitrait and multitrait animal model REML analyses for early growth traits in a multibreed beef cattle population. Although many genetic parameters estimates are now available in the literature from different breeds and production conditions (Mohiuddin, 1993; Koots *et al.*, 1994a; b), studies involving estimation of variance and covariance components and genetic parameters on data collected in multibreed populations under various production environments are lacking. Such estimates may furthermore differ according to breed of cattle and production system (Robinson, 1996a). The objective of this work therefore was to estimate (co)variances, heritabilities and genetic correlations for preweaning growth traits in a multibreed beef cattle herd by separating direct genetic, maternal genetic and maternal permanent environmental effects by fitting unitrait and multitrait animal models.

2.2 MATERIALS AND METHODS

Data were obtained from multibreed beef calves born and raised on the Johannesburg Metropolitan Council's farms during the period 1968 to 1992. The beef herd is kept on two different farms, *viz.* the Olifantsvlei farm and the Northern farm, which are located in the Gauteng province of South Africa. The beef herd is raised on a restricted pasture feeding system using irrigated annual and perennial rye grass pastures supplemented with *Eragrostis curvula* hay, maize meal, distillers grain and silages of maize, sorghum and grass (Paterson *et al.*, 1980a) when necessary.

2.2.1 Animals

Four foundation sire breeds were included in this particular crossbreeding programme, namely Hereford, Charolais, Angus and Bonsmara. Charolais represented the large frame-sized while Hereford, Angus and Bonsmara represented small to medium-sized breeds. Initially, a large proportion of purebred and crossbred dams of the above-mentioned breeds were purchased from commercial farms for this project.

2.2.2 Breeding systems

A crossbreeding program has originally begun in 1962 with a diversity of foundation cattle breeds. The objective of the initial crossbreeding was to produce various crosses of animals under a classical crossbreeding programme, including two-breed and three-breed terminal and rotational systems (Schoeman & Jordaan, 1999). After the termination of the initial crossbreeding programmes in 1981, development of a composite population started when all crossbred groups were pooled and selection was based on performance traits such as female reproduction, weaning weight, post-weaning gain and breeding soundness, without taking breed composition into consideration. The aim was ultimately to obtain a high producing multibreed population of varying breed composition. In total 4119 calves involving combinations of these breeds were born. The number born by each mating type is presented in Table 2.1. The data structure is therefore characterised by a lack of certain combinations, such as purebreds and reciprocals.

Table 2.1: Number of calves born by each mating type.

Dam genotype	Sire genotype							
	A	B	BAH	C	CAH	CH	H	HA
A	0	0	0	236	0	0	155	0
AB	0	0	0	58	0	0	0	0
AC	0	0	0	227	19	5	112	0
ACH	0	0	0	193	15	9	65	0
AH	23	0	0	414	17	17	520	0
B	9	0	0	187	0	1	108	0
BAH	0	0	0	0	0	0	21	0
BC	0	0	9	55	0	7	0	0
BH	15	0	0	24	0	0	81	0
C	0	3	0	0	0	0	48	2
CAH	0	10	0	0	0	0	1	1
CH	0	14	0	358	24	13	323	0
H	42	22	3	159	5	2	452	35
Total	89	49	12	1911	80	54	1886	38

A, Angus; B, Bonsmara; C, Charolais; H, Hereford

Artificial insemination was used in all females using the same sires across both farms and since 1981 mating was carried out at random without taking breed composition into account. Age at first calving for heifers was approximately two years.

2.2.3 Recording procedures

Birth weight, birth date, weaning weight and weaning date as well as breed composition were recorded for each individual calf born during this period. Breed composition of each animal was obtained by tracing pedigrees back to the base population. Cows calved almost throughout the year. However, the majority of calves were born in winter (June -October) while the remaining calves were born during November to May. Hence, season of birth was recorded as either “summer born” or “winter born”. After editing the data by removing extreme values of weights and calves with unknown parents, 4119 records were available for analysis. Those calves deviating more than three standard deviations from the mean weight for BW and WW were excluded from the analysis. The records included birth weight (BW), weaning weight (WW) and preweaning average daily weight gain (ADG). The characteristics of the dataset are presented in Table 2.2.

Table 2.2: Characteristics of the data set for BW, WW and ADG (birth to weaning) of calves.

	Number of			Standard	
	records	Minimum	Maximum	Mean	deviation
Birth weight (kg)	4119	22.00	55.00	35.80	6.20
Weaning weight (kg)	4119	102.00	358.00	192.40	34.89
Average daily gain (kg)	4119	0.28	1.92	0.75	0.14
Calf age at weaning (days)	4119	106.00	310.00	210.70	26.90
Dam age at parturition (years)				5.64	2.30
Number of calves/sire				56.40	
Number of calves/dam				2.10	

The numbers of sires and dams used were 73 and 1973, respectively. Dam ages ranged between 2 to 17 years old. Closer ages having comparable birth and weaning weights were pooled together. Cows aged 2 and 3 years, 4, 5 and 6 years, those aged 7 and 8 years and those 9 and older were pooled together into 4 categories, respectively. Before pooling the data, average age of dam was 5.9 years and after pooling, it was 5.6 years.

2.2.4 Statistical procedures

In an initial analysis data were analysed using the General Linear Model (GLM) procedures of the Statistical Analysis Systems (1996). The models fitted included the fixed effects of dam age (4 levels), genotype of calf (58 levels), sex of calf (2 levels) and herd-year-season (66 levels). Weaning age of calf was included as a covariate for WW. All fixed effects and their interactions that had no ($P > 0.05$) influence on BW, WW and ADG were excluded from the final analyses according to a step down procedure.

Estimates of (co)variance components from unitrait and multitrait analyses were performed by using the REML VCE packages of Groeneveld (1996, 1997), fitting four animal models. Models 3 and 4 allowed for a covariance between direct and maternal genetic effects. These models in matrix notation were:

$$\text{Model 1: } Y = X\mathbf{b} + Z_1\mathbf{a} + \mathbf{e}$$

$$\text{Model 2: } Y = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{c} + \mathbf{e}$$

$$\text{Model 3: } Y = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + \mathbf{e}$$

$$\text{Model 4: } Y = X\mathbf{b} + Z_1\mathbf{a} + Z_2\mathbf{m} + Z_3\mathbf{c} + \mathbf{e}$$

where Y = a vector of the calf's record for each trait.

X = a known incidence matrix relating the observations to the fixed effects.

\mathbf{b} = a vector of fixed effects

Z_1, Z_2 and Z_3 = known incidence matrices relating the observation (Y) to the unknown random effects of \mathbf{a} , \mathbf{m} and \mathbf{c} .

- a** = denotes a random vector for the animals own additive genetic effects.
- m** = a random vector of maternal additive genetic effects
- c** = a random vector of permanent maternal environmental effects
- e** = a vector of random residual errors.

It is furthermore assumed that:

$$\text{Var}(\mathbf{a}) = \mathbf{A}\sigma_a^2$$

$$\text{Var}(\mathbf{m}) = \mathbf{A}\sigma_m^2$$

$$\text{Var}(\mathbf{c}) = \mathbf{I}\sigma_c^2$$

$$\text{Var}(\mathbf{e}) = \mathbf{I}\sigma_e^2$$

$$\text{Cov}(\mathbf{a}, \mathbf{m}) = \mathbf{A}\sigma_{am}$$

where, **A** = the numerator relationship matrix between the animals

σ_a^2 = the direct additive genetic variance

σ_m^2 = the maternal additive genetic variance

σ_c^2 = the variance of maternal permanent environmental effects

σ_e^2 = the variance of residual error

σ_{am} = the genetic covariance between direct and maternal genetic effects

I = an identity matrix.

Heritabilities were estimated as follow:

(a) Heritability for the direct additive genetic effects

$$h_a^2 = \sigma_a^2 / \sigma_p^2, \text{ where } \sigma_p^2 \text{ is the phenotypic variance.}$$

(b) Heritability for the maternal effects

$$h_m^2 = \sigma_m^2 / \sigma_p^2$$

(c) Total heritabilities (h_T^2)

$$h_T^2 = (\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am}) / \sigma_p^2, \text{ (Willham, 1972).}$$

The genetic correlation between direct and maternal genetic effects was estimated by

$$r_{am} = \sigma_{am} / (\sigma_a^2 \sigma_m^2)^{1/2}$$

2.3 RESULTS AND DISCUSSION

2.3.1 Fixed effects

An analysis of variance and proportional contribution of individual fixed effects on BW, WW and ADG are presented in Table 2.3. Age of dam, genotype of calf, sex of calf and herd-year-season were significant sources of variation in BW, WW and ADG of calves.

Table 2.3: Least squares analysis of variance and proportional contribution of fixed effects (FE%) to the total variance for BW, WW, and ADG.

Source of variation	DF	BW		WW		ADG	
		F value	FE (%)	F value	FE (%)	F value	FE (%)
Age of dam	3	34.6***	1.5	17.6***	0.7	11.9***	0.6
Calf genotype	57	20.6***	16.4	16.8***	11.6	12.1***	11.2
Sex of calf	1	307.5***	4.3	312.8***	3.8	233.2***	3.8
Herd-year-season	65	8.3***	7.5	14.5***	11.4	14.6***	15.4
Weaning age	1			1113.7***	13.4		
R ² model		0.44		0.52		0.35	
EMS ^a		22.14		603.90		0.01	

*** P<0.001; ^a EMS, error mean square

Although age of dam was a significant (P<0.001) source of variation for BW, WW, and ADG, it only accounted for 1.5, 0.7 and 0.6% of the variation in BW, WW and ADG, respectively. Several other studies also reported a significant influence of age of dam on early growth traits of beef cattle (Burfenig *et al.*, 1978; Dillard *et al.*, 1980; Paterson *et*

al., 1980a, b; Lawlor *et al.*, 1984; Roberson *et al.*, 1986; Van Zyl, 1990; Schoeman *et al.*, 1993).

Genotype of calf was one of the most important factor influencing all the traits, accounting for 16.4, 11.6 and 11.2% of variation for BW, WW and ADG, respectively (Table 2.3). The contribution of calf genotype seems relatively larger in BW than in WW. Among the possible reasons for differences in performance of the calf genotype are breed additive, breed maternal, individual heterosis and maternal heterosis contributions to their performances. These results are in accordance with those of Gotti & Benyshek (1988), Van Zyl (1990), Schoeman *et al.* (1993) and Plasse *et al.* (1995).

The sex of calf effect was also significant ($P < 0.001$) for all traits studied but accounted for only 4.3% of the variation in BW and 3.8% in both WW and ADG (Table 2.3). Van Zyl (1990) reported that the sex effect explained 4.4 and 5.5% of the variation in BW and WW, respectively, which is comparable to these results. Male calves were heavier at birth and weaning and had a higher ADG than female calves. In general the results are also in agreement with findings of Gregory *et al.* (1978a; b), Dillard *et al.* (1980) and Reynolds *et al.* (1980).

Herd-year-season was also a significant ($P < 0.001$) source of variation in the traits studied (Table 2.3). It accounted for 7.5, 11.4 and 15.4% of the variation in BW, WW and ADG, respectively. The influence of herd-year-season was comparatively larger at weaning than at birth.

Weaning age of calves had a significant ($P < 0.001$) influence on WW of calves (Table 2.3). It accounted for 13.4% of the variation. Where mating occurs in a restricted season and calves are weaned all time, age of calf at weaning may become an important production trait, influencing the weight and value of calf produced (Koger *et al.*, 1975). Comparable results were also reported by Gray *et al.* (1978) and Dillard *et al.* (1980).

2.3.2 Univariate analysis

Table 2.4 presents the (co)variance components and genetic parameters for BW, WW and ADG. Estimates of heritabilities for all traits agreed with the values in the literature summarised by Meyer (1992a), although the estimates reported varied according to the differences in type of records analysed (Wright *et al.*, 1987), methods of estimation (Nelsen *et al.*, 1986) and models used for the analysis (Mohiuddin, 1993). The variance components of direct effects (σ^2_a) and the resulting direct heritabilities (h^2_a) from Model 1 for BW, WW and ADG were substantially higher than those of the other models. The h^2_a estimates of Model 1 were in agreement with reports of Gutierrez *et al.* (1997) and Schoeman & Jordaan (1999) and lies within the range of the estimates in the literature reviewed by Mohiuddin (1993) for BW of 0.14 to 0.61 and for WW of 0.07 to 0.66. Fitting the additive genetic effects as the only random effects besides the random error, resulted in high h^2_a values. In other words, ignoring maternal effects most likely inflated h^2_a for all traits considered. Waldron *et al.* (1993) also concluded that animal models, which ignored maternal effects, tend to overestimate direct heritabilities of early growth traits.

To assess this potential bias, where either a maternal permanent environmental effect (Model 2) or maternal additive genetic effect (Model 3) or both (Model 4) were included in the models, h^2_a estimates were considerably reduced. This may be an indication that h^2_a from Model 1 was overestimated for each trait. Fitting a maternal permanent environmental effect, as the log likelihood value suggested (Groeneveld 1996, 1997), Model 2 provides a better fit to the data for all traits. The maternal environmental effect accounted for 14.8, 23.6 and 25% of the total phenotypic variation in BW, WW and ADG, respectively. Meyer (1992a) also reported maternal permanent environmental effects of 10.7% and 29% in Hereford cattle for BW and WW, respectively while Waldron *et al.* (1993) reported estimates of 11.4% for BW and 29.5% for WW in Hereford cattle. In this study, the contribution of maternal environmental effects for WW and ADG were more important than for BW. The estimates of c^2 were higher than h^2_a for WW and ADG, whereas the opposite holds true for BW.

Table 2.4: Estimates of (co)variance components (kg^2) and genetic parameters for BW, WW and ADG from univariate analysis fitting different animal models.

Model	Parameters											Log likelihood
	σ_a^2	σ_m^2	σ_{am}	σ_c^2	σ_e^2	σ_p^2	h_a^2	h_m^2	r_{am}	c^2	h_T^2	
Birth weight												
Model 1	15.08				10.37	25.45	0.59				0.59	4910.50
Model 2	6.05			3.44	13.75	23.25	0.26			0.15	0.26	4881.78
Model 3	2.30	3.07	1.53		15.76	22.66	0.10	0.13	0.58		0.30	7728.99
Model 4	2.47	1.89	1.31	1.42	15.52	22.61	0.10	0.08	0.61	0.06	0.25	7726.28
Weaning weight												
Model 1	339.30				334.99	674.29	0.50				0.50	4364.08
Model 2	78.06			146.36	394.74	619.16	0.13			0.24	0.13	4262.35
Model 3	84.91	190.86	-54.46		404.01	625.31	0.15	0.33	-0.43		0.16	7137.67
Model 4	85.73	39.87	-30.87	134.83	390.40	619.96	0.15	0.07	-0.53	0.23	0.10	7115.36
Average daily gain												
Model 1	0.007				0.007	0.014	0.48				0.48	5571.72
Model 2	0.001			0.003	0.008	0.012	0.10			0.24	0.10	5466.99
Model 3	0.002	0.004	-0.001		0.008	0.013	0.13	0.35	-0.49		0.19	8344.28
Model 4	0.001	0.000	-0.001	0.003	0.008	0.011	0.12	0.04	-0.79	0.26	0.00	8320.28

σ_a^2 , direct additive genetic variance; σ_m^2 , maternal additive genetic variance; σ_{am} , direct-maternal genetic covariance; σ_c^2 , maternal permanent environmental variance; σ_e^2 , error variance; σ_p^2 , phenotypic variance; h_a^2 , direct heritability; h_m^2 , maternal heritability; r_{am} , direct and maternal genetic correlation; c^2 , σ_c^2/σ_p^2 ; h_T^2 , total heritability.

Fitting maternal genetic effects rather than maternal environmental effects also resulted in a reduction of h^2_a in all traits. Model 3 and 4 provided a lower estimate of h^2_a for BW than most of the values reported in the literature reviewed by Mohiuddin (1993), but correspond to those reported by Quaas *et al.* (1985) for Simmentaler and Cantet *et al.* (1988) for Hereford cattle. Estimates of h^2_a for WW and ADG are also in agreement with most of the values reported in the literature for beef cattle (Meyer, 1992a; Cantet *et al.*, 1993). In Model 3 maternal heritabilities (h^2_m) and maternal genetic variances (σ^2_m) were higher than the corresponding h^2_a and σ^2_a for all traits. Nelsen *et al.* (1984) reported a h^2_m of 0.82 and a h^2_a of 0.36 for BW in a Hereford herd. In another study for the same trait, Kriese *et al.* (1991) estimated a h^2_m of 0.55 and a h^2_a of 0.22 for Beefmaster cattle. However, in contrast to these results, several contradictory results were also reported (Koch, 1972; Burfening *et al.*, 1981; Trus & Wilton, 1988; Waldron *et al.*, 1993). Maternal heritabilities for WW and ADG were also higher than h^2_a (Model 3). Corresponding estimates under the animal model were also reported by Meyer (1992a) for Hereford beef cattle. Wright *et al.* (1991) found a higher value of h^2_m for WW in Senepol cattle when fitting sire-dam and sire-maternal-grand-sire (SMGS) models. In other studies, by fitting sire-dam and SMGS models, Bertrand & Benyshek (1987), Brown *et al.* (1990) and Johnston *et al.* (1992) reported higher h^2_a than h^2_m estimates.

The total heritability estimated from Model 4 for ADG was zero, which was unexpected. This may be owing to the high negative genetic correlation between direct and maternal effects. The c^2 was larger than the h^2_m under this model for WW and ADG. Meyer (1992a) and Tosh *et al.* (1999) also reported a higher c^2 for WW than the h^2_m in a beef cattle population. In other studies, estimates of h^2_m were higher than c^2 for WW (Rodriguez-Almeida *et al.*, 1995; Schoeman & Jordaan, 1999; Skrypzeck *et al.*, 2000b). Gutierrez *et al.* (1997) also reported higher h^2_m than c^2 for both WW and ADG. The reason for the relatively high c^2 may be attributed to the genotypes that are not included in the model could be grouped with the c^2 as permanent environment is of a repetitive nature and is normally seen as non-genetic effect. In addition, high c^2 may be related to the postnatal environments provided by the young dams (heifers) to their progenies.

The genetic correlations between the direct and maternal effects (r_{am}) were positive and large for BW while they were large and negative for WW and ADG, respectively. These

values for BW were in contrast to the list of estimates from previous published studies presented by Meyer (1992a), which were mostly negative. Both Waldron *et al.* (1993) and Meyer (1994) also reported positive estimates of r_{am} for BW. These differences may arise from the fact that in the present study data from a multibreed herd were used where animals differed considerably in size (*e.g.* the Charolais compared to the Angus). Baker (1980) pointed out that SMGS models did not account for negative correlations between the permanent environment of a dam and the permanent environment of her daughters, which resulted in bias estimates of r_{am} . Possibly, the difference between SMGS and animal model estimates may suggest that more accurate estimates were obtained from animal models in the estimation of the genetic parameters. Waldron *et al.* (1993) also suggested that the difference in the sign of σ_{am} indicates that the animal model estimates of σ_{am} are less affected by negative environmental correlations than in sire model estimates. Positive r_{am} estimates may arise from the same genes tending to possess the same effects on both direct and maternal genetic effects of BW.

Estimates of r_{am} for WW and ADG were highly negative. Comparable large negative genetic correlations were reported for WW in other beef cattle studies such as those by Wright *et al.* (1991), Cantet *et al.* (1993), Meyer, (1993b) and Schoeman *et al.* (2000). Comparable negative estimates of r_{am} were also reported for ADG in Simmental, Angus and Hereford cattle (Trus & Wilton, 1988). The average value obtained for r_{am} for WW from several studies summarised by Mohiuddin (1993) was -0.15. In this study, the larger negative r_{am} possibly suggests that selection for genetically superior animals for WW resulted in genetically inferior for the maternal genetic components of WW. As pointed out by Meyer (1992a), a number of reasons might have involved for such genetic relationship, for instance, environmental factors related to management systems and husbandry practices may be contributed for high direct and maternal genetic correlations. It was furthermore indicated by Schoeman & Jordaan (2001) that such large negative r_{am} estimates were considerably reduced in a crossbreed population by the inclusion of the breed proportions and non-additive effects in the model fitted. The large negative estimates obtained in this study as well as those reported estimates are thus most likely not reflecting a true antagonism, but are biased estimates of the true relationship between direct and maternal genetic effects.

2.3.3 Multitrait analysis

Estimates of (co)variance components and total heritabilities (h^2_T) are presented in Table 2.5, while estimates of h^2_a , h^2_m , c^2 , direct genetic correlations and maternal genetic correlations are presented in Table 2.6 for BW, WW and ADG from the multitrait analysis. The h^2_T estimates from the multitrait analysis varied from 0.15 to 0.59. The h^2_T for ADG (Model 4) under the univariate analysis was zero, while under the multitrait analysis it was 0.15. This difference may partly arise from the difference in the estimation of r_{am} between the two analyses. Heritabilities from multitrait analysis for the traits lie within the range of estimates of Mohiuddin (1993), which vary from -0.02 to 0.68 for BW and from 0.02 to 0.81 for WW. Estimates of h^2_T for ADG also correspond with literature estimates reported in the review of Meyer (1992a).

Table 2.5: Estimates of (co)variance components (kg^2) and total heritabilities (h^2_T) of BW, WW and ADG.

Model	Parameters						h^2_T
	σ^2_a	σ^2_m	σ_{am}	σ^2_c	σ^2_e	σ^2_p	
Birth weight							
Model 1	15.03				10.41	25.44	0.59
Model 2	5.79			3.49	13.89	23.17	0.25
Model 3	2.40	3.37	1.24		15.70	22.71	0.26
Model 4	2.57	2.37	1.02	1.25	15.47	22.68	0.23
Weaning weight							
Model 1	346.64				331.10	677.74	0.51
Model 2	114.24			137.84	376.81	628.89	0.18
Model 3	114.93	158.95	-29.27		389.09	633.70	0.26
Model 4	119.18	21.61	-12.58	128.31	372.65	629.17	0.18
Average daily gain							
Model 1	0.007				0.007	0.014	0.48
Model 2	0.002			0.003	0.008	0.013	0.15
Model 3	0.002	0.003	0.000		0.009	0.014	0.25
Model 4	0.002	0.000	0.000	0.003	0.008	0.013	0.15

The direct heritabilities (h^2_a) were high under Model 1, while they were low to medium under the alternative models (Table 2.6). The exclusion of the maternal effects most likely inflated h^2_a for all traits. The results of Model 1 that yielded high heritabilities in this study agree with Mackinnon *et al.* (1991) who reported a h^2_a of 0.78 (BW), 0.56 (WW) and 0.50 (ADG) in tropical cattle when fitting a model accounting for direct genetic effects only. Schoeman & Jordaan (1999) found a h^2_a of 0.62 for BW and a 0.52 for WW in the same multibreed beef cattle herd but using a different subset of the data and fitting a multitrait animal model, which accounted for direct effects only. The direct heritabilities estimated for each trait from Models 2, 3 and 4 were low. When the maternal effects were included in the models, the values varied from low (0.10 for BW; Model 3) to medium (0.25 for BW; Model 2). The present estimates of h^2_a for BW and WW were lower than the unweighted means reported by Koots *et al.* (1994a) for BW (0.35) and WW (0.27) when Models 2, 3 and 4 were fitted. All h^2_a values of this analysis appeared to be in agreement with those of the corresponding estimates of the unitrait analysis.

The direct genetic correlations (r_g) as shown in Table 2.6, varied from 0.37 to 0.76 for the traits, indicating a medium to high genetic association between them. The correlation between the direct genetic components of BW and WW were larger than BW and ADG under all the models. The correlations between WW and ADG for the different models were almost unity. Although the correlations between the traits were positive, differences in estimates among the models were observed for all traits. As indicated by Meyer (1992b), the difference in estimates between the different models may be related to the inclusion of environmental covariances or possible negative sampling correlations and large sampling errors. Mackinnon *et al.* (1991) reported direct genetic correlations between BW and WW, BW and ADG, and WW and ADG of 0.43, 0.24 and 0.94, respectively. Likewise, Koots *et al.* (1994b) reported mean positive genetic correlations between BW and WW (0.50) and BW and ADG (0.26). The results of this study together with literature results suggested that selection for higher WW or ADG would increase BW, which may be associated with dystocia and loss of productivity. For such genetic relationships other selection criteria should be sought when the objective is to increase WW without an adverse effect of BW in this herd. For example, Schoeman & Jordaan (1999) suggested an index or cow efficiency as the best appropriate selection criteria when the aim is to improve WW without a corresponding increase in BW.

Maternal heritabilities (h^2_m) varied from 0.02 in Model 4 to 0.26 in Model 3 (Table 2.6). The inclusion of the maternal environmental effect (c^2) in Model 4 thus reduced the h^2_m estimates for all traits compared to Model 3. In the study of Schoeman & Jordaan (1999), the inclusion of c^2 had almost no effect on h^2_m estimates of pre-weaning related traits, except for pre-weaning relative growth rate. These estimates are in agreement with the results of Mostert *et al.* (1998) who found a h^2_m of 0.06 to 0.15 for BW and 0.08 to 0.19 for WW fitting a multitrait model accounting for both direct and maternal effects in five beef cattle breeds in South Africa. Koots *et al.* (1994a) reported a weighted mean of 0.14 for BW and 0.13 for WW.

Maternal genetic correlations as indicated in Table 2.6, were positive, ranging from a low of 0.04 between maternal components of BW and ADG to a high of 0.99 between WW and ADG. Apart from the correlation between WW and ADG, others were lower than the corresponding direct genetic correlations. Generally, the maternal genetic component of one trait is positively correlated with the maternal components of another trait. The correlation between BW and WW obtained from Model 4 is in agreement with those of Swalve (1993) who estimated maternal correlations ranging from 0.30 to 0.83 in the Australian Simmentaler beef cattle. The value of Model 3 was somewhat lower than the weighted mean literature value of 0.39 between BW and WW (Koots *et al.*, 1994b), but agree with the value from Model 4. The correlation between maternal effects for BW and WW obtained by Rust *et al.* (1998) was 0.24 for the Simmentaler cattle population in South Africa. Hence, differences in values estimated among the models, all the genetic correlations of the maternal components indicated the existence of positive relationships between the traits.

The permanent maternal environmental effect (c^2) varies slightly between Models 2 and 4 for BW, but was almost similar for WW and ADG (Table 2.6). For BW (Model 4), h^2_m tended to be slightly higher than c^2 . This is in agreement with previous findings, *e.g.* Meyer (1992a, 1993b) for Hereford and Angus Australian beef cattle and Swalve (1993) for Simmentaler. Maternal heritabilities were lower than c^2 for WW and ADG (Model 4). The results obtained for WW correspond with the estimates of Meyer *et al.* (1993c), Waldron *et al.* (1993) and Tosh *et al.* (1999) but varied from the reports of Bertrand & Benyshek (1987), Swalve (1993) and Schoeman & Jordaan (1999). Estimates of c^2 have tended to be

higher in most studies using field data, like in this study. For instance, in Polled Hereford and Charolais field data Meyer (1993a; b) estimated c^2 for WW from an animal model to be 0.22 and 0.23, whereas h^2_m estimates were 0.10 and 0.04, respectively. The maternal permanent environmental effect plays an important role in the preweaning growth traits of this beef cattle population. As described earlier, the relatively high c^2 estimates could be a reflection of the permanent maternal effect due to large differences caused by young heifers calving for the first time.

Table 2.6: Estimates of direct (left, on diagonal) and maternal (right, on diagonal) heritabilities and c^2 (right, on diagonal in bracket), direct genetic correlations (left, above diagonal), maternal genetic correlations (right, above diagonal) from multitrait analyses of BW, WW and ADG fitting different animal models.

	Direct components			Maternal components			
	BW	WW	ADG	BW	WW	ADG	
BW							
Model 1	0.59	0.55	0.37				
Model 2	0.25	0.76	0.58	(0.15)*			
Model 3	0.10	0.69	0.49	0.14	0.17	0.04	
Model 4	0.11	0.69	0.48	0.10	(0.05)	0.41	0.22
WW							
Model 1		0.51	0.97				
Model 2		0.18	0.96		(0.22)		
Model 3		0.19	0.96		0.26	0.99	
Model 4		0.19	0.95		0.04	(0.21)	0.98
ADG							
Model 1			0.48				
Model 2			0.15			(0.22)	
Model 3			0.14			0.21	
Model 4			0.15			0.02	(0.23)

* (), permanent maternal environmental effect ($c^2 = \sigma^2_e / \sigma^2_p$)

The genetic correlation between the direct and maternal effects and cross-correlations among traits are presented in Table 2.7. The direct and maternal correlations (r_{am}) were also (when fitting both Models 3 and 4) positive for BW but negative for WW and ADG. As compared to the univariate analysis, the multivariate analysis yielded lower positive (BW) and negative (WW and ADG) estimates of the genetic correlations. The direct-maternal correlations for BW were larger than literature reports of Mohiuddin (1993), but correspond with the reports of Trus & Wilton (1988) who reported for Shorthorn a r_{am} of 0.55. The negative r_{am} values estimated for WW are consistent with those reported by Bertrand & Benyshek (1987) and Swalve (1993), but lower negative than the estimates of Mostert *et al.* (1998), Rust *et al.* (1998) Robinson (1996a) and Meyer (1993b) reported for WW.

Table 2.7: Genetic correlations between direct and maternal effects and their cross-correlations for BW, WW and ADG fitting Models 3 and 4.

Trait		Direct genetic		
		BW	WW	ADG
Maternal genetic	BW			
	Model 3	0.44	0.72	0.78
	Model 4	0.42	0.77	0.84
	WW			
	Model 3	-0.12	-0.22	-0.12
	Model 4	-0.23	-0.25	-0.11
	ADG			
	Model 3	-0.15	-0.26	-0.17
	Model 4	-0.35	-0.43	-0.23

In Table 2.7 the off-diagonal components of the direct-maternal correlation matrix, which are the correlations between the direct effect of one trait and the maternal effect of other trait or *vice versa* (cross-correlation) are shown. The estimate of the correlation between the direct effect of BW and maternal effect of WW (Model 3) agreed well with the average literature estimate of -0.12 (Koots *et al.*, 1994b). The estimate from Model 4 was somewhat higher than this average, but lie within the -0.20 to -0.58 values estimated by Mostert *et al.* (1998). On the other hand, the correlation between the maternal effect of BW

and the direct effect of WW was large positive (Model 3 =0.72, Model 4 =0.77) compared to the average value of -0.05 reported by Koots *et al.* (1994b). Likewise, the direct effect of BW was negatively correlated with the maternal effect of ADG while the maternal effect of BW was positively correlated with the direct effect of ADG. The reason for this difference is not obvious. The correlation between direct or maternal effects for WW and maternal or direct effects for ADG were both negative. Selection for direct breeding values of WW would thus increase maternal breeding values of BW, while selection for increased maternal breeding values of WW and ADG would decrease direct breeding values for BW.

2.4 CONCLUSION

Models for analysing genetic parameters of early growth traits need to include permanent maternal effect. Estimates of heritabilities from a simple animal model tend to be larger than in most comparable studies, although large genetic variation in this multibreed herd may be a reason for fairly high heritabilities. Direct heritabilities from models included maternal genetic and/or permanent environmental effects tend to be lower and most likely less biased. The magnitude of heritability estimates indicated that opportunity exists to improve these traits through selection. Maternal environmental effects were considerably more important than maternal genetic effects for weaning weight and average daily gain.

Estimates of correlations between direct and maternal genetic effects varied between univariate and multivariate analyses. Positive estimates obtained for BW is unexpected and were larger than values in many literature reports. WW and ADG were negatively associated for direct and maternal genetic components. These large negative r_{am} estimates could be effected by unknown differences in management practices not taken into account in the analysis. Possible reasons for the high positive r_{am} for BW as well as the permanent maternal environmental effects in this multibreed cattle may need further investigation. Moreover, other traits of importance as alternative selection criteria such as cow efficiency and carcass traits should also be evaluated in further analyses. Although multivariate animal model analyses are computationally demanding, it is the most appropriate way of estimating (co)variance components and genetic parameters of growth traits.

CHAPTER 3

THE EFFECT OF SIRE BREED, PUREBRED AND CROSSBRED DAMS ON PREWEANING GROWTH TRAITS OF CALVES.

3.1 INTRODUCTION

Crossbreeding has been widely proposed for genetic improvement under different production conditions. This approach in beef production, particularly in the commercial herd in South Africa, has become widely accepted by producers as a means of improving productivity (Harwin, 1989). It involves combining of two or more breeds selected for their economic benefit to optimize simultaneously the use of both non-additive (heterosis) and additive (breed difference) effects. Effective exploitation of these effects requires understanding and evaluation of beef cattle breeds to be used for crossbreeding systems. The important questions regarding beef production in the future are not whether or not crossbreeding will be employed, but rather what breeds should be used in different crossbreeding systems in different feed and production situations (Long, 1980; Harwin, 1989; Bourdon, 2000).

Birth and weaning weights are economically important traits in commercial beef cattle production. Evaluation of factors influencing these traits in a diversity of environmental conditions is important to design well-planned crossbreeding systems aimed at maximizing productivity of the herd. The type of both sire and dam breed clearly determine the performance of their progeny, although the environment is also very important. The utilization of some of the large sire breeds in crossbreeding is associated with increased dystocia due to high birth weights of calves and a subsequent reduction in productivity (Brinks *et al.*, 1973; Laster *et al.*, 1973; Long & Gregory, 1974; Smith *et al.*, 1976). This problem has received a lot of attention in the beef cattle industries. Breed types also have a pronounced influence on weaning weights of their progeny. For example, Harwin (1989) indicated that the weaning weight of a calf is approximately two-third the result of milking ability of the dam and one-third the result of the inherent growth potential of the calf. This confirms that the maternal contribution to the performances of the progeny is considerably

large, and breeders should take into account the milk production and milking abilities of the dams in planning crossbreeding systems. Various results from different countries have demonstrated the potential benefit in increasing milk production and production from crossbred cows (Thorpe & Cruickshank, 1981; Light *et al.*, 1982).

Commercial beef cattle producers need information concerning the productive potential and means of efficient utilization of breeds or breed genotypes under various environmental conditions, because the performances of individual breeds or breed combinations are not expected to be the same under all environments owing to genotype-environmental interactions. Thus, the relative performances of breeds and breed combinations should be evaluated in various environmental and management conditions. The purpose of this study was to evaluate the influences of crossbred dams and sire breed on birth and weaning weights of calves under intensive beef cattle production conditions.

3.2 MATERIALS AND METHODS

Data were obtained from a multibreed beef cattle herd of the Johannesburg Metropolitan Council farms (the Northern farm and the Olifantsvlei farm). More detail of the project was given in Chapter 2.

Hereford and Charolais sires were mated to purebred and crossbred dams and the crossbreeding systems implemented were two-breed and three-breed terminal and rotational crossbreeding systems. Semen of both sire breeds were used across the two farms to artificially inseminate the females. The number of sires used was 40 with an average of 63.4 calves per sire, of these 28 were Charolais and 12 were Hereford.

The dam genotypes used in the analysis included Angus (A), Hereford (H), Bonsmara (B), two-breed crosses of equal proportions, Angus x Charolais (AC), Hereford x Angus (HA), Charolais x Bonsmara (CB), Hereford x Bonsmara (HB), Hereford x Charolais (HC), backcross cows of Hereford x Angus (HA), Hereford x Charolais (HC) and three-breed crosses of Charolais x (Angus x Hereford) (CAH). Twelve dam genotypes (three purebred and nine crossbreed) were available. Dam ages ranged between 2 to 17 years old, and were categorized into four age groups. Closer ages having a similar birth and weaning weights

were pooled together as was described in the previous chapter. The average age of dams was 6.8 ± 2.86 years. The data consisted of 2535 birth and weaning weight records collected from 1968 to 1982. The number of dams used was 1162 with an average of 2.20 calves per dam. Heifers were first inseminated so as to calf for the first time at approximately two years of age. The farms purchased a large percentage of the base cows and data were not adequately recorded so as to allow identification of reciprocal crosses among some of the crossbred cows.

About 70% of the calves were born from June to October while the remaining were born from November to May. As described in Chapter 2 season of birth was recorded as 'winter born' or 'summer born'. Calves represented in each breed of sire and breed genotypes of dam combination are illustrated in Table 3.1. The traits evaluated were birth weight (BW) and weaning weight (WW) of calves.

Table 3.1: Number of observations by breed genotype of sire and dam for BW and WW of calves.

Dam genotype	Sire breed		
	C	H	Total
A	236	155	391
B	187	108	295
H	136	452	588
1/2A1/2C	114	27	141
1/2H1/2A	355	259	614
1/2C1/2B	40	5	45
1/2H1/2B	25	29	54
1/2H1/2C	87	14	101
1/2C1/4A1/4H	159	16	175
3/4C1/8A1/8H	8	41	49
3/4H1/4A	5	50	55
3/4H1/4C	13	14	27
Total	1365	1170	2535

3.2.1 Statistical procedures

Data were analysed using General Linear Model (GLM) procedures of the Statistical Analysis System (1996). The models were fitted according to the step down procedures in which fixed effects and interactions not making a significant ($P > 0.05$) contribution to the variance were excluded from the final analysis. The model included the fixed effects of breed of sire, breed genotype of dam, sex of calf, herd-year-season and dam age. Interactions (sire x HYS for BW and dam x HYS for WW) were ignored from the final analysis because the model was overspecified and unable to estimate least squares means.

The final reduced model was as follow:

$$Y_{ijklm} = \mu + S_i + D_j + X_k + H_l + A_m + e_{ijklm}, \text{ where}$$

Y_{ijklm} = the value of the appropriate trait (BW, WW) under consideration

μ = population mean for the appropriate trait

S_i = effect of the i^{th} breed of sire ($n = 2$)

D_j = effect of the j^{th} breed genotype of dam ($n = 12$)

X_k = effect of the k^{th} sex of calf ($n = 2$)

H_l = effect of the l^{th} herd-year-season ($n = 53$)

A_m = effect of the m^{th} age of dam ($n = 4$)

e_{ijklm} = random residual effects

For WW, weaning age of calf was included as a covariate.

3.3 RESULTS AND DISCUSSION

An analysis of variance for BW and WW are presented in Table 3.2. The environmental effect of herd-year-season, sex of calf, age of dam, all had significant influences ($P < 0.001$) on BW and WW. Weaning age of calves was also significant for WW ($P < 0.001$). This was to be expected and is in accordance to what was found in other studies (McDonald & Turner, 1972; Thrift *et al.*, 1978).

Table 3.2: Analysis of variance for BW and WW of calves.

Source of variation	DF	BW	WW
		F value	F value
Breed of sire	1	368.2***	231.9***
Dam genotype	11	12.5***	12.8***
Sex of calf	1	197.8***	237.0***
Age of dam	3	19.0***	18.9***
Herd-year-season	52	5.2***	11.9***
Weaning age of calves	1		129.1***
Mean		35.5	191.2
SD		4.6	23.7
R ² model (%)		45.9	56.1

*** P<0.001

3.3.1 Breed of sire

The effect of sire breed on BW was a significant ($P<0.001$) source of variation (Table 3.2). Least squares means for BW and WW are presented in Table 3.3. The Charolais sired calves were significantly heavier ($P<0.001$) by 5kg than Hereford sired calves at birth. Charolais sires are known to sire calves of large size at birth compared to *Bos indicus* and some *Bos taurus* breed sires (Laster *et al.*, 1973; Smith *et al.*, 1976; Paterson *et al.*, 1980a). Furthermore, Pahnish *et al.* (1969) reported that the Charolais as breed of sire produced heavier calves at birth than did the Charolais as breed of dams. The incidence of dystocia in Charolais sired calves due to high BW was well recognized by a number of authors in beef cattle investigations (Laster *et al.*, 1973; Smith *et al.*, 1976). To minimize the rate of dystocia sire breed effects on BW should be thoroughly evaluated in the designing of crossbreeding systems. High BW of Charolais sired calves may be largely attributed to the large positive direct additive effect of the Charolais. Positive direct additive effects of Charolais on BW of calves have been reported in several crossbreeding studies (Alenda *et al.*, 1980; Dillard *et al.*, 1980; Newman *et al.*, 1993). For Hereford, the direct additive for BW was positive in some reports (Gregory *et al.*, 1978b; Schoeman *et al.*, 1993), but negative in other crossbreeding studies (Alenda *et al.*, 1980; Skrypzeck *et al.*, 2000a).

Skrypzeck *et al.* (2000b) assessed the contribution of the Hereford breed in the same multibreed beef cattle herd and suggested higher levels of Hereford in crossbreeding for the prevention of dystocia. In another investigation, Hereford sires were also used on heifers to decrease the incidence of dystocia (Tawonzvi *et al.*, 1988).

Table 3.3: Least squares means and standard errors for BW and WW of calves by breed of sire.

Breed of sire	n	BW (kg) \pm SE	WW(kg) \pm SE
Charolais	1365	38.4 \pm 0.26 ^a	197.1 \pm 1.28 ^a
Hereford	1170	33.4 \pm 0.27 ^b	177.5 \pm 1.36 ^b
Mean		35.9 \pm 0.27	187.3 \pm 1.32

^{a, b} Least squares means differ significant at P<0.001.

Weaning weight of calves sired by Charolais was 19.6kg or 11.0% heavier (P<0.001) than those sired by Hereford. Pahnish *et al.* (1969) also evaluated Charolais and Hereford sires and found that calves sired by Charolais sires were 19.3kg heavier than Hereford sired calves. Likewise, Paterson *et al.* (1980a) also found the same magnitude of difference between calves sired by Charolais and Hereford. It is suggested that the superiority of the Charolais in this regard lies in large breed additive effects compared to the Hereford. The additive effects of Charolais were positive for WW in a number of investigations, such as those reported by Alenda *et al.* (1980), Dillard *et al.* (1980) and Olson *et al.* (1993). For Hereford, positive additive effects for WW of calves were also reported by Schoeman *et al.* (1993), while negative estimates of breed additive effects were also evident in some other investigations (Gregory *et al.*, 1978b; Alenda *et al.*, 1980; MacNeil *et al.*, 1982; Skrypzeck *et al.*, 2000a).

The non-additive genetic effects resulted from crossing of different breeds are substantially larger in WW than BW depending on the breeds used and the crossbreeding systems implemented (Dillard *et al.*, 1980). Individual heterosis effects derived from crossing of Hereford sires to Afrikaner and Simmentaler dams were positive in the reports of Schoeman *et al.* (1993) and Skrypzeck *et al.* (2000a). Dillard *et al.* (1980) predicted

negative direct heterosis of -2.5% and -3% when Charolais sires were mated to Hereford and Angus dams, respectively. However, when Hereford and Angus sires were crossed to Charolais dams, the resulting heterotic effects were large positive.

The inclusion of Charolais genes in crossbreeding of Angus, Hereford and Bonsmara boost the performances of WW of calves that may also be associated with the improvement of milking abilities of the crossbred dams. Using the Hereford as breed of sire in a well planned systematic crossbreeding seems more advantageous than its use as dam breed. This suggestion was also supported by Alenda *et al.* (1980) and Long & Gregory (1974) who reported Hereford sires excel Hereford dams in WW of crosses.

3.3.2 Dam genotypes

The effect of dam genotype on BW and WW of calves was a significant ($P < 0.001$) source of variation (Table 3.2). Least squares means for BW and WW of calves by dam genotype are presented in Table 3.4. At birth, the progeny of purebred Angus dams were significantly ($P < 0.05$) smaller than those of Hereford, Bonsmara and crossbred dams. Calves from Hereford and Bonsmara dams and their crosses ($1/2H1/2B$) did not differ significantly ($P > 0.05$). Differences in BW of calves were observed between Bonsmara and Bonsmara-Charolais crossbred dams ($P < 0.05$). Among the crossbred cows, the $1/2A1/2H$ produced the lowest BW while the three-breed cross $3/4C1/8A1/8H$ dams produced the highest BW ($P < 0.05$). There was a tendency for Charolais crossbred cows to produce calves of heavier BW than other crossbred and purebred dams. Another noticeable feature in this study was the non-significant differences in BW of calves from $1/2C1/2H$, $1/2C1/2A$ and $1/2C1/2B$ dams, but these crossbred cows had calves with significantly ($P < 0.05$) heavier BW than those of Hereford, Angus and Bonsmara dams. It was also indicated by Dillard *et al.* (1980) that when Charolais is the breed of dam, heterosis values are larger than when Charolais is the breed of sire for BW and WW.

In general, the absence of significant differences in BW of calves for the majority of the crossbred dams may confirm the investigations of MacDonald & Turner (1972), Alenda *et al.* (1980) and McElhenney *et al.* (1986), that the influence of maternal heterosis on BW is either non-existing or negligible. The maternal effect of Charolais on BW was negative in

the studies of Alenda *et al.* (1980). Likewise, the maternal effects of Hereford were also reported to be negative in the investigations of Gregory *et al.* (1978b) and Skrypzeck *et al.* (2000a). The Angus maternal effect estimated for BW by Gregory *et al.* (1978b) was negative while it was positive in the studies reported by Dillard *et al.* (1980).

Table 3.4: Least squares means and standard errors for BW and WW of calves by genotype of dam.

Dam genotype	n	BW(kg) ±SE	WW(kg) ±SE
Angus	391	32.7±0.35 ^a	175.2±1.77 ^a
Bonsmara	295	35.0±0.37 ^{cd}	186.9±1.84 ^d
Hereford	588	34.6±0.30 ^c	176.2±1.51 ^a
1/2A1/2C	141	37.6±0.45 ^f	193.8±2.20 ^e
1/2H1/2A	614	33.9±0.31 ^b	179.7±1.50 ^b
1/2C1/2B	45	37.7±0.75 ^{fg}	196.7±3.75 ^{ef}
1/2H1/2B	54	34.7±0.68 ^{bcd}	189.5±3.38 ^{de}
1/2H1/2C	101	36.6±0.51 ^{ef}	187.7±2.54 ^d
1/2C1/4A1/4H	175	35.9±0.44 ^{de}	185.2±2.20 ^{cd}
3/4C1/8A1/8H	49	38.3±0.76 ^f	205.7±3.76 ^f
3/4H1/4A	55	35.9±0.68 ^{cdeg}	177.8±3.38 ^{abc}
3/4H1/4C	27	37.1±0.94 ^{ef}	193.3±4.68 ^{de}

Least squares means with at least one common superscript, do not differ significantly at $P>0.05$.

Bonsmara dams weaned heavier ($P<0.05$) calves than either Hereford or Angus dams. Calves of crossbred dams were on average 5.7% heavier at weaning than calves of purebred dams. Amongst the crossbred dams, those with high Charolais proportions (1/2C1/2B and 3/4C1/8A1/8H) weaned the heaviest calves. Among the dams evaluated for WW, Angus and Hereford dams produced the lowest WW. Dams of 1/2A1/2H produced slightly heavier ($P<0.05$) calves than the parent breeds, while higher level of Hereford (3/4H1/4A) in backcross dams did not differ from the parent breeds. Among the two-breed crosses involving Charolais, the 1/2C1/2A and 1/2C1/2B were superior to the 1/2C1/2H dams. Even though reciprocal crosses and some backcrosses were not available, it is possible to hypothesize on the maternal heterosis of WW from the observed means. The difference

between mid-parent value and observed mean is calculated to be 4kg for the 1/A1/2H crosses. Likewise, the difference between mid-parent value and 1/2B1/2H value was 8kg. The crosses were thus able to sustain WW of calves above the mid-parent value of the respective purebreds. Therefore, maternal heterosis exists and validates the value of the crossbred dams in producing heavier WW.

In almost all comparable studies, the direct maternal effects of Hereford for WW were strongly negative (Alenda *et al.*, 1980; Schoeman *et al.*, 1993; Skrypzeck *et al.*, 2000a). This large negative Hereford maternal effect considerably overrides the positive breed additive effect of the Hereford (Schoeman *et al.*, 1993). The lower WW attained by calves of the Angus and Hereford dams compared to others dams, probably substantiate the conclusion of Dillard *et al.* (1980) that Angus and Hereford dams do not provide enough milk and maternal ability to maximize growth in Charolais crossbred calves. Jenkins & Ferrel (1992) also reported low milk producing ability of Hereford compared to Angus and Charolais cows. The Hereford and the majority of Hereford crossbred dams noticeably produced lower WW of calves in this study and also in other studies.

3.4 CONCLUSION

Differences between Charolais and Hereford sires mated to the same dam genotypes may reflect difference in direct additive effects and individual heterosis effects exhibited in the crossbred calves. The Charolais sired calves excelled Hereford sired calves both in birth weight and weaning weight. In the light of this study the choice of sire breed should be made to complement those characteristics that are weak in other breeds by additive means and through exploitation of heterosis.

The performance of crossbred dams are encouraging, and with understanding of their better performance as crossbreds, use of crossbred dams is advocated depending on effective breed combination to utilize additive and non-additive genetic effects. In several investigations the maternal effects of Hereford were largely negative, hence, high levels of Hereford in composite or crossbred dams do not seem to be of any advantage in this herd.

However, inclusion of Charolais genes in these crossbreeding programmes improved the performances of crossbred cows.

CHAPTER 4

THE CONTRIBUTION OF CHAROLAIS AND ANGUS BREEDING LEVEL ON THE PERFORMANCE OF PREWEANING GROWTH TRAITS

4.1 INTRODUCTION

The large varieties of beef cattle breeds of the world differ in performance traits. This suggests a great possibility of creating certain breed combinations to increase productivity and efficiency. The breed differences arise partly from selection for differing objectives or under different environments and partly from cumulative random changes in gene frequency (Hill, 1984). Dickerson (1969) described in the theoretical considerations of crossbreeding that breed differences are important sources of genetic improvement. This could be achieved through grading up to superior breeds, heterosis generation (systematic crossbreeding) and the development of composite breeds. Crossbreeding systems such as terminal crossing usually require the respective purebred populations to be maintained. An alternative approach is the formation of a multibreed composite population. Combining different breeds into one population provides an excellent opportunity to exploit the advantage of the contributing breeds (Lin, 1996).

A composite breed represents a population made up of two or more component breeds and designed to benefit from hybrid vigour and breed complementarity. They are expected to be bred to their own kind, to retain a level of heterosis normally associated with traditional crossbreeding systems, but without continues crossbreeding. It is expected that they would be better than the parent breeds for composite traits in performances, but intermediate for some individual contributing traits, and showed greater genetic variability (Gregory & Cundiff, 1980; Alenda & Martin, 1981). Additionally, developing synthetic breeds provide more consistency in production compared to traditional crossbreeding systems, producers have the potential to produce their own replacement herd and overcome some of the major problems encountered in conventional crossbreeding (Gregory & Cundiff, 1980; Schoeman & Jordaan, 1999; Bourdon, 2000).

The proportion of individual breeds going into a composite is the critical step in composite breed formation and may be well determined whether a composite breed succeeds or fails. Each breed should be therefore evaluated with respect to its contribution with other breeds for the desired traits under specific production environments. The objective of this study was to evaluate the contribution of Angus and Charolais in a cross cattle population, to estimate (co)variance components and to determine the optimum breeding levels of the two breeds for early growth traits in this multibreed beef cattle population.

4.2 MATERIALS AND METHODS

Data were obtained from multibreed beef calves of the Johannesburg Metropolitan Council collected during the period of 1968 to 1992. The beef herd is kept on two different farms (Olifantsvlei farm and Northern farm) on an intensive management system. These farms form part of the wastewater management scheme of the greater Johannesburg Metropolitan Council. Breeding systems, animals management, recording and selection procedures of the herd were described more in detail in Chapter 2.

After editing the data, 4119 records were available and were included in the analyses. The records included birth weight (BW), weaning weight (WW) and pre-weaning average daily weight gain (ADG). The number of sires used was 73, with an average of 56.4 calves per sire, which varied between 1 and 347 calves per sire. The number of dams used was 1973 with an average of 2.1 calves per dam, which varied between 1 to 8 calves per dam.

Animals with varying contributions of Angus, Bonsmara, Charolais and Hereford were included in the investigation. The contribution of Angus and Charolais in the composition of individual calves varied from 0 to 75% breeding. The total number of breed combinations, or calf genetic groups in this study was 56. The proportion of each breed in each calf was calculated from the original pedigrees. The number of calf genetic groups with different proportion of Angus and Charolais were 8 and 7, respectively. Linear regressions were fitted for Angus and Charolais only, ignoring the varying contribution of

Hereford and Bonsmara. The total number of calves considered in relation to the proportions of the breeds is presented in Table 4.1.

Table 4.1: Number of calves born in relation to the proportion of Angus and Charolais.

Breed	Breed proportion (%)								
	0	6.25	9.4	12.5	25	37.5	50	62.5	75
Angus	1407	692	13	577	934	16	457	0	23
Charolais	1462	0	0	219	218	249	1138	13	820

4.2.1 Statistical procedures

The data were initially analysed using the GLM procedures of Statistical Analysis Systems (SAS) (1996). The models were fitted for several fixed effects according to the step down procedures. All fixed effects and their interactions that had no significant ($P > 0.05$) influence on BW, WW and ADG were excluded from the final genetic analysis. In the final models the following fixed effects were fitted: age of dam, proportion of Angus, proportion of Charolais, sex of calves and herd-year-season, and weaning age of calves as a covariate for WW. The models fitted to each trait are presented in Table 4. 2.

The Restricted Maximum Likelihood (REML) VCE package of Groeneveld (1996, 1997) was used for variance components analyses. Unitrait animal models accounting for direct and maternal additive genetic effects and permanent maternal environmental effects as random effects in addition to the random residual error were fitted.

The basic model in matrix notation comprised the following:

$$\mathbf{Y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{Z}_3\mathbf{c} + \mathbf{e}$$

where \mathbf{Y} = a vector of a calf record for the traits

\mathbf{X} = a known incidence matrix relating the observation to the fixed

effects.

b = a vector of fixed effects.

Z_1, Z_2 and Z_3 = known incidence matrices relating elements of **a**, **m** and **c** to **Y**

a = a random vector of direct additive genetic effects.

m = a random vector of maternal additive genetic effects.

c = a random vector of permanent maternal environmental effects

e = a random vector of residual error.

Table 4.2: Models fitted for statistical analyses of birth weight (BW), weaning weight (WW) and average daily gain (ADG) of calves.

Effects	Type	Number of levels	Traits		
			BW	WW	ADG
Herd-year-season	Fixed	65	X	X	X
Age of dam	Fixed	4	X	X	X
Sex of calf	Fixed	2	X	X	X
Proportion of Angus	Fixed	8	X	X	X
Proportion of Charolais	Fixed	7	X	X	X
Weaning age	Covariate	1		X	
Maternal environment	Random	1973	X	X	X
Maternal	Animal	5740	X	X	X
Animal	Animal	5740	X	X	X

The direct and maternal heritabilities estimated were subsequently used to predict individual breeding values (BLUP) of each calf for BW, WW and ADG. Direct and maternal mean breeding values per genetic group estimated were then regressed on proportion of Angus and Charolais breeds. Likewise, Best Linear Unbiased Estimates (BLUE) of the traits were also calculated for each calf and mean values per genetic group were regressed on proportion of their breeding.

4.3 RESULTS AND DISCUSSION

The mean proportions of Angus and Charolais contribution per year of calf born are presented in Figure 4.1. The mean contribution of Angus steadily declined from 1968 to 1982 due to the use of a small number of Angus sires during the first few years of the crossbreeding programme only. The increased mean contribution of Angus since 1983 was due to the use of some purebred and crossbred sires.

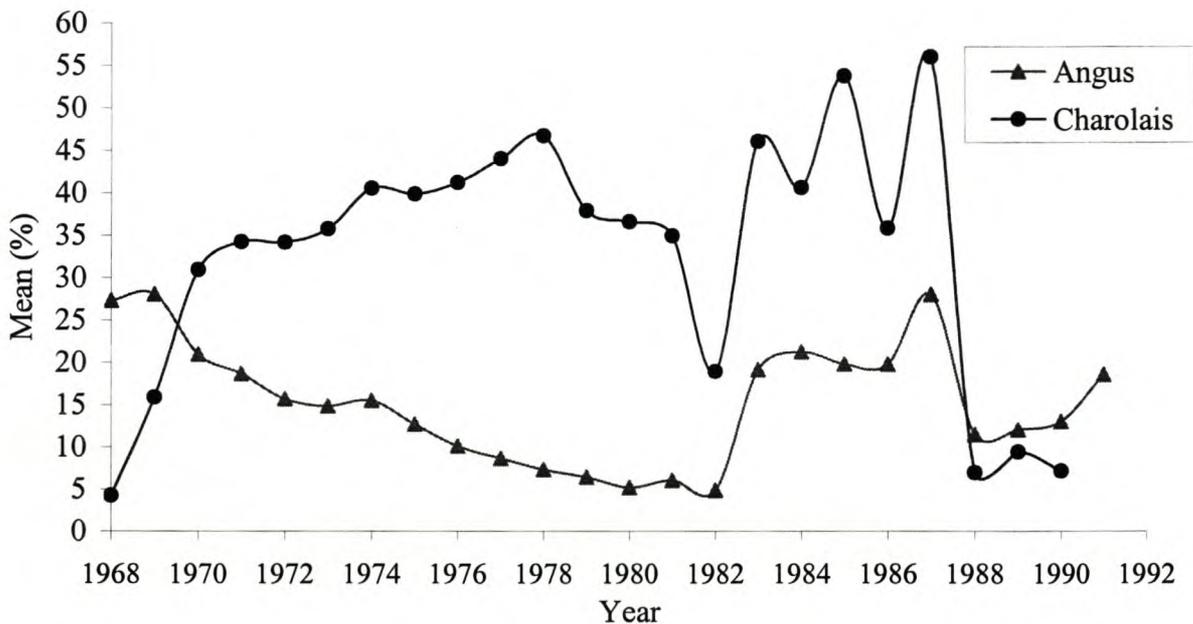


Figure 4.1: Changes in mean Angus and Charolais contribution (%) per year of calves born.

Charolais mean proportion increased from 1968 to 1978, whereafter it declined. The decline in contribution of Charolais since 1978 were caused by two major reasons, firstly due to the termination of the conventional crossbreeding systems and secondly due to the introduction of other breeds to the multibreed herd. On the other hand, the increase in Charolais mean contribution from 1983 to 1987 was due to the use of Charolais crossbred sires and some purebred Charolais sires. After 1987 the mean contribution of both breeds largely decreased.

Changes in variances of Angus and Charolais proportions per year of calves born are presented in Figure 4.2. Variance for Angus gradually declined as the herd became more uniform in composition from 1968 to 1982, but after this period the variance lack consistency. In case of the Charolais, the variance progressively increased until 1977, but decreased thereafter. Variation in Charolais proportion was high in 1984 while it declined rapidly thereafter as the herd become more similar in composition for Charolais. The breed proportion variances were not stable for both breeds. It is obvious that once an optimal combination is obtained and *inter se* mating produces a composite breed, the proportion of Angus and Charolais would be expected to remain constant. However, this point or genetic equilibrium was not reached for both Angus and Charolais.

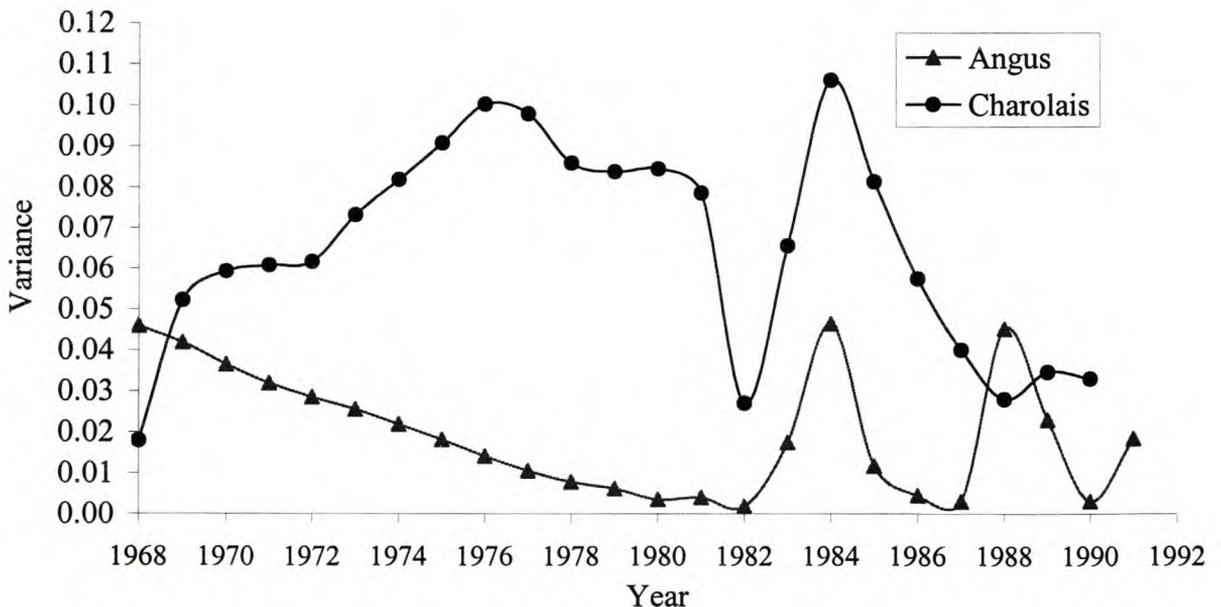


Figure 4.2: Change in variance of Angus and Charolais proportion per year of calves born

Estimates of direct (h^2_a) and maternal (h^2_m) heritabilities and the correlations between direct and maternal effects (r_{am}) and the permanent maternal environmental effects (c^2) for BW, WW and ADG are presented in Table 4.3. The h^2_a estimate for BW was lower compared to those in the literature for various composite beef cattle herds as summarised in Table 4.4. The direct heritability of BW was also lower than literature means (0.30 by Mohiuddin, 1993 and 0.31 by Koots *et al.*, 1994a), but corresponds with the reports of Quaas *et al.* (1985) and Cantet *et al.* (1988). While within the range of literature values (Meyer, 1992a),

direct heritabilities of WW and ADG were lower than reported means (0.24 and 0.29 for WW and ADG, respectively; Koots *et al.*, 1994a). Maternal heritability (h^2_m) estimates of all traits lie within in the range of the estimates in literature summarised in Table 4.4.

Table 4.3: Estimates of direct (h^2_a) and maternal (h^2_m) heritabilities and the correlations between direct and maternal genetic effects (r_{am}) and the permanent maternal environmental effects (c^2) for BW, WW and ADG.

Trait	h^2_a	h^2_m	r_{am}	c^2
BW	0.10	0.10	0.48	0.06
WW	0.20	0.12	-0.58	0.22
ADG	0.15	0.10	-0.72	0.25

Schoeman & Jordaan (1999) and Skrypzeck *et al.* (2000b) reported high heritabilities from a large set of the same data comprising 15 different breeds. These high heritability estimates could arise from large genetic variances due to the multibreed composition of the herd, since the model in their study did not account for this effect. In another investigation Schoeman & Jordaan (2001) found that in both univariate and two-trait analyses there were considerable reductions in heritability estimates in the models where the breed group effects and non-additive breed effects were accounted for. The reason for the lower heritability estimates for BW as compared to others comparable studies may be related to environmentally induced large phenotypic variance estimates of the traits in this study. Variable estimates of heritabilities were also observed in three synthetic lines of beef cattle differing in mature size by Rodriguez-Almeida *et al.* (1995). These results suggest that variable estimates may result from the inclusion of the non-additive genetic (dominance, additive x additive) variances, in which most of the non-additive genetic variance in the traits studied is accounted for by the dominance genetic effect.

Table 4.4: Selected literature estimates for genetic parameters on early growth traits in different composite beef cattle populations.

Country	Model	Parameters				Reference
		h^2_a	h^2_m	r_{am}	c^2	
Birth weight						
Australia	AMM	0.61	0.11	0.01		Mackinnon <i>et al.</i> (1991)
Cameroon	AMM	0.65	0.22	-0.93		Tawah <i>et al.</i> (1993)
USA	AMMPe	0.54	0.11	-0.01	0.03	Rodriguez-Almeida <i>et al.</i> (1995)
Canada	AMMPe	0.51	0.09	0.17	0.02	Tosh <i>et al.</i> (1999)
South Africa	AM	0.62				Schoeman & Jordaan (1999)
South Africa	AMMPe	0.72	0.14	-0.40	0.06	Skrypzeck <i>et al.</i> (2000b)
Australia	AMMPe	0.49	0.05	0.12	0.04	Meyer <i>et al.</i> (1993c)
Weaning weight						
Australia	AMM	0.20	0.32	0.00		Mackinnon <i>et al.</i> (1991)
Cameroon	AMM	0.29	0.27	-0.39		Tawah <i>et al.</i> (1993)
USA	AMMPe	0.29	0.13	0.00	0.04	Rodriguez-Almeida <i>et al.</i> (1995)
Canada	AMMPe	0.33	0.13	-0.11	0.20	Tosh <i>et al.</i> (1999)
South Africa	AMMPe	0.57	0.13	-0.37	0.09	Schoeman & Jordaan (1999)
South Africa	AM	0.54	0.21	-0.65	0.12	Skrypzeck <i>et al.</i> (2000b)
Australia	AMMPe	0.29	0.07	-0.13	0.12	Meyer <i>et al.</i> (1993c)
Average daily gain						
Australia	AMM	0.16	0.31	.000		Mackinnon <i>et al.</i> (1991)

AM, animal model; AMM, animal model including maternal genetic effect; AMMPe, animal model including maternal genetic and permanent environment.

Permanent maternal environmental effects (c^2) were larger than both the direct and maternal heritabilities for WW and ADG, indicating that the maternal environment plays an important role in the expression of these traits. In general, the c^2 estimates were larger than those of Table 4.4 for the traits considered. The reasons for relatively high c^2 were suggested earlier in Chapter 2.

The genetic correlation between direct and maternal genetic effects (r_{am}) for BW (0.48) was positive while it was large negative for both WW (-0.58) and ADG (-0.72). Positive estimates of direct and maternal genetic correlations are also evident in other investigations for BW (Table 4.4). Trus & Wilton (1988), Meyer (1992a) and Waldron *et al.* (1993) also reported variable positive values of the direct-maternal genetic correlation for BW. Average estimates in the literature, as were reported in reviews by Meyer (1992a), Mohiuddin (1993) and Koots *et al.* (1994b) were all negative for BW, WW and ADG. The negative correlations between direct and maternal genetic effects of WW and ADG may be not only due to the true genetic antagonism but also to negative environmental dam-offspring covariances (Baker, 1980), sire x sire interactions (Robinson, 1996b) or selective reporting of data (Mallinckrodt *et al.*, 1995). Such sources of error are more likely in field data, like this study than in data derived under controlled experiments.

The regressions of Best Linear Unbiased Estimates (BLUEs) of BW on proportion of Angus and Charolais are presented in Figures 4.3a-b, respectively. Birth weight decreased with increasing proportion of Angus (Figure 4.3a), while it increased linearly with an increasing proportion of Charolais (Figure 4.3b). Birth weight was exceptionally high at 9.4% (13 calves) proportion of Angus; the contributor breed in addition to Angus was only Hereford. This high value is therefore relative to Hereford and not relative to Charolais. In general, the relatively high BW at lower Angus contributions can be explained by the contribution of Bonsmara, Hereford and particularly Charolais. In the characterisation of beef cattle breeds Schoeman (1996) reported mean BW of 36, 35, 41 and 33kg for Bonsmara, Hereford, Charolais and Angus, respectively. In contrast to Angus, as it is illustrated in Figure 4.3b, Charolais contribution increased BW of calves.

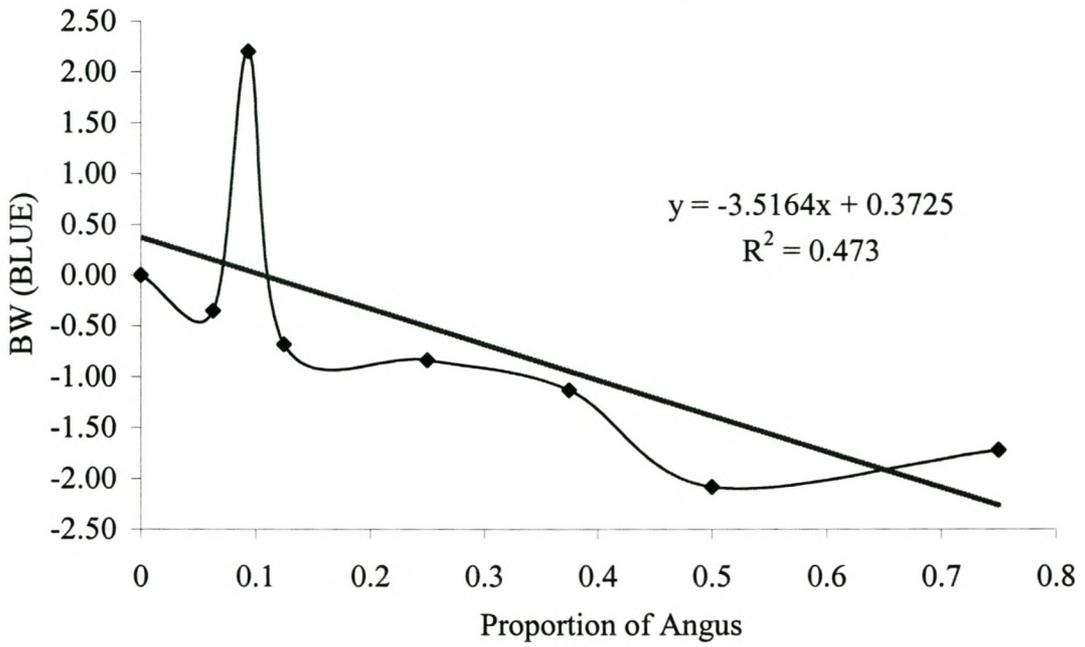


Figure 4.3a Regression of BW (BLUEs) on Angus breed contribution.

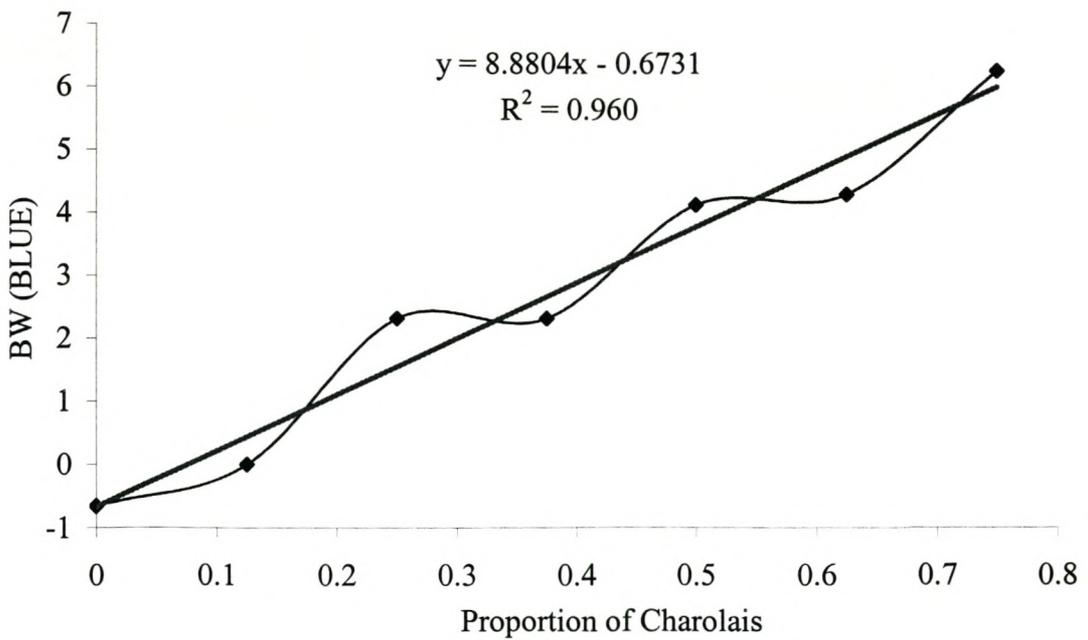


Figure 4.3b Regression of BW (BLUEs) on Charolais breed contribution.

The regressions of direct and maternal breeding values on Angus and Charolais proportions for BW are presented in Figures 4.4a-b and Figures 4.5a-b, respectively. The direct breeding value of BW was positively associated with an increased proportion of Angus breeding (Figure 4.4a). Likewise, the maternal breeding value (Figure 4.4b) also increased with increasing Angus contribution. The high average direct breeding values at 37.5% Angus breeding level may be partly attributed to the contribution of other breeds in the combination. In addition to 37.5% Angus, breeds contributed included Charolais and Hereford with 50% and 12.5% proportions, respectively.

The Charolais direct breeding value (Figure 4.5a) increased and attained maximum breeding value at 35% contribution, after which it declined again. Maternal breeding values (Figure 4.5b) increased with increasing Charolais proportion. The direct breeding value at 75% proportion of Charolais was very low. Though the reason for this is not obvious to explain, this may be indicating the low breeding value of Charolais at higher proportions under these environmental conditions. Of the total calves (4119) considered in this study, only 820 (20%) were of 75% Charolais breeding.

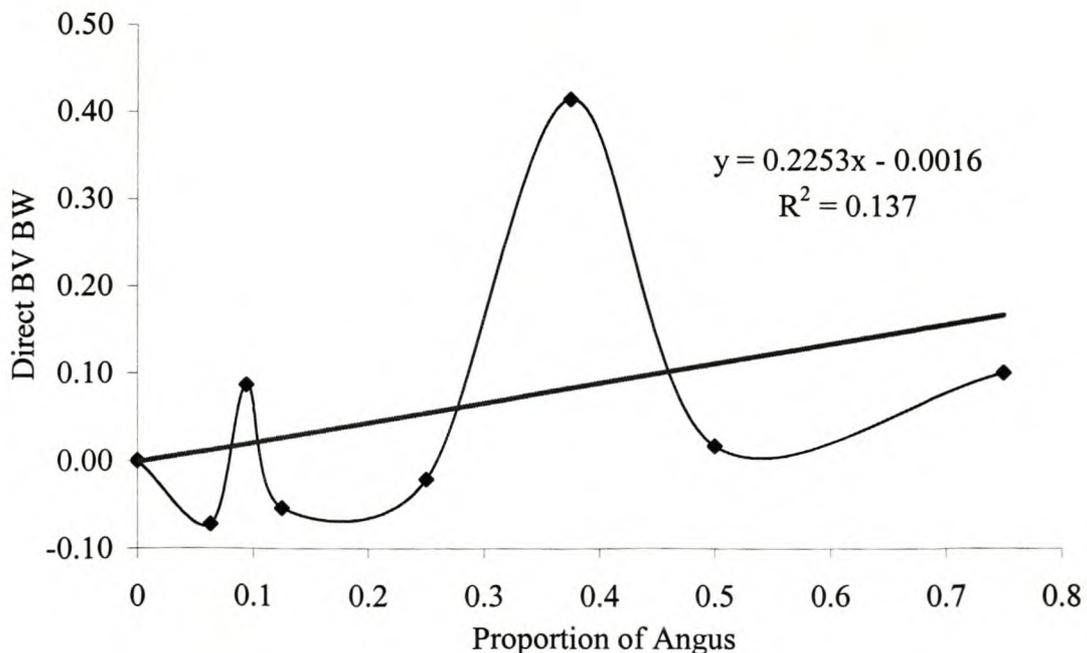


Figure 4.4a Regression of direct breeding value of BW on proportion of Angus breeding.

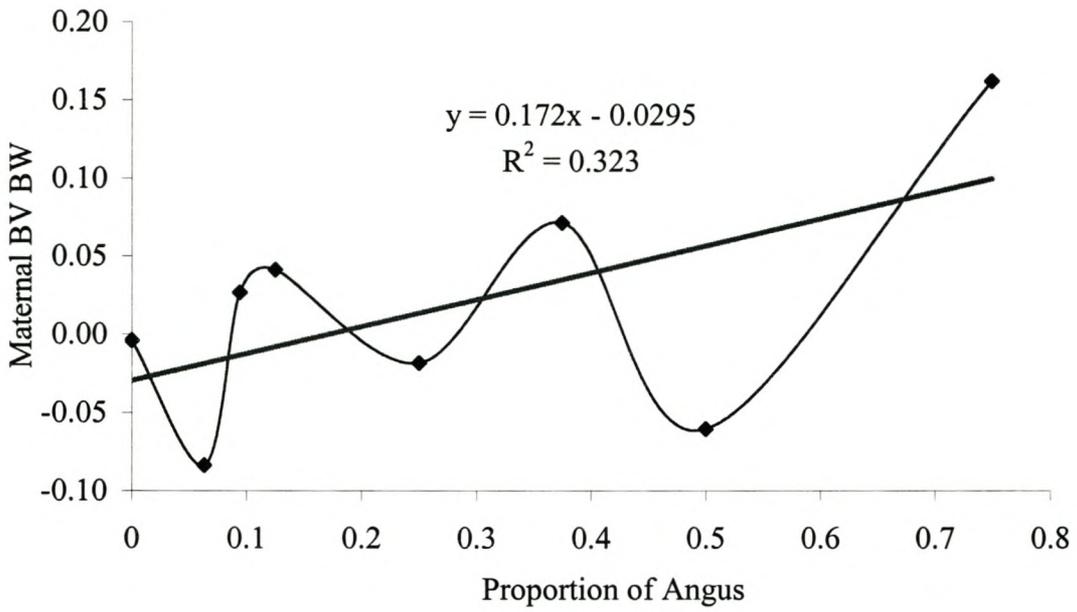


Figure 4.4b Regression of maternal breeding value of BW on proportions of Angus breeding.

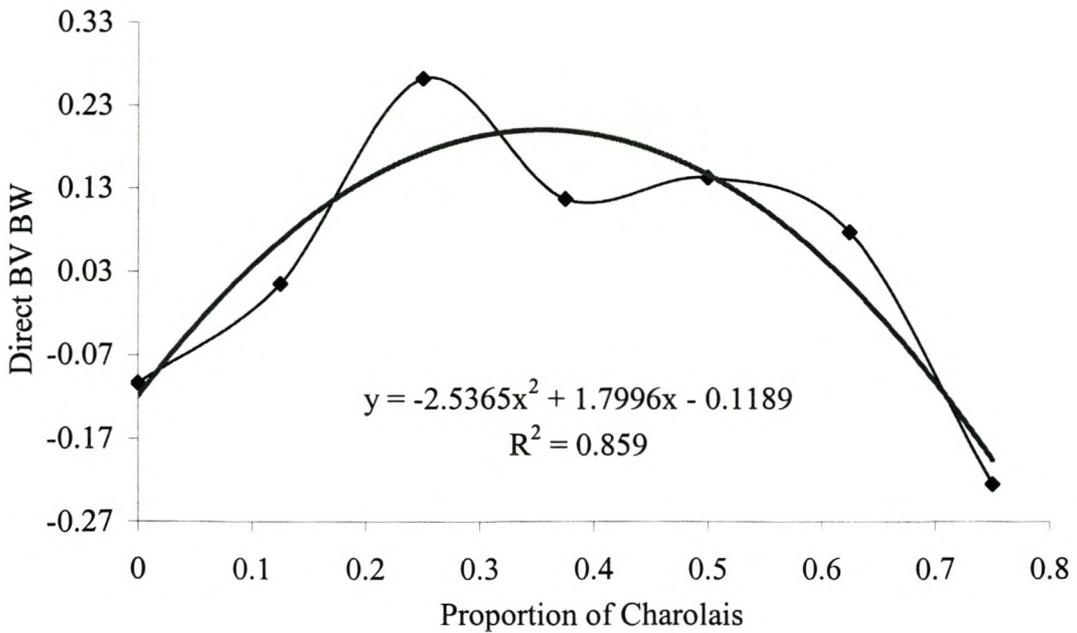


Figure 4.5a Regression of direct breeding value of BW on proportion of Charolais breeding.

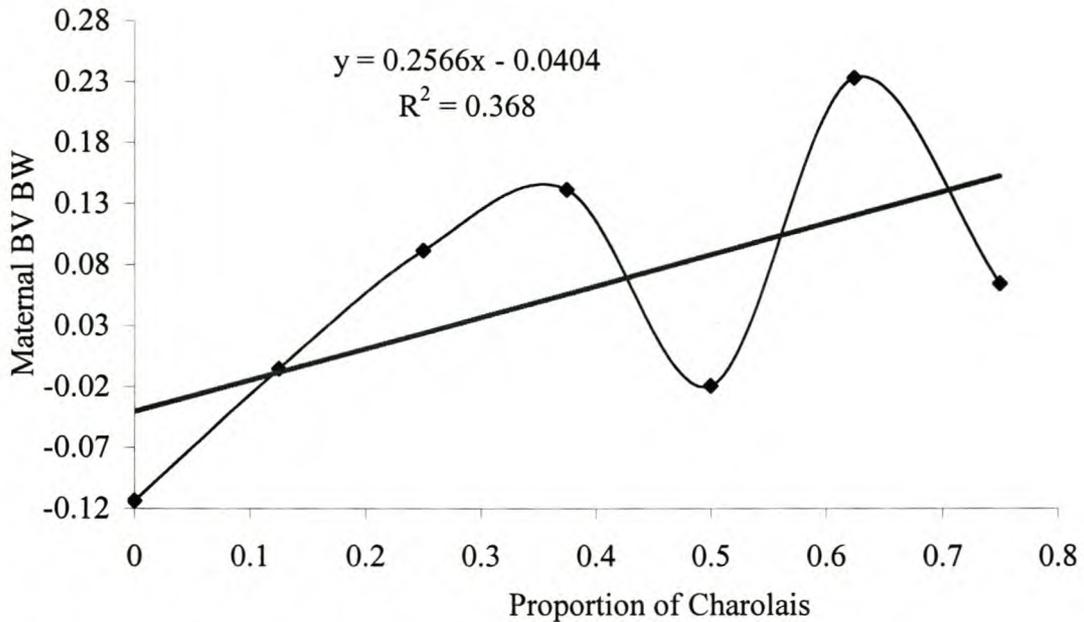


Figure 4.5b Regression of maternal breeding value of BW on proportion of Charolais breeding.

In several beef cattle crossbreeding studies, positive additive direct effects for Charolais were reported (Alenda *et al.*, 1980; Dillard *et al.*, 1980; Newman *et al.*, 1993; Olson *et al.*, 1993), while others reported negative estimates (Cunningham & Magee, 1988). Some investigations reported negative direct effects for Angus (Alenda *et al.*, 1980; Dillard *et al.*, 1980; Cunningham & Magee, 1988) relative to the breeds with which it was compared. The direct or maternal breeding values of the traits predict the genetic potential of an animal, as well as those of its offspring, representing only that part of the genetic value that can be transmitted from parent to offspring. The average BW of Charolais cattle taking part in the National Beef Cattle Performance and Progeny Testing Scheme was the highest compared to other breeds evaluated, with the exception of South Devon (Schoeman, 1996). The results also suggested that breeds such as Charolais with birth weights higher than their predicted value to be inclined to cause more dystocia problems compared to Bonsmara, Angus and Hereford with mean BW lower than their respective predicted values. Smith *et al.* (1976) evaluated sire breeds for calving difficulty and found that calves sired by Charolais and Simmentaler had significantly higher incidences of dystocia compared to Hereford and Angus. In another investigation, Schaeffer & Wilton (1977) evaluated and ranked breed of sires for calving difficulties and the result showed that Angus and Hereford

being easy calving breeds and Simmentaler and Charolais being difficult calving breeds. Notter *et al.* (1978) also reported that breeding values for calving difficulty in Charolais as sire breeds were large compared to Angus.

Positive maternal breed effects were evident in a number of findings for both Charolais and Angus (Dillard *et al.*, 1980; Cunningham & Magee, 1988). The increase in maternal breeding value with increasing gene proportions of both breeds may reflect the potential of the Angus and Charolais dams not to restrict growth of the fetus by way of specific physiological mechanisms in their uterine environment. In synthetic herds of beef cattle, in the light of this study, Charolais contribution may be advantageous at intermediate breeding level only. Increasing levels of Angus in crossbreeding or synthetic breed development, however, would decrease the incidence of dystocia.

The regressions of WW (BLUEs) on Angus and Charolais proportions are presented in Figures 4.6a-b, respectively. Performance levels of WW were negatively associated with an increase in Angus breeding levels (Figure 4.6a). In contrast, WW linearly increased with an increase in Charolais proportion (Figure 4.6b).

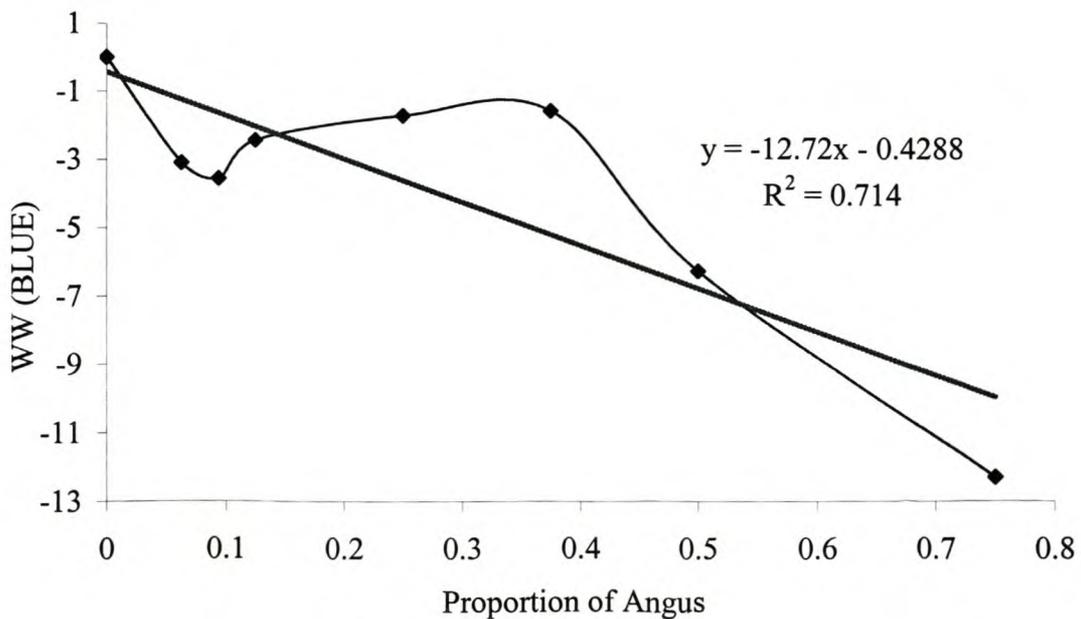


Figure 4.6a Regression of WW (BLUEs) on Angus breed contribution.

The BLUEs of Angus were mostly negative while it was positive for Charolais for BW, WW and ADG. The relatively high WW at lower proportions of Angus largely related to the Charolais contribution, as it is evident in Figure 4.6b. Weaning weights of Angus and Bonsmara were similar while it was lower in the Hereford (Schoeman, 1996). The low WW at lower proportion of Charolais indicated the relatively low potential of the other contributing breeds (Hereford and Bonsmara) used in the combinations.

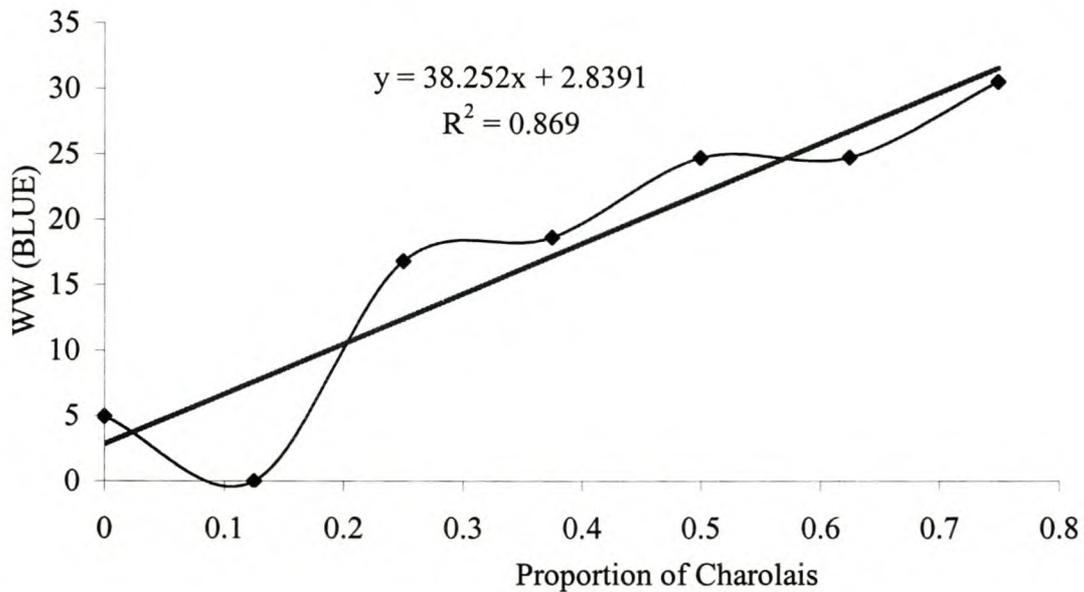


Figure 4.6b Regression of WW (BLUEs) on Charolais breed contribution.

Regressions of direct and maternal breeding values on Angus and Charolais proportions for WW are presented in Figures 4.7a-b and Figures 4.8a-b, respectively. The decline in performance levels of WW as the proportion of Angus increased was in accordance with the decrease of mean direct breeding values (Figure 4.7a), but in contrast with the increasing in maternal breeding values (Figure 4.7b). Generally, the estimated maternal breeding values of WW and ADG were negative for both Angus and Charolais. The contradiction in the direction of change between direct and maternal breeding values for Angus may reflect the possibility of an environmentally induced high negative direct-maternal genetic correlation (Table 4.3).

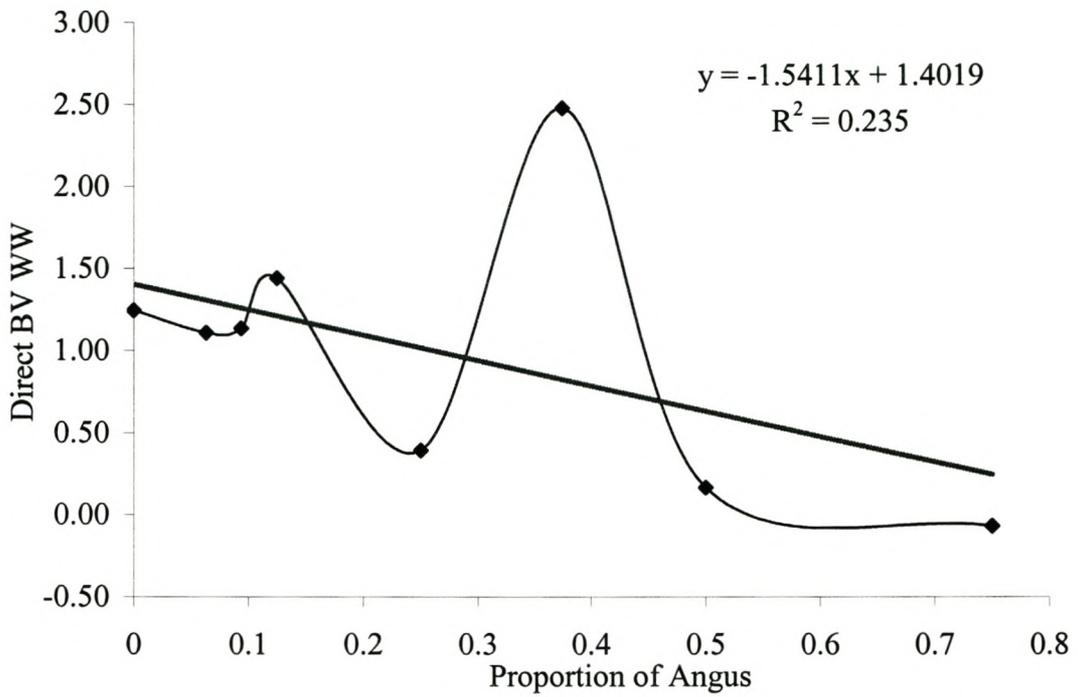


Figure 4.7a Regression of direct breeding value of WW on Angus breeding.

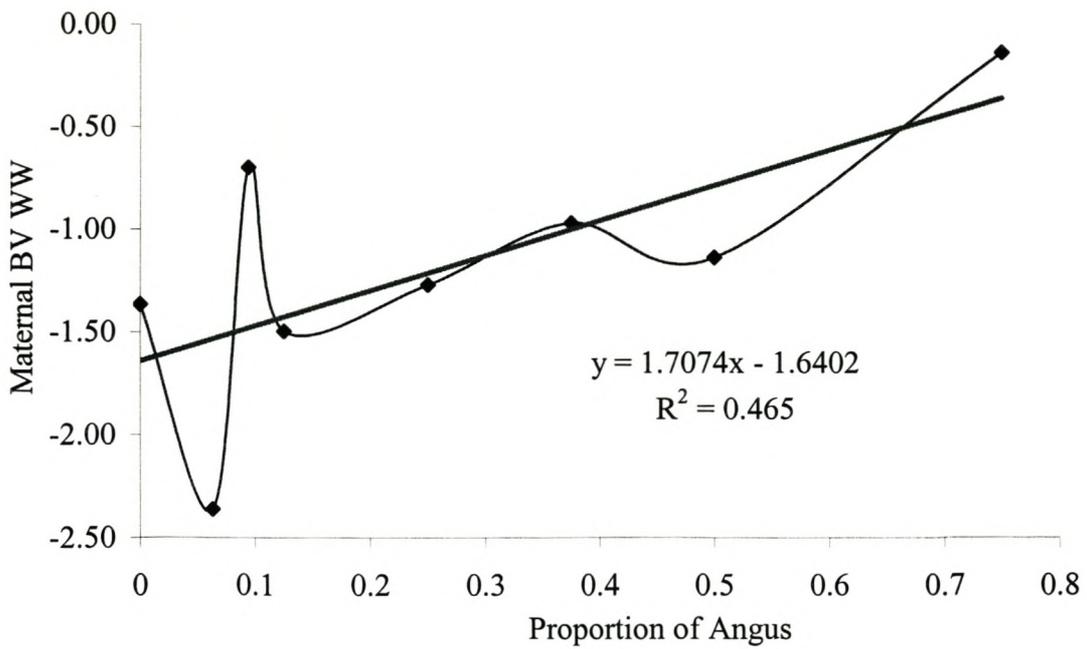


Figure 4.7b Regression of maternal breeding value of WW on Angus breeding.

As indicated in Figure 4.8a the mean direct breeding value increased with increasing Charolais proportion and reached a maximum level at 38% Charolais contribution and declined thereafter. The mean maternal breeding value (Figure 4.8b) of WW was positively associated with an increase in the proportion of Charolais contribution. The reason for the lower direct breeding values of Charolais with greater than 38% proportions may be partly associated with environmental influences, in which performance records were a weak indicator of underlying breeding value at higher levels of Charolais. Both Schoeman *et al.* (2000) and Skrypzeck *et al.* (2000b) in their studies on part of the same dataset underlined the unfavourable environment under which the herd is managed which partly influences the performance of the herd.

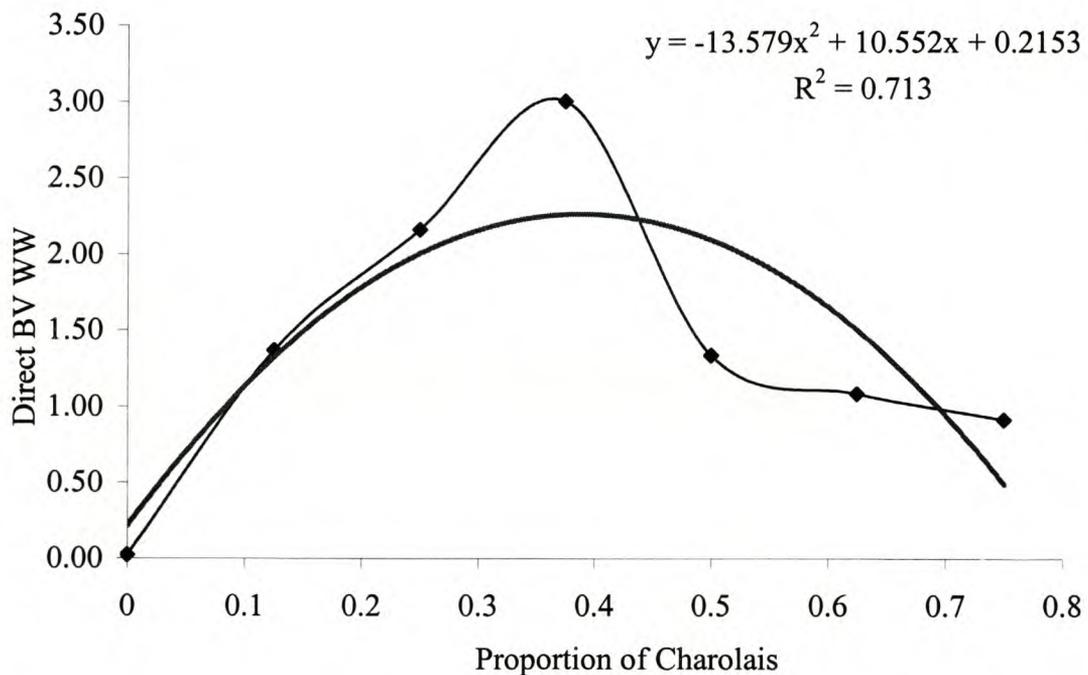


Figure 4.8a Regression of direct breeding value of WW on Charolais breeding.

In several crossbreeding studies, different signs and magnitudes of direct and maternal effects were reported for Angus and Charolais, depending on the breeds with which they compared. Estimates of Charolais direct effects were positive in most studies (Alenda *et al.*, 1980; Dillard *et al.*, 1980; MacNeil *et al.*, 1982; Newman *et al.*, 1993; Olson *et al.*, 1993), while other reported negative estimates (Cunningham & Magee, 1988). The estimates of

direct additive genetic effects of Angus were consistently negative (Alenda *et al.*, 1980; Dillard *et al.*, 1980; MacNeil *et al.*, 1982; Cunningham & Magee, 1988).

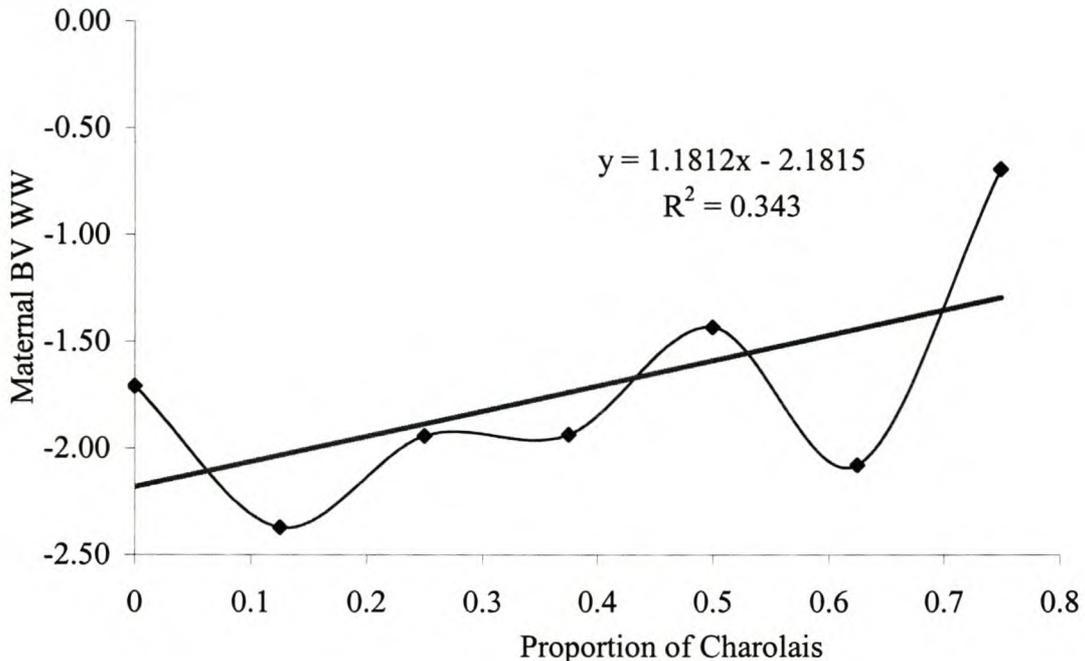


Figure 4.8b Regression of maternal breeding value of WW on Charolais breeding.

The overall results of this study indicated that Charolais and Angus maternal breeding values increased with increasing of their gene proportion in this herd. In this regard, the estimated maternal breeding values of WW obtained from the National Beef Cattle Performance Testing Scheme indicated a large potential of these breeds as maternal lines (Bergh & Gerhard, 1999). This clearly indicates the genetic potential of the two breeds for higher milk production and their maternal abilities to wean heavier calves. In a number of beef cattle studies such as those reported by Alenda *et al.* (1980), Dillard *et al.* (1980) and MacNeil *et al.* (1982) positive maternal effects were revealed for Charolais. Likewise, positive maternal effects for Angus were also more apparent in the literature than negative maternal effects (Dillard *et al.*, 1980; MacNeil *et al.*, 1982; Cunningham & Magee, 1988). Jenkins & Ferrell (1992) reported that Angus produced slightly less milk than Charolais, while Hereford produced considerably less milk than both Charolais and Angus. Weaning weight performance levels and direct breeding values decreased while maternal breeding

value increased with increasing proportions of Angus. The breeding level of Angus that optimises utilisation of its genetic potential in this multibreed herd is not identified in this investigation. For Charolais, the predicted growth potential of animals was maximum at 37.5% Charolais whereafter it declined. It may therefore be suggested that increasing the proportion of Charolais to intermediate levels in a composite herd would tend to optimise the genetic potential of preweaning traits under this environment without an adverse effect on birth weight. Alternatively, in a systematic crossbreeding programme higher proportions of Charolais in dam breeds maximise the utilisation of maternal effects.

Regressions of average daily gain (BLUEs) on Angus and Charolais breeds proportions are presented in Figures 4.9a-b, respectively. The mean ADG increased and reached maximum value at 20% Angus proportion (Figure 4.9a), while it increased linearly with increasing Charolais proportion (Figure 4.9b). The overall trends of mean performance levels of ADG are comparable to WW performances for both breeds. This reflected the high genetic correlation between WW and ADG as were observed in chapter 2.

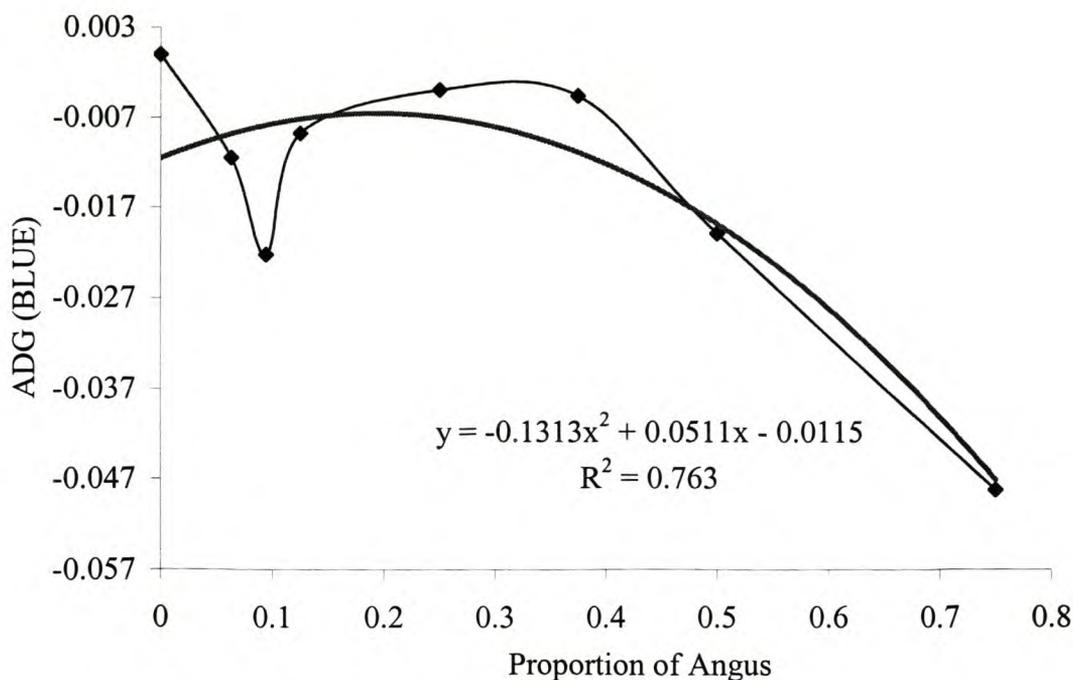


Figure 4.9a Regression of average daily gain (BLUEs) on Angus breed contribution.

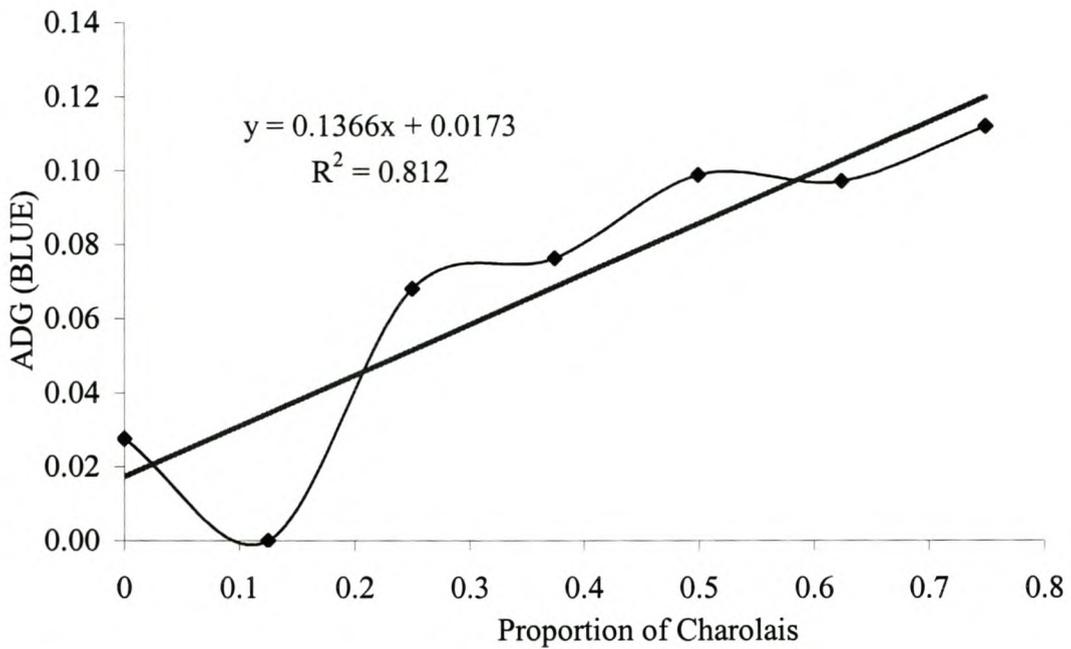


Figure 4.9b Regression of average daily gain (BLUEs) on Charolais breed contribution.

The regression of direct and maternal breeding values of ADG on Angus and Charolais proportions are presented in Figures 4.10a-b and Figures 4.11a-b, respectively. Mean direct breeding values (Figure 4.10a) are negatively associated with increasing proportions of Angus, while mean maternal breeding values are (Figure 4.10b) positively associated with increasing Angus contributions.

Figure 4.11a illustrates that the mean direct breeding value of Charolais increased and attained a maximum value at 45% Charolais contribution, whereafter it declined. The mean maternal breeding values decreased slightly and reached a minimum value at 31.4% proportion of Charolais, whereafter it increased with increasing proportions of Charolais.

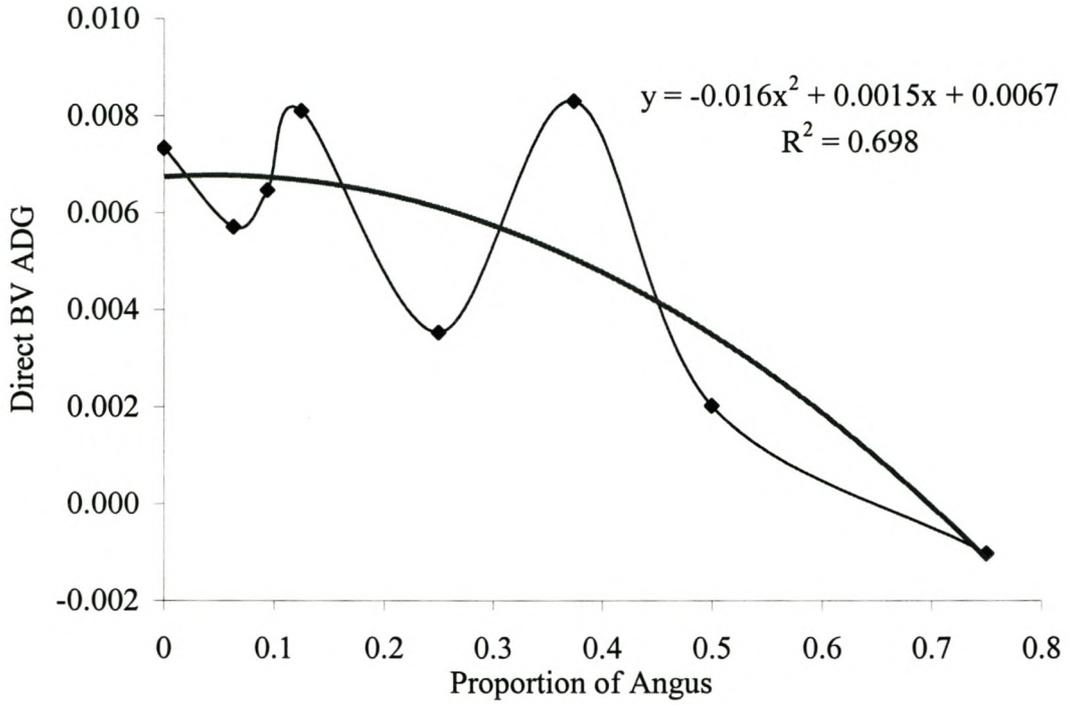


Figure 4.10a Regression of direct breeding value of ADG on Angus breeding.

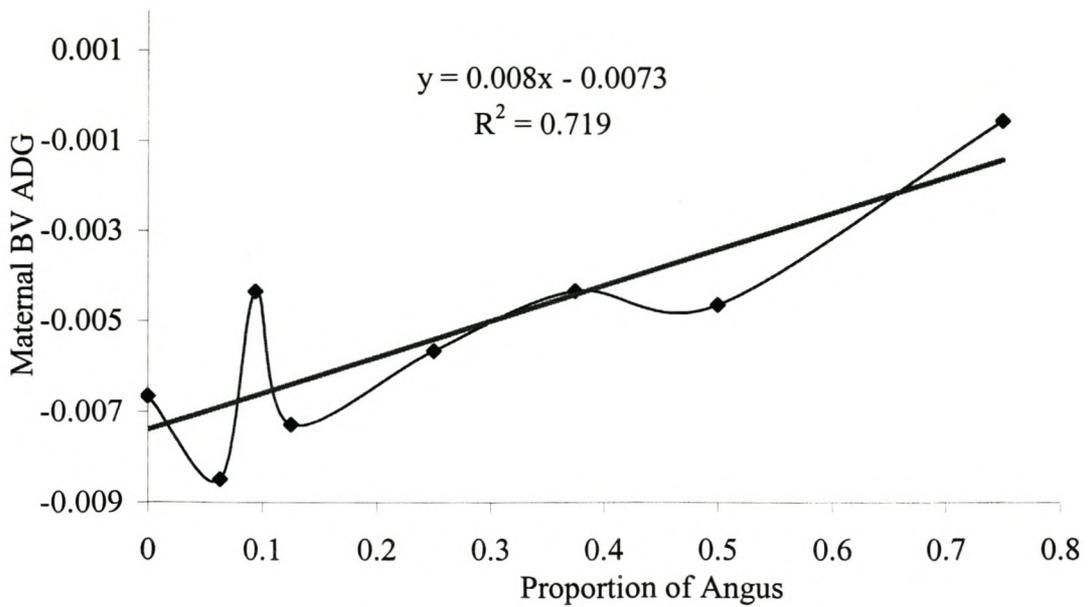


Figure 4.10b Regression of maternal breeding value of ADG on Angus breeding.

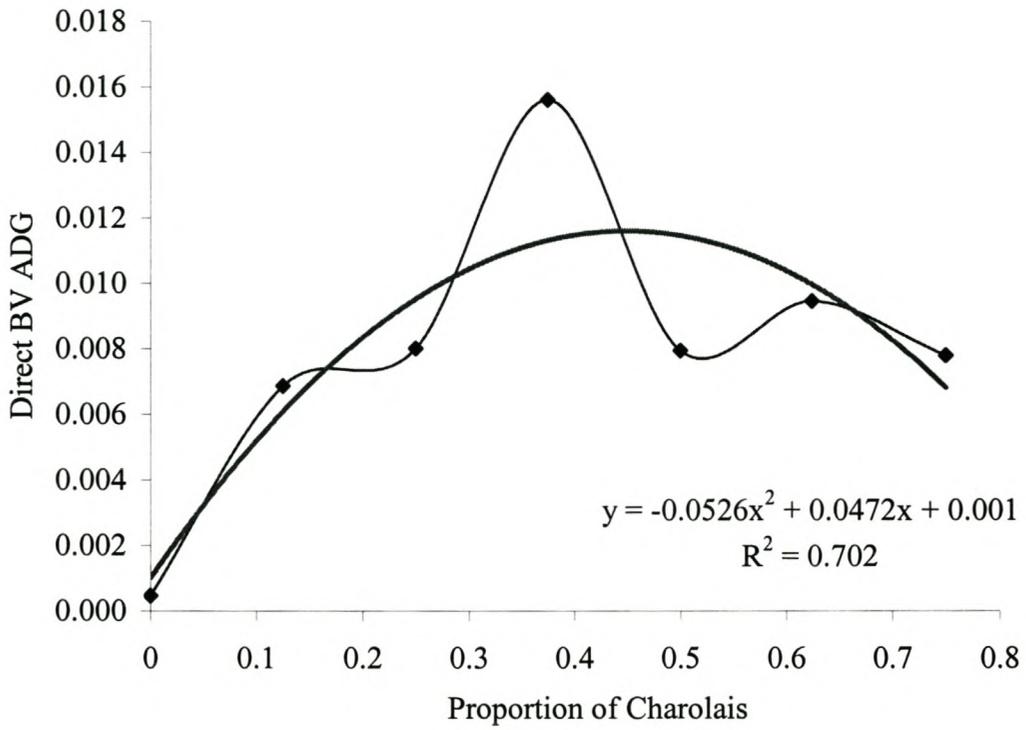


Figure 4.11a Regression of direct breeding value of ADG on proportion of Charolais.

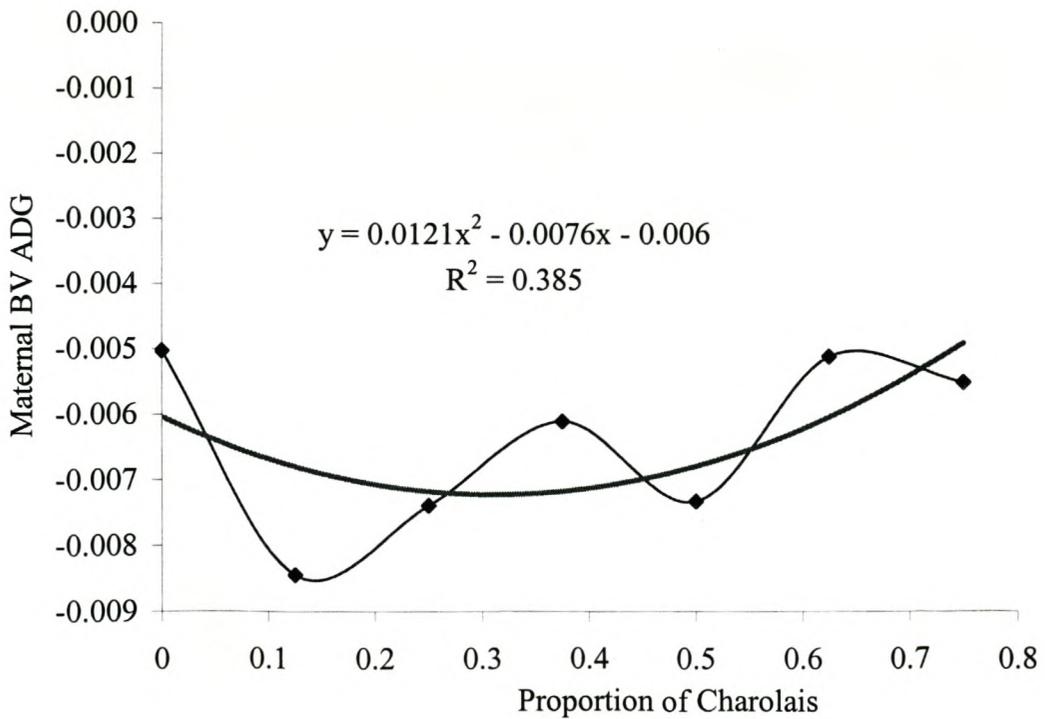


Figure 4.11b Regression of maternal breeding value of ADG on proportion of Charolais.

Dillard *et al.* (1980) reported positive direct effects of ADG for Angus and Charolais, expressed as a deviation from the Hereford additive direct value. The additive and maternal effects for Angus compared to the polled Hereford were negative and positive, respectively (Neville *et al.* (1984). Cunningham & Magee (1988) found positive estimates of maternal effects for both breeds. Increasing of the maternal breeding values with increasing proportion of both breeds in this study were indicative of the superior maternal abilities relative to the breeds with which they compared. Using crossbred cows with some Angus and Charolais breeding would result in increased preweaning growth due to the superior maternal abilities provided by their genes in this herd.

4.4 CONCLUSION

In a composite involving varying contributions of Angus, Hereford, Bonsmara and Charolais, increasing the genetic proportion of Angus decreases the performance levels of BW, WW and ADG. However, increasing the proportion of Charolais increased the performances of all the traits. The BLUEs of Angus were negative while it was positive for Charolais for the traits studied. These results generally showed an increase in maternal breeding values with increasing proportions of Angus and Charolais for BW, WW and ADG. Nevertheless, direct breeding values did not have such consistency for all the traits. Increasing the genetic proportion of Angus and Charolais in the dams would improve the milk production and maternal abilities of the cows to wean heavier calves. The results clearly confirmed earlier studies characterizing the Angus as an ideal maternal line. In this multibreed herd it may be suggested that increasing the proportion of Charolais to intermediate levels would tend to improve the performances of preweaning traits. Further investigations involving other traits of economic importance such as calving ease, carcass and cow efficiency traits should also be considered in future evaluations.

CHAPTER 5

GENERAL CONCLUSION

Heritabilities and genetic correlations estimated for birth weight, weaning weight and average daily gain in this study lie within the range of past estimates for beef cattle. Direct heritability estimates were larger under the most simple animal models accounted only for direct additive genetic effects as the only random effect, besides that of the random error. When a maternal permanent environmental effect and/ or maternal additive genetic effect were fitted in the models, the direct heritability estimates declined. This may lead to the conclusion that direct heritability estimates from a simple animal model were overestimated. In general, direct and total heritability estimates varied from low to high while the corresponding maternal heritability estimates varied from low to medium. In this herd, any of the traits can be expected to respond to selection, though the genetic correlation between direct and maternal effects were negative for weaning weight and average daily gain. From a crossbreeding point of view, there should be a clearer classification between “sire lines” and “dam lines” amongst beef cattle breeds, with selection on maternal traits in dam lines and on growth performance in sire lines.

The relationships between the direct genetic components of the traits were positive. The same genes tend to influence the traits and selection for one trait will improve the other as a correlated response (*i.e.* selection for higher weaning growth rate may be associated with higher birth weight, which may be undesirable, depending on the breeds).

For birth and weaning weights the Charolais sired calves were heavier than the Hereford sired calves. These differences may be attributed to difference in direct genetic effects and individual heterosis effects exhibited in crossbred calves. The choice of sire breed in an effective breeding programme should be made to complement those characteristics that are weak in other breeds by direct additive means and by way of exploitation of heterosis. All calves of crossbred dams were on average superior at weaning than purebred dams. Among the crossbred dams, crosses with the Charolais breed tended to wean heavier calves while

the majority of Hereford crossbred dams produced lower weaning weight of calves in this study and also in other beef cattle investigations.

The proportion of Angus and Charolais breeding levels in this multibreed herd influenced the performance of all the traits. Increasing the proportion of Charolais increased the performance levels of the traits considered in the study. In contrast, increasing the proportion of Angus generally decreased the performance levels of the traits. The direct breeding values decreased at higher proportion of Charolais. In this herd, it may be suggested that an intermediate breeding level seems more advantageous than higher proportions of Charolais. For Angus, the direct breeding values decreased as its proportions increased. Thus, it should be noted that higher growth rates would not be expected at higher proportions of Angus in this specific environment. The results of this study clearly illustrated increasing of maternal breeding values with increasing proportions of both breeds. This confirmed the superior maternal abilities of Angus and Charolais relative to the breeds with which they were compared, which was mainly Hereford. Crosses with higher breeding levels of Angus could be used as an ideal maternal line.

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