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THE VALUE OF RECORDING BODY MEASUREMENTS IN BEEF CATTLE

by

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In partial fulfilment of the requirements for the degree

MAGISTER SCIENTIAE AGRICULTURAE

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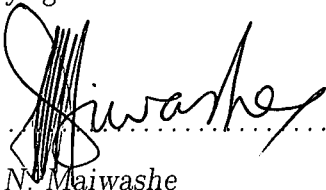
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DECLARATION

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Abstract

Body size and shape are objectively described using body measurements in beef cattle. How these measures of size and shape relate to the functioning of the individual is of paramount importance to livestock producers. Changes in these parameters that lead to inefficient animals are never welcomed by farmers. Therefore, constant checks on the relationships between body measurements and performance traits are vital in selection programs.

To estimate heritabilities and genetic correlations among body measurements and growth traits, data of 7 266 performance records of Bonsmara bull calves participating in on-farm growth tests (Phase D) were used. The data set was extracted from the Integrated Registration and Genetic Information System (INTERGIS) of South Africa. The data covered a 25-year period i.e. from 1972 - 1996. Data were recorded from 45 herds, with 439 sires and 5 180 dams involved. Traits analyzed were scrotal circumference (SC), body length (BL), shoulder height (SH), birth weight (BW), weaning weight (WW), final weight (FW) and average daily gain (ADG) from weaning to final test date.

Multivariate REML methodology was used to estimate (co)variances and genetic components for different traits. In cases where there were more than one value for an estimate, the values were pooled, weighting each estimate by the inverse of its sampling variance. Different models were, however, fitted for each trait. The permanent environmental effect was found to be important for most of the post-weaning traits, but it could, however, not be considered in the multivariate runs. This was due to computational limitations imposed by the data set. A simple model considering only direct animal effect and random error

was fitted for all post-weaning traits.

Heritability estimates for body measurements ranged from medium for body length (0.27 ± 0.05) to high for shoulder height (0.42 ± 0.05) and scrotal circumference (0.46 ± 0.06). Corresponding estimates for performance traits were: direct (0.31 ± 0.05) and maternal birth weight (0.10 ± 0.03), direct (0.29 ± 0.05) and maternal weaning weight (0.04 ± 0.02), average daily gain (0.19 ± 0.04) and final weight (0.30 ± 0.05).

Generally, body measurements were favourably and positively correlated with performance traits (0.03 to 0.83). However, scrotal circumference was found to be genetically weakly correlated to maternal birth weight (-0.22 ± 0.15) and average daily gain (0.10 ± 0.13). A close to zero genetic correlation was found between average daily gain and maternal weaning weight (0.03 ± 0.17). These results suggest that selection for fast growing bulls may not influence maternal performance at weaning.

Considering the favourable genetic correlations between body measurements and performance traits, it could be inferred that selection for body measurements is compatible with that of performance traits. However, a further study should be conducted to evaluate which of those traits considered in this study are of economic importance so that an appropriate selection index can be developed.

Opsomming

Liggaamsgrootte en -vorm van vleisbeeste kan objektief beskryf word m.b.v. liggaamsmates. Die verband tussen hierdie mates en die funksionering van die dier is van groot belang vir produsente. Veranderinge in hierdie parameters wat lei tot oneffektiewe diere sal nie deur boere verwelkom word nie. Dit is dus nodig om die verband tussen liggaamsmates en produksie eienskappe te monitor in seleksieprogramme.

Oorerfbaarhede en genetiese korrelasies tussen liggaamsmates en groei eienskappe is bepaal. Produksierekords van 7 266 Bonsmara bulkalwers, afkomstig van 45 kuddes, met 439 vaders en 5 180 moeders, wat in op-die-plaas groeitoetse (Fase D) deelgeneem het, is gebruik. Die data was afkomstig van die geïntegreerde registrasie en genetiese informasie sisteem (INTERGIS) van Suid-Afrika en strek oor 'n 25 jaar periode (1972 tot 1996). Eienskappe wat bestudeer is sluit in skrotumomvang (SC), liggaamslengte (BL), skouerhoogte (SH), geboortegewig (BW), speengewig (WW), finale gewig (FW) en gemiddelde daaglikse toename (ADG).

Meereienskap REML metodologie is gebruik om (ko)variansie komponente te beraam vir die verskillende eienskappe. In gevalle waar daar meer as een beramer vir 'n komponent was, is die waardes gepoel en geweeg deur die invers van die variansie. Verskillende modelle is vir elke eienskap gepas. Volgens enkeleienskap analyses was die permanente omgewings effek belangrik vir meeste van die na-speense eienskappe, maar dit kon nie in ag geneem word in die meereienskap lopies nie, weens rekenaarbeperkings veroorsaak deur die grootte van die datastel. 'n Eenvoudige model wat slegs die direkte effek en toevallige

fout komponent in ag neem, is gepas vir alle na-speense eienskappe.

Oorerflikhede vir liggaamsmates varieer van medium vir liggaamslengte (0.27 ± 0.05) tot hoog vir skouerhoogte (0.42 ± 0.05) en skrotumomvang (0.46 ± 0.06). Ooreenstemmende beramers vir produksie eienskappe is: direkte (0.31 ± 0.05) en maternale geboortegewig (0.10 ± 0.03), direkte (0.29 ± 0.05) en maternale speengewig (0.04 ± 0.02), gemiddelde daaglikse toename (0.19 ± 0.04) en finale gewig (0.30 ± 0.05).

Oor die algemeen is liggaamsmates gunstig en positief gekorreleer met produksie eienskappe (0.03 tot 0.83). Skrotumomvang was geneties laag gekorreleer met maternale geboortegewig (-0.22 ± 0.15) en gemiddelde daaglikse toename (0.10 ± 0.13). 'n Genetiese korrelasie naby nul is tussen gemiddelde daaglikse toename en maternale speengewig (0.03 ± 0.17) gevind. Hierdie resultate suggereer dat seleksie vir vinnig groeiende bulle waarskynlik nie 'n verandering in maternale prestasie by speen sal veroorsaak nie.

Aangesien daar 'n gunstige genetiese korrelasie is tussen liggaamsmates en produksie eienskappe kan dit afgelei word dat seleksie vir liggaamsmates verenigbaar is met die van produksie eienskappe. Daar word dus aanbeveel dat 'n verdere studie onderneem word om die eienskappe wat ekonomies belangrik is, te bepaal en om 'n seleksie indeks te ontwikkel.

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Chapter 1

General introduction

Since the beginning of scientific animal production major changes have occurred in the size of farm animals. This is because of the physical laws of nature dictate the limits within which various body dimensions or physiological functions of animals may vary (Brown *et al.*, 1983). For example, animals which are too large for a particular environment are less well adapted. Therefore, animals adapted to particular environments should be found and their type should be described by objective measurements.

In the South African beef industry, the need for objective measurements has been acknowledged since 1959 when the National Beef Cattle Performance Testing Scheme was initiated (Gerhard and Bergh, 1999). Since 1963 certain body measurements have been recorded on young bulls participating in the Phase C (standardized, intensive central growth tests) of the National Beef Cattle Performance Testing Scheme. These measurements (body length, shoulder height, scrotal circumference and skin thickness) were taken at the beginning and end of the growth test. Shoulder height and body length are skeletal measurements while skin thickness is related to the adaptability of cattle to a tropical environment (Bonsma, 1980). Shoulder height has been used mostly to identify different maturity types in cattle. Research has shown that short-statured, wide bulls are earlier

maturing than tall, narrow bulls (Brown *et al.*, 1973).

Scrotal circumference in young bulls is a potentially useful indicator of reproductive potential in beef cattle production (Bourdon and Brinks, 1986). It is easy to measure, repeatable and highly heritable (Latimer *et al.*, 1982; Neely *et al.*, 1982; Knights *et al.*, 1984). Scrotal circumference of young bulls is favourably related to semen quality (Brinks *et al.*, 1978) and age at puberty of their female half sibs (Lunstra, 1982; King *et al.*, 1983; Toelle and Robison, 1985). Lunstra *et al.* (1978) also indicated that yearling bulls with a larger scrotal circumference than their contemporaries often mature earlier, suggesting that short-statured wide bulls may also have large scrotums.

1.1 Performance testing in South Africa

Performance testing refers to the measuring, recording and evaluation of the growth, carcass quality and reproductive performance of individual animals. Animals are measured under the same environmental conditions in different herds so that their genetic potential forms the sole basis of comparison amongst individuals. Practically, animals are mostly subjected to diverse environmental and management conditions peculiar to their respective herds.

The measurement and recording of individual performance in beef cattle in South Africa was approved by the Minister of Agriculture on 4 December 1959 (Gerhard and Bergh, 1999). The National Beef Cattle Performance Testing Scheme (NBCPTS) is presently run by the Agricultural Research Council. The objective of the National Beef Cattle Performance Testing Scheme is to supply the beef industry with objective performance information that could be used to improve the biological and economic efficiency of beef production, through genetic improvement and improved management practices.

The NBCPTS is classified into five phases, which can be summarized as follows (NBCPTS, 1996):

1. Phase A - evaluation of the cow herd

The performance of all cows and their calves are evaluated through the recording of weights at different stages i.e. at birth and weaning (approximately 7 months of age). Traits evaluated are ease of calving, birth weight, mothering ability and preweaning growth (weaning weight), cow efficiency (weaning weight/metabolic cow weight) and fertility (age at first calving and inter-calving period).

2. Phase B - evaluation of post-weaning growth

Weights of young bulls, steers and heifers raised under existing farm conditions are recorded at 12 and 18 months of age. Scrotal circumference of young bulls is also recorded.

3. Phase C - standardized growth tests

Post-weaning performance of young bulls is evaluated at central testing stations under standardized (intensive) conditions for a period of 84 days (112 days prior to 1999) following an adaptation period of 28 days. Post-weaning growth is evaluated as average daily gain and feed efficiency as feed needed per kilogram gain on test. Body measurements such as shoulder height, body length and scrotal circumference are also measured.

4. Phase D - on-farm growth tests

Ten (fifteen prior to 1999) young bulls of the same breed from one or more breeders are tested on the farm of a breeder or at a central venue for post-weaning growth and efficiency. The tests are run over a period of 84 days (112 days prior to 1999) and up to 270 days (365 days prior to 1999) depending on the nutritional regime of the bulls. Body measurements similar to those taken in Phase C are recorded.

Phase D growth tests are very popular in South Africa. Since 1971 a total of 150 533 bulls of all breeds have been tested under farm conditions (Phase D). In total 184 473 bulls have been tested in Phases C and D of the Scheme since 1963 (Gerhard and Bergh, 1999). It is thus apparent that a large number of bulls are evaluated under farm conditions.

5. Phase E - carcass evaluation

Qualitative and quantitative carcass traits of a progeny group (at least 8 progeny of the same sex) of a sire are evaluated following a growth test. Traits evaluated include carcass weight, dressing percentage, percentage fat, muscle and bone in carcass as well as meat tenderness and marbling.

Various changes regarding testing procedures have occurred since the introduction of the Scheme. The number of breeds participating in the Scheme has also increased to 28 for beef cattle, with the Bonsmara being the main breed.

1.2 The purpose of the study

The Bonsmara is the main breed participating in the NBCPTS (43% of the total number of cows of all breeds, 45% of Bonsmara bull calves tested in centralized growth tests and 56% of on-farm growth test) (Gerhard and Bergh, 1999). Consequently, numerous studies have been done with regard to its growth traits (Neser, 1996; Nephawe, 1998). However, since the beginning of the recording of body measurements in South Africa, few studies have involved the estimation of genetic components for body measurements, except for breeds like Hereford and Simmentaler (Bosman, 1997; Van Marle-Köster *et al.*, 1999). Therefore, information is limited on the genetic parameters for body measurements in Bonsmara cattle.

The objectives of this study were to (1) estimate (co)variance components and heritabilities for body measurements and growth traits of Bonsmara bulls participating in Phases A and D and (2) determine whether there is any association amongst body measurements and between body measurements and growth traits.

The findings of this study will be of practical value to the livestock producers with regard to selection of their stock. It will also enable producers to predict correlated responses in body measurements from selection on growth traits or *vice versa*.

Chapter 2

Non-genetic factors influencing body measurements and growth traits

2.1 Introduction

The success of a selection program relies heavily on how accurately breeding values can be estimated from the performance of an individual. The performance of an individual is, however, due to the unobservable genetic component (additive and non-additive genetic effects) and a set of environmental factors to which the individual is exposed.

Environmental factors may be eliminated either experimentally or statistically. However, more often data used in animal breeding originate from field populations of livestock. Such data are usually highly unbalanced and generally involve confounding between genetic and environmental factors. Therefore, elimination of environmental factors may be achieved through statistical manipulations. Though some environmental factors may be adjusted for, some are unquantifiable and could not be adjusted for, hence the random error term associated with each observation. The most common sources of environmental variation include age of dam, season of the year, sex and actual age of the animal when

the trait is measured. For example, animals born on different days are often measured on the same day, implying that a proportion of the difference in a trait measured is due to age differences.

Adjusting for fixed effects is achieved by the use of linear models that allows estimation of linear functions of the effects. Solutions may also be found for classified variables though interpretation of the solution may be difficult since solutions are not unique (Mrode, 1996). Furthermore, mixed model methods can provide simultaneously estimates of fixed effects and predictions of random variables (BLUP).

Since environmental factors tend to be unique to specific locations and production systems, this chapter gives a full description of environmental factors affecting traits of economic importance in Bonsmara bull calves.

2.2 Materials and methods

2.2.1 Environment

Herds considered in this study were distributed over diverse environmental conditions. Differences in these environments are mainly due to the location, climatic conditions and veld types. The environments can be briefly described as follows:

Sweet grassveld. This veld type is located in the Thabazimbi and Pietersburg areas of the Northern Province. Total seasonal rainfall is low and erratic, varying from 350 - 500mm per annum while the temperature ranges from 5 - 40 °C. The dominant trees are *Grewia flaxa*, *Acacia* spp., *Boscia albitrunca*, *Combretum* spp. and *Colophospermum mopane*. The most abundant grasses are *Eragrostis* spp., *Aristida* spp., *Panicum maximum*, *Schimidtia pappophoroides* and *Urochloa* spp. (Acocks, 1988). The sweet grassveld is less stable than mixed and sour grassveld, but is highly resilient and recovers rapidly following disturbance

such as drought (Tainton, 1999).

The potential for crop production is limited by low and erratic rainfall and thus sweet grassveld is suited to extensive livestock systems. In general, cattle are the animals which are best adapted to using and maintaining this area. However, dryland pastures may be integrated into production systems and reduce the effects of erratic rainfall.

Forage quality is higher than in sourveld and remains fairly uniform throughout the year. The digestibility of the ingested forage may range from 56% and 60% in summer and drop to between 46% and 57% in winter (Tainton, 1999). Growing stock tend to maintain condition during the winter and may continue to gain weight. Average daily gain in the range of 1.0 kg/day in summer and 0.8 to 0.9 kg/day in winter may be expected and yearling beef animals may gain between 150 and 200 kg in liveweight over spring and summer (Tainton, 1999).

Sour grassveld. The sour grassland of South Africa is approximately 13 million ha in extent and occurs mostly as fire climax grassveld (Tainton, 1981). It is dominated by *Cymbopogon plurinodis*, *Themeda triandra*, *Elionurus argenteus* and *Hyparrhenia* spp. Soils are sandy loam and rainfall ranges from 350 - 650 mm per annum.

Generally the sourveld is stable and shows less signs of erosion and deterioration than other veld types. This is due to the dense grass cover, and its rapid maturity and consequent unpalatability. The sourveld, because much of it is a fire climax and because of the large variety of unpalatable species which may dominate the sward under bad management, has complex management requirements. The most useful stage for animal production is intermediate between the climatic climax community of scrub or forest and the stage of unpalatable secondary grass species. However, palatability and quality decline rapidly as the plants mature so that its feed value is low in winter, particularly where the rainfall is high since here the grasses tend to mature early in the growing season (Tainton, 1999). In such areas livestock lose weight during winter, even when provided with a protein-rich

supplement.

Most classes of cattle are well adapted to produce on sourveld during spring and summer. For example, in spring, young beef animals can produce liveweight gains of up to 1kg per day if sufficient grazing is available, and beef cows which calve in spring will wean calves weighing between 180 and 240 kg in April/May. The cows will also maintain condition provided they are stocked at an appropriate stocking rate.

Mixed shrub and grass. It has developed in the more tropical regions of the country where the rainfall is seasonal with a pronounced dry period in the winter and where temperatures are high in summer. This veld type range structurally from those with grassland interspersed with a few large, umbrella-shaped trees to those with large numbers of shrubs and trees which may form impenetrable thickets (Tainton, 1999). There is, however, a delicate balance between the tree and grass component of this vegetation. The grass is by nature tall, dominated by *Themeda triandra* and *Cymbopogon plurinodis*, with much *Aristida diffusa*, *Stipagrostis uniplumis*, *Eragrostis lehmanniana*, *Heteropogon contortus*, *Digitaria eriatha*, *Chrysopogon serrulatis* and *Eutachys* spp.

Both grazers and browsers are adaptable to this veld type. However, the forage supply from year to year is extremely variable and, within years, there are generally severe bottle-necks. Bush encroachment is regarded as one of the most serious veld management problems in these areas.

Highveld. This veld type covers the area of Kroonstad, Frankfort, Vrede, Ventersdorp and Koppies. It is an extremely dense Themeda veld, with no other species playing an important part. The rainfall is greater than 650 mm per annum and is confined to summer months (Acocks, 1988). Thus, the growing season extends from September to April and the grass is sour and only palatable during this period. This veld type is suited to both indigenous and exotic breeds.

2.2.2 Management

Calves considered in this study participated in the Phase A of the NBCPTS. Phase A evaluates the mothering ability of the dam and growth potential of their offspring. After weaning, breeders place a selected group of weaner bull calves (normally selected on weaning performance and structural soundness) on the on-farm growth test which is called Phase D. The Phase D tests are divided into the following three classifications:

- Phase D1 (single herd growth test)
- Phase D2 (centralized multiple herd growth test)
- Phase D3 (shortened single or multiple herd growth test)

The first two phases (D1 and D2) have been in existence since the inception of the on-farm growth test in 1972. Various changes have occurred in the testing procedure since inception (NBCPTS, 1996). In summary, the two phases last a minimum of 140 days (intensive) to a maximum of 365 days (extensive), after an adaptation period of 21 to 90 days. The adaptation period is short for intensive tests and long for extensive tests. Individuals within a test group are not allowed to vary by more than 120 days of age. The maximum individual age at the start of the adaptation period is 365 days, although tests generally start at weaning. Phase D is a post-weaning on-farm growth test.

Phase D3 was introduced in 1991 as a modification to the 140 days intensive test, hence its test period of 112 days after an adaptation period of 28 to 35 days. The bull calves are intensively fed a concentrated feed ration. The maximum individual starting age is 270 days.

The main objective of these tests is to determine the production potential of young bulls under farm conditions, and thus offer a breeder an objective selection aid to identify animals 'superior' in respects of traits of economic importance. Growth rate and feed efficiency (measured as the Kleiber ratio) are measured on individual bull calves. Other

traits measured are shoulder height, body length, scrotal circumference and final weight on test.

Only data from single-herd Phases D1 and D3 growth tests were considered. This strategy was employed to keep the contemporary group as intact as possible from birth to test. Thus, records were from bull calves that were born and raised in the same herd.

Linear body measurements analyzed were shoulder height (SH), body length (BL) and scrotal circumference (SC). Growth traits considered were birth weight (BW), weaning weight (WW), final weight (FW) measured at the end of test and average daily gain (ADG) from weaning to end of test period. Average daily gain was calculated as weight gained on test divided by number of days on test. The procedure followed for the measuring of body measurements at end of test was as follows (NBCPTS, 1996):

- Shoulder height - measured distance (vertical) from the ground to the shoulder expressed in millimeters (*mm*).
- Body length - distance between shoulder point and pin bone (*mm*).
- Scrotal circumference - greatest distance around the scrotum (*mm*).

Recorded information included age of dam, age of animal at weighing and pedigree information.

2.2.3 Data

Performance data of 91 659 Bonsmara bull calves were extracted from the Integrated Registration and Genetic Information System (INTERGIS) of South Africa. Data were recorded between 1972 and 1996. The data were collected from 316 herds with 4 110 sires and 51 057 dams involved.

The pedigree and data files were examined for errors. For example, parents had to be born before their offspring and records were restricted within certain ranges (± 3 standard

deviations from the mean). All animals with missing date of birth or age of dam were excluded. Embryo calves and twins were eliminated from the data. Only bull calves that were born and tested in the same herd were considered. Bull calves with incomplete records for test measurements were not considered.

To ensure proper linkages between herds, all herds that were not linked by a common sire were eliminated. Common sires were considered as those sires that had progeny in more than one herd. Direct genetic connections between levels of fixed effects were thus established. Only sires with more than four progeny in the data set were considered.

Contemporary group for birth (BCG) was defined by the effects of herd, year and season. The calving year stretched from December of one year to November of the following year. A 90-day season grouping was used with four seasons defined in a calving year. The weaning contemporary group (WCG) was formed on the basis of herd, weigh date (year, month and day) and management group code. The management group code differentiates between creep-fed and non-creep-fed calves. BCG and WCG were independent to ensure that birth weights of calves that died before weaning were also considered. The test contemporary group (TCG) included all bull calves that were in the same weaning contemporary group and had the same test number. Single-sire birth contemporary groups were deleted.

Contemporary group size were restricted to a minimum of five bull calves per contemporary group for birth and weaning, while the test contemporary group consisted of at least ten bull calves.

2.2.4 Statistical analyses and modeling

The GLM procedure of SAS was used in the analyses to develop fixed effects models for the traits considered (SAS, 1996). Preliminary analyses were performed on the effects (non-random) of contemporary groups (as previously defined for birth, weaning, and test) for all traits under consideration. Covariables of age of calf at weighing and age of dam

were fitted as both linear and quadratic regressions. The effect of the technician was not considered for body measurements, since the same person took all measurements for a particular contemporary group. This effect was thus confounded with the contemporary group effect. The linear model fitted was as follows:

$$Y_{ij} = \mu + cg_i + b_1A + b_2A^2 + b_3D + b_4D^2 + e_{ij} \quad (2.1)$$

where:

Y_{ij} = an observation of a trait on an animal from the i -th contemporary group

μ = the population mean

cg_i = fixed effect of the i -th contemporary group

b_1A = linear regression on age of calf at recording

b_2A^2 = quadratic regression on age of calf at recording

b_3D = linear regression on age of dam

b_4D^2 = quadratic regression on age of dam

e_{ij} = random error associated with the ij -th observation with zero mean and $I\sigma_e^2$

2.3 Results and discussions

2.3.1 Data

All edits performed on the original data set reduced the number of records available for further analysis by a substantial percentage. The final data set comprised 7 266 records i.e. only 7.93% of the original data set. Of the 316 herds that were initially available, only 45 herds remained. There were 14 herds in the sweet grassveld, 18 in the sour grassveld, 11 in the mixed shrub and 2 in the highveld. These herds were connected by 54 sires and a total of 349 different sires and 5 180 different dams were used. The characteristics of the data structure are summarized in Table 2.1

Table 2.1: Characteristics of the data structure

Trait	BW	WW	On test traits ^a
No. records	7 072	6 754	3 645
No. dams	5 063	4 882	2 950
No. sires	341	348	344
No. animals	12 437	11 939	6 902
No. CG ^b	193	235	232
Avg. CG size	37	29	16

^a Since only complete records were considered for traits measured on test, the numbers are equal for all the traits measured on test; e.g. number of sires for FW are equal to those of ADG, SH, BL and SC.

^b Contemporary group

2.3.2 Statistical analyses

Summary statistics regarding the mean, distribution and standard error associated with the mean are given in Table 2.2.

Table 2.2: Summary statistics of all the traits

Trait	Mean($\pm SE$)	SD ^a	CV(%) ^b	Min ^c	Max ^d
BW(kg)	37.03(0.06)	4.67	10.77	23	50
WW(kg)	228.90(0.44)	36.50	9.43	124	335
FW(kg)	429.99(0.85)	51.31	6.66	282	585
ADG(g/day)	1273.18(4.16)	250.86	11.39	555	2036
SH(mm)	1206.61(0.55)	33.25	2.10	1110	1300
BL(mm)	1404.84(0.89)	53.63	2.67	1250	1506
SC(mm)	343.88(0.43)	25.91	6.32	265	420

^a Standard deviation

^b Coefficient of variation

^c Minimum

^d Maximum

The coefficient of variation (CV) shows that BW, WW and ADG were phenotypically more variable than the other traits (FW, SH, BL and SC).

Analyses of variance

An analysis of variance was performed on all the traits as indicated in Table 2.3 through Table 2.9.

Birth weight. The results of the analysis of variance for BW are given in Table 2.3. It is evident that all the variables fitted affected BW significantly ($P < 0.0001$). The importance of the contemporary group (BCG) was expected since different management and/or environmental conditions encountered in different herds mostly lead to differences in mean performance levels. BCG contributed only 3.3% of the variation accounted by the model.

Table 2.3: Analysis of variance for birth weight

Source of variation	df	Mean Squares
BCG	192	188***
Age of dam (linear)	1	3378***
Age of dam (quadratic)	1	2084***
Error	6877	16

*** $P < 0.0001$

$R^2 = 0.29$; $CV = 10.77\%$

Age of dam (linear and quadratic) was shown to be more important than BCG in that it contributed a large percentage (96.7%) of the variation accounted for by the model. Massey and Benyshek (1981) also showed that birth weight increased as the age of the dam increased, with the largest calves produced by the 5- and 6-year-old cows. Similar results were also reported by Pabst *et al.* (1977).

Though all variables were highly significant ($P < 0.0001$), the model accounted for only a small proportion of the total phenotypic variance ($R^2=0.29$). Nevertheless, these results were consistent with those reported for the same breed by Nephawe (1998).

Weaning weight. Analysis of variance results are shown in Table 2.4. Contemporary group (WCG) highly influenced variation in weaning weight ($P < 0.0001$). The effects of age of dam and age of calf were important sources of variation for weaning weight ($P < 0.0001$). These results are consistent with other results reported in literature (Brinks *et al.*, 1962; Veseley and Robison, 1971; Pabst *et al.*, 1977; Jürgens, 1995). The effect of age of dam on weaning weight is largely due to differences in milk production between young immature heifers and mature dams (Ojala, 1984). The model accounted for an appreciable amount of variation of the total phenotypic variance ($R^2=0.66$).

Table 2.4: Analysis of variance for weaning weight

Source of variation	df	Mean Squares
WCG	234	17757***
Age of dam (linear)	1	184485***
Age of dam (quadratic)	1	110935***
Age of calf (linear)	1	41047***
Age of calf (quadratic)	1	10315***
Error	6515	466

*** $P < 0.0001$

$R^2 = 0.66$; $CV = 9.43\%$

Average daily gain. Table 2.5 shows that the effect of the contemporary group (TCG) was highly significant for average daily gain. However, the age of dam (adjusted for the effects of contemporary group and age) was not significant. These results concur with published results from similar studies (Brinks *et al.*, 1962; Swiger *et al.*, 1963; Anderson *et al.*, 1973; Chavraux and Bailey, 1977; Mavrogenis *et al.*, 1978; Massey and Benyshek, 1981; Collins-Lusweti and Curran, 1985; Urick *et al.*, 1991). The effect of age of dam on ADG could have been minimized by the adaptation period practiced in the NBCPTS. Swiger (1961) found that calves from younger dams tend to gain faster or compensate for their pre-weaning environment in the first 28-day period and this effect was actually reversed towards the end of the test. However, Shelby *et al.* (1963) and Flower *et al.* (1964) found significant effects of age of dam on post-weaning growth rate.

Table 2.5: Analysis of variance for average daily gain

Source of variation	df	Mean Squares
TCG	231	653061***
Age of dam (linear)	1	7848
Age of dam (quadratic)	1	8939
Age of calf (linear)	1	45884*
Age of calf (quadratic)	1	4152
Error	3409	21011

*** $P < 0.0001$

* $P < 0.1$

$R^2 = 0.68$; $CV = 11.39\%$

Age of the calf at the beginning of the test was found to be slightly important ($P < 0.1$). Similar results were reported in other studies (Patterson *et al.*, 1955; Moore *et al.*, 1961; Shalles and Marlowe, 1967; Brown and Keaton, 1974; Nelsen and Kress, 1979). Tong (1982) suggested that the importance of age of calf might be brought about by its impact on compensatory growth. Several other studies have however reported that age was not significant for post-weaning ADG (Moore *et al.*, 1961; Brown and Gifford, 1962; Lewis and Jones, 1978; Steane *et al.*, 1978; Cain and Wilson, 1983; Ojala, 1984). The inconsistent results with respect to initial age on test are related to initial age range and genetic variation of growth patterns of bulls (Tong, 1982). Thus, minimizing the range of initial ages ensures that bulls are not compared at drastically different physiological ages.

Shoulder height. All the variables had significant influence on shoulder height (Table 2.6). The effect of contemporary group (TCG) and age of dam (linear and quadratic) had more influence on shoulder height ($P < 0.0001$), while the influence of age of calf was marginal ($P < 0.01$ and $P < 0.1$).

The significant effect of age of dam on shoulder height is in contrast to the notion that traits observed late in life are less dependent on the age of dam. These results might be explained by the carry-over effect that occurs from weaning to maturity. With wide age ranges (301-540 days) considered in this study, it was highly expected that age of the calf

Table 2.6: Analysis of variance for shoulder height

Source of variation	df	Mean Squares
TCG	231	7102***
Age of dam (linear)	1	15722***
Age of dam (quadratic)	1	8811***
Age of calf (linear)	1	4696**
Age of calf (quadratic)	1	1534*
Error	3409	611

*** $P < 0.0001$

** $P < 0.01$

* $P < 0.1$

$R^2 = 0.48$; $CV = 2.10\%$

will have an influence on all the traits measured at the end of test hence its importance in shoulder height.

Body length. Age of the dam had the largest effect on body length, followed by contemporary group and the age of the calf (Table 2.7). The importance of age of the calf and dam on body length are probably due to the high phenotypic correlation that exists between body length and weight (Brown *et al.*, 1973).

Table 2.7: Analysis of variance for body length

Source of variation	df	Mean Squares
TCG	231	21898***
Age of dam (linear)	1	55291***
Age of dam (quadratic)	1	33871***
Age of calf (linear)	1	12440**
Age of calf (quadratic)	1	3070*
Error	3409	1405

*** $P < 0.0001$

** $P < 0.01$

* $P < 0.1$

$R^2 = 0.54$; $CV = 2.67\%$

Scrotal circumference. Contemporary group effects were highly significant though it did not contribute much to the overall phenotypic variance (Table 2.8). Age of dam was also significant and was the most important effect in the model. This result was consistent with the findings of Bourdon and Brinks (1986) and Kriese *et al.* (1991a) who reported that yearling scrotal growth rate in Hereford bulls increased with increasing age of their dams. According to Bourdon and Brinks (1986) the effect of age of dam on scrotal circumference is probably the result of differences in weight among bulls.

Table 2.8: Analysis of variance for scrotal circumference

Source of variation	df	Mean Squares
TCG	231	2970***
Age of dam (linear)	1	11619***
Age of dam (quadratic)	1	7884***
Age of calf (linear)	1	5658***
Age of calf (quadratic)	1	2838**
Error	3409	472

*** $P < 0.0001$

** $P < 0.01$

$R^2 = 0.34$; $CV = 6.32\%$

Age of the calf (linear and quadratic) was found to contribute significantly in explaining variation in scrotal circumference. Latimer *et al.* (1982) found that bulls that were older at the start of the test tended to have larger scrotal circumference as yearlings, regardless of their starting weight. Van Marle-Köster *et al.* (1999) reported a similar result on yearling scrotal circumference in Hereford cattle. De Rose *et al.* (1988) only included the linear term of the age of calf in the model for scrotal circumference.

Final weight. All the effects fitted significantly influenced final weight (Table 2.9). The model fitted accounted for a large percentage of the total variance ($R^2=0.71$).

Mavrogenis *et al.* (1978) and Simm *et al.* (1985) also found age of dam to be a significant source of variation in final weight. Brown *et al.* (1972) indicated that the persistence of dam effects might be the result of compensatory growth during the post-weaning phases

Table 2.9: Analysis of variance for final weight

Source of variation	df	Mean Squares
TCG	231	25993***
Age of dam (linear)	1	63301***
Age of dam (quadratic)	1	42261***
Age of calf (linear)	1	13567***
Age of calf (quadratic)	1	3141**
Error	3409	819

*** $P < 0.0001$

** $P < 0.01$

$R^2 = 0.71$; $CV = 6.66\%$

being related to the pre-weaning maternal effects. Furthermore, Rutledge *et al.* (1972) working with mice, found no evidence of post-natal maternal effects on 42 to 84-day gain, and thus ascribed the persistency of maternal effects on post-weaning weight to differences acquired prior weaning or 42 days.

2.4 Conclusions

The results of this study confirm the vital role of non-genetic factors in explaining variation in different traits in beef cattle. It has also been shown that environmental factors such as maternal influence (in the form of age of the dam) may have a lasting effect on the performance of the animal despite the fact that calves are only dependent on their dams during pre-weaning stages. It is therefore essential that known environmental effects be adjusted for so that animals may be compared fairly. Fixed effects models were identified that will be fitted in the subsequent statistical (genetic) analyses. However, inconsistencies observed in different studies as compared to the results obtained in this study, attest to the fact that each population is unique.

Chapter 3

(Co)variance components and heritability estimates for body measurements and growth traits

3.1 Introduction

Advances in computer technology and statistical modeling have led to great improvements in estimation of (co)variance components in animal breeding. Widespread use is being made of maximum likelihood techniques that allow complex models, incorporating various fixed and random effects and make optimal use of information from all relatives.

Knowledge of the magnitude of the variance and covariance components of traits of economic importance is critical for the genetic evaluation of animals and the development of sound breeding programs (Willham, 1980; Shi *et al.*, 1993). Few estimates of (co)variance components and heritabilities have been produced for body height, length and scrotal circumference, especially in populations of performance-tested bulls. Furthermore, occurrence of inflated direct-maternal genetic correlation in field data is a major concern for selection

programs (Bertrand and Benyshek, 1987; Garrick *et al.*, 1989; Meyer, 1993; Swalve, 1993; Robinson, 1996*b*; Lee and Pollak, 1997). Although a slightly negative relationship between direct and maternal effects is considered plausible, many authors are skeptical of some of the high negative correlations reported in the literature (Mallinckrodt *et al.*, 1995; Robinson, 1996*b*; Meyer, 1997). An inflated negative correlation has been hypothesized to be due to factors such as:

- the negative dam-offspring environmental correlation (Baker, 1980; Meyer, 1992).
- greater variations between sires than dams, due either to greater genetic variance or confounding environmental effects such as paddock with sire (Robinson, 1996*b*).
- data structure and data problems (Mallinckrodt *et al.*, 1995; Lee and Pollak, 1997).

The fitting of detailed models is necessary for accurate genetic evaluation. Sire \times herd or year interactions have been shown to influence parameter estimates in previous studies (Notter *et al.*, 1992; Lee and Pollak, 1997). They have also been shown to provide a better fit than models excluding them (Neser, 1996; Nephawe, 1998). Neser (1996), analyzing weaning weight in Bonsmara cattle, showed that models including sire \times herd-year-season interactions could be superior to those including only sire \times herd interactions. Furthermore, this effect has also been shown to reduce the correlation between direct and maternal genetic effects (Lee and Pollak, 1997; Nephawe, 1998).

The primary objective of this study was to estimate (co)variances and heritabilities for body measurements and growth traits in Bonsmara bull calves participating in the on-farm growth tests of the South African NBCPTS. A second aim was to examine the effect of sire \times herd-year-season interactions on the covariance between direct-maternal genetic effects for birth and weaning weights.

3.2 Materials and methods

3.2.1 Data

The characteristics pertaining to numbers of records, sires and dams involved for a particular trait, have been given in Chapter 2.

3.2.2 Statistical analyses

Models

Two sets of analyses were performed on the data set. In the first analysis, six different models were fitted for all the traits in this study to compare the estimated (co)variance components. The second analysis examined the influence of the sire \times herd-year-season interactions on the direct-maternal genetic covariance.

In the first analysis, Model 1 was a 'simple' animal model fitting animals' direct additive genetic effects only. Model 2 allowed for a maternal effect in addition but attributed it solely to the permanent environmental effect of the dam. Conversely, Model 3 assumed all maternal influence was of genetic origin. Whereas model 3 assumed direct and maternal genetic effects to be uncorrelated, Model 4 allowed for a respective non-zero covariance. Models 5 and 6 corresponded to Models 3 and 4, respectively, but fitted both dams' genetic and permanent environmental effects (i.e. three random factors altogether). These models are similar to those described by Meyer (1993). The second analysis fitted the sire \times herd-year-season interactions in the 'best' model fitted for birth and weaning weights.

The following population parameters were derived from the (co)variance component estimates : direct heritability (h_a^2); maternal heritability (h_m^2); permanent environmental heritability (h_c^2) and the total heritability of both genetic effects (h_T^2). Formulae used for calculating heritability estimates were as follows (Willham, 1972):

$$h_a^2 = \sigma_a^2 / \sigma_P^2;$$

$$h_m^2 = \sigma_m^2 / \sigma_P^2;$$

$$h_c^2 = \sigma_c^2 / \sigma_P^2$$

and

$$h_T^2 = (\sigma_a^2 + 1.5\sigma_{am} + 0.5\sigma_m^2) / \sigma_P^2$$

where the phenotypic variances were

$$\sigma_P^2 = \sigma_a^2 + \sigma_{am} + \sigma_m^2 + \sigma_c^2 + \sigma_e^2 \text{ or } \sigma_P^2 = \sigma_a^2 + \sigma_e^2 \text{ (for direct effect only)}$$

The most comprehensive model fitted for both pre-weaning and post-weaning traits was as follows:

$$\mathbf{Y} = \mathbf{X}\beta + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{Z}_3\mathbf{c} + \mathbf{e} \quad (3.1)$$

where \mathbf{Y} is the vector of phenotypic observations; β is the vector of fixed effects consisting of the contemporary group, age of dam at birth (linear and quadratic regressions) and age at weighing (linear and quadratic regressions); \mathbf{a} is the vector of unknown random additive direct genetic effects; \mathbf{m} is the vector of unknown random additive maternal genetic effects; \mathbf{c} is the vector of unknown random permanent maternal environmental effects; and \mathbf{e} is the vector of unknown random residual effects. \mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 , and \mathbf{Z}_3 are known incidence matrices relating observations to the respective fixed and random effects.

The distribution of random components in the model are $[\mathbf{a}', \mathbf{m}', \mathbf{c}', \mathbf{e}', \mathbf{y}']' \sim N([\mathbf{0}' \mathbf{0}' \mathbf{0}' \mathbf{0}' \mathbf{0}' (\mathbf{X}\beta)']', \Sigma)$, where

$$\Sigma = \begin{bmatrix} A\sigma_a^2 & A\sigma_{am} & 0 & 0 & AZ_1'\sigma_a^2 \\ A\sigma_{am} & A\sigma_m^2 & 0 & 0 & AZ_2'\sigma_m^2 \\ 0 & 0 & I\sigma_c^2 & 0 & Z_3'\sigma_c^2 \\ 0 & 0 & 0 & I\sigma_e^2 & I\sigma_e^2 \\ Z_1A\sigma_a^2 & Z_2\sigma_m^2 & Z_3\sigma_c^2 & I\sigma_e^2 & V \end{bmatrix} \quad (3.2)$$

σ_a^2 is the direct additive genetic variance; σ_{am} is the covariance between the additive direct and maternal genetic effects; σ_m^2 is the maternal additive genetic variance; σ_c^2 is the permanent maternal environmental variance; σ_e^2 is the residual variance, and $V = Z_1AZ_1'\sigma_a^2 + Z_2AZ_2'\sigma_m^2 + (Z_1AZ_2' + Z_2AZ_1'\sigma_{am}) + Z_3Z_3'\sigma_c^2 + I\sigma_e^2$.

Two methods can be used to evaluate genetic models, these include the log likelihood ratio test (LRT) and the standard error of the estimate (SE). The method most commonly used for comparing parameters estimated by the Restricted Maximum Likelihood (REML) is the LRT. The LRT allows two models that differ in terms of the inclusion and exclusion of the parameter of interest to be compared. The LRT is achieved through multiplying the differences between two models to be compared by -2 and comparing this value to the χ^2 - test statistic with one degree of freedom (Swalve, 1993).

The ASREML package developed by Gilmour *et al.* (1996) was used to estimate variance components. ASREML allows the fitting of different models for individual traits in a multivariate analysis. This package estimates variance components under a general mixed model by restricted maximum likelihood (REML).

3.3 Results and discussions

3.3.1 Birth weight

Based on likelihood values, the order of fit improved from the simple animal model to the most complex model i.e. Model 6 (Table 3.1). The fitting of the simple model with only the direct additive component and the residual effect yielded a substantially higher estimate of σ_a^2 compared to the other models. This was expected since the maternal genetic variance and the direct-maternal covariance are often confounded with the direct additive effect in the simple animal model. The importance of the maternal effects was confirmed by the change in log likelihood (Models 2 and 3), which showed a significantly better fit

to the simple animal model. Models 2 and 3 further show that both maternal genetic and permanent environmental effects are overestimated when only one of them is considered (see Table 3.1). As the log likelihood clearly demonstrates, the data were described 'best' by Model 6, which included all random components as well as the covariance between direct and maternal additive effects.

Model 6 estimates of h_a^2 , h_m^2 , and h_c^2 were 0.32, 0.13 and 0.09, respectively. However, the effects of h_m^2 tended to be higher than h_c^2 . These estimates are comparable with recent estimates reported in the literature (Koots *et al.*, 1994; Van der Westhuizen, 1997; Nephawe, 1998). Robinson (1996*b*) found slightly higher estimates of 0.47, 0.18 for h_a^2 and h_m^2 but a slightly lower estimate of 0.07 for h_c^2 in Angus cattle. Similar estimates of the direct heritability and slightly lower maternal estimates were reported for Angus cattle by Meyer (1992).

Table 3.1: Estimates of (co)variance components (in kg^2) and genetic parameters for birth weight using different models

Parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ_a^2	7.62	5.37	4.98	5.37	4.70	5.33
σ_m^2			1.85	2.71	1.16	2.08
σ_{am}				-1.10		-1.45
σ_c^2		1.98			1.17	1.44
σ_e^2	9.45	9.26	9.88	9.72	9.54	9.20
σ_P^2	17.07	16.61	16.70	16.71	16.57	16.58
σ_e^2/σ_P^2	0.55	0.55	0.59	0.58	0.58	0.56
SE	± 0.04	± 0.04	± 0.04	± 0.04	± 0.04	± 0.04
σ_{am}/σ_P^2				-0.07		-0.09
SE				± 0.04		± 0.04
h_c^2		0.12			0.07	0.09
SE		± 0.02			± 0.03	± 0.03
r_{am}				-0.29		-0.44
h_a^2	0.45	0.32	0.30	0.32	0.28	0.32
SE	± 0.04	± 0.04	± 0.04	± 0.05	± 0.04	± 0.05
h_m^2			0.11	0.16	0.07	0.13
SE			± 0.02	± 0.04	± 0.03	± 0.04
h_T^2			0.35	0.30	0.32	0.25
$LogL$	-13195.3	-13181.1	-13178.5	-13177.2	-13175.1	-13172.5
$\Delta LogL$	-22.8***	-8.6***	-6.0***	-4.7***	-2.6**	0

σ_a^2 , direct additive genetic variance; σ_m^2 , maternal additive genetic variance; σ_{am} , direct-maternal genetic covariance; σ_c^2 , permanent maternal environmental variance; σ_e^2 , residual error variance; σ_P^2 , phenotypic variance; r_{am} , direct-maternal genetic correlation; h_a^2 , direct heritability; h_m^2 , maternal heritability; h_c^2 , permanent environmental effect expressed as a ratio of the total phenotypic variance; h_T^2 , total heritability; SE, standard error; $LogL$, log likelihood; $\Delta LogL$, log likelihood expressed as deviation from the model with the lowest value.

*** $P < 0.01$

** $P < 0.05$

Allowing for the covariance between direct and maternal additive effects resulted in corresponding increases in both h_a^2 and h_m^2 (Model 6), which is in agreement with the findings of Nephawe (1998) for the same breed. Meyer (1992, 1993) indicated that these changes may be attributed to the effects of sampling variation on the partitioning of the phenotypic variance. The negative estimate of the genetic correlation between direct and maternal additive effects is common in beef cattle, as is reported elsewhere (Baker, 1980; Cantent *et al.*, 1988; Garrick *et al.*, 1989; Núñez-domínguez *et al.*, 1993; Robinson, 1996a; Nephawe,

1998; Ferreira *et al.*, 1999; Varona *et al.*, 1999). As pointed out by Trus and Wilton (1988), these results suggest a genetic antagonism between a heifer's prenatal growth potential and the subsequent quality of her intra-uterine environment. In contrast to this finding, Meyer (1992) found the direct-maternal additive correlations to be small and statistically unimportant in Hereford and Angus cattle, as did Rust, T. (personal communication) with Afrikaner cattle in South Africa.

According to Robinson (1996b), a negative covariance between direct and maternal additive effects may be biased by other sources of variation, such as the confounding of the environmental effects with the sire. It was, thus, decided to include an additional random effect, namely the sire \times herd-year-season interaction in Model 6.

The results of these analyses are shown in Table 3.2. Estimates of h_a^2 and h_m^2 were 0.32 and 0.13 respectively, in the model omitting the sire \times herd-year-season interaction. However, the inclusion of a sire \times herd-year-season, as an additional random effect, resulted in a reduction in both the direct and maternal genetic components, which became 0.23 and 0.11, respectively. The effect of a sire \times herd-year-season interaction was more pronounced on the additive direct variances than the additive maternal variances, with little or no effect on the error, phenotypic or permanent environmental variance. It is possible that the sire component was considered in the interaction (Neser, 1996), which inevitably resulted in a reduction in the heritability estimates and the estimates of the correlations between direct and maternal genetic effects. The latter reduction was from -0.44 to -0.32 (i.e. a reduction of 27.3%).

Although a sire \times herd-year-season interaction provided a marginally better fit ($P < 0.01$) to the data set than the model omitting it, it accounted for only a small proportion of the total phenotypic variance (3%). However, a very large reduction in the estimates of direct and, to a lesser extent, maternal additive heritabilities from 0.32 to 0.23 and 0.13 to 0.11, respectively, was observed. The nature of a sire \times herd-year-season interaction is not well-understood (Lee and Pollak, 1997). Since the sire \times herd-year-season interaction had such

Table 3.2: Estimates of (co)variance components (in kg^2) and genetic parameters for birth weight with and without sire \times HYS

Parameter	Model 6	
	without S \times HYS	with S \times HYS
σ_a^2	5.33	3.82
σ_m^2	2.08	1.79
σ_{am}	-1.45	-0.84
σ_c^2	1.44	1.55
$\sigma_{S \times HYS}^2$	-	0.53
σ_e^2	9.20	9.69
σ_P^2	16.58	16.63
σ_e^2/σ_P^2	0.56	0.57
SE	± 0.04	± 0.04
σ_{am}/σ_P^2	-0.09	-0.05
SE	± 0.04	± 0.04
$\sigma_{S \times HYS}^2/\sigma_P^2$	-	0.03
SE	-	± 0.04
h_c^2	0.09	0.09
SE	± 0.03	± 0.03
r_{am}	-0.44	-0.32
h_a^2	0.32	0.23
SE	± 0.05	± 0.05
h_m^2	0.13	0.11
SE	± 0.04	± 0.04
h_T^2	0.25	0.21
LogL	-13172.1	-13166.6
ΔLogL	-5.5***	0

See Table 3.1 for abbreviations

a dramatic effect on the direct and maternal additive genetic variances, it was decided to omit this interaction from the operational model. As pointed out by Lee and Pollak (1997) further research is warranted to investigate the nature of this interaction before changing models.

3.3.2 Weaning weight

The estimate of direct heritability from Model 1 was high (Table 3.3). Partitioning the direct genetic effect into direct and maternal components by fitting Models 2, 3 or 5 significantly ($P < 0.01$) increased the log likelihood. Furthermore, considering Models 1 and 2, it could be seen that σ_a^2 was reduced substantially. This indicates that the exclusion of maternal effects (either genetic or environmental) in the model leads to overestimation of the direct additive variance. The omission of the permanent environmental effect had an impact on the phenotypic variance as can be seen in Models 3 and 4. Therefore, the permanent environmental effect of the dam has some influence on the efficacy of correcting for systematic environmental effects in the fixed part of the model (Meyer, 1992).

Likelihood values clearly indicated that Model 6 (including maternal components and genetic correlation between direct and maternal effects) provided the 'best' fit for the data. Estimates from this model were 0.25, 0.18 and 0.12 for h_a^2 , h_m^2 , and h_c^2 , respectively. These estimates are in good agreement with recent findings reported for the same breed (Neser, 1996; Nephawe, 1998). Robinson (1996a), working with Angus cattle, reported similar estimates of 0.29, 0.14 and 0.15 for h_a^2 , h_m^2 , and h_c^2 , respectively. However, in contrast to the results found here, the permanent environmental effect was slightly higher than the maternal additive effect.

A high negative correlation between direct and maternal additive effects of -0.54 was estimated (Model 6). A similar estimate of -0.53 was reported for the same breed (Neser, 1996). Wright *et al.* (1991) found an estimate of -0.57 , which closely agrees with the results found here. Generally, negative estimates of direct-maternal correlations have been reported (Garrick *et al.*, 1989; Meyer, 1992; Keeton *et al.*, 1996; Robinson, 1996a; Lee and Pollak, 1997; Ferreira *et al.*, 1999; Miller and Wilton, 1999; De Mattos and Bertrand, 2000). The estimate of the correlation between direct and maternal additive effects was higher than the -0.30 reported in Limousin cattle by Bertrand and Benyshek (1987). Koots *et al.* (1994) reported an average genetic correlation of -0.25 from nine studies.

Table 3.3: Estimates of (co)variance components (in kg^2) and genetic parameters for weaning weight using different models

Parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ_a^2	205.02	117.15	95.92	117.91	88.98	117.94
σ_m^2			81.17	125.54	49.02	88.09
σ_{am}				-54.18		-54.87
σ_c^2		88.18			52.60	57.76
σ_e^2	294.05	276.24	307.30	296.63	289.17	272.93
σ_P^2	499.10	481.6	484.4	485.9	479.8	481.9
σ_e^2/σ_P^2	0.59	0.57	0.63	0.61	0.60	0.57
SE	± 0.04	± 0.03	± 0.03	± 0.04	± 0.03	± 0.04
σ_{am}/σ_P^2				-0.11		-0.11
SE				± 0.05		± 0.04
h_c^2		0.18			0.011	0.12
SE		± 0.02			± 0.03	± 0.03
r_{am}				-0.45		-0.54
h_a^2	0.41	0.24	0.20	0.24	0.19	0.25
SE	± 0.04	± 0.04	± 0.04	± 0.04	± 0.04	± 0.04
h_m^2			0.17	0.26	0.10	0.18
SE			± 0.02	± 0.04	± 0.03	± 0.04
h_T^2			0.28	0.20	0.24	0.17
$\text{Log}L$	-23607.2	-23576.9	-23571.3	-23567.8	-23563.8	-23558.8
$\Delta \text{Log}L$	-48.4***	-18.1***	-12.5***	-9***	-5**	0

See Table 3.1 for abbreviations

Negative estimates of -0.40, -0.41, -0.59 and -0.68 were found in the South African National Genetic Evaluation for Angus, Hereford, Simmentaler and Bonsmara, respectively (Mostert, B.E., personal communication).

Bennett and Gregory (1996) and Meyer (1992) have reported low positive estimates of direct-maternal additive effects of 0.13 and 0.22 for Angus and a Composite breed of cattle, respectively. Differences between estimates may be attributed to differing levels of genetic variation between populations, the restricted nature and effects of selected data, sex, feeding management and method of estimation (Koots *et al.*, 1994; Mallinckrodt *et al.*, 1995; Keeton *et al.*, 1996; Lee and Pollak, 1997).

It was clear that the high direct-maternal additive correlation was in general agreement

with other studies. However, the possibility of this estimate being an overestimation could not be ruled out, as was observed with birth weight. Thus, a further random effect of a sire \times herd-year-season interaction was fitted to investigate its influence on the direct-maternal additive correlation.

Table 3.4: Estimates of (co)variance components (in kg^2) and genetic parameters for weaning weight with and without sire \times HYS

Parameter	Model 6	
	without S \times HYS	with S \times HYS
σ_a^2	117.94	51.00
σ_m^2	88.09	69.20
σ_{am}	-54.87	-19.97
σ_c^2	57.76	55.91
$\sigma_{S \times HYS}^2$	-	30.43
σ_e^2	272.93	295.28
σ_P^2	481.9	481.8
σ_e^2/σ_P^2	0.57	0.61
SE	± 0.04	± 0.04
σ_{am}/σ_P^2	-0.11	-0.04
SE	± 0.04	± 0.04
$\sigma_{S \times HYS}^2/\sigma_P^2$	-	0.06
SE	-	± 0.01
h_c^2	0.12	0.12
SE	± 0.03	± 0.03
r_{am}	-0.54	-0.34
h_a^2	0.25	0.11
SE	± 0.04	± 0.04
h_m^2	0.18	0.14
SE	± 0.04	± 0.04
h_T^2	0.17	0.12
LogL	-23558.8	-23539.4
ΔLogL	-19.4***	0

See Table 3.1 for abbreviations

Results of an analyses omitting and fitting a sire \times herd-year-season interaction to Model 6 are shown in Table 3.4. The fitting of an over-parameterized model, including a sire \times herd-year-season interaction, led to a drastic reduction (56%) in h_a^2 and (22%) in h_m^2 . The inclusion of a sire \times herd-year-season interaction accounted for a substantial

proportion of the total variance (6%), leading to a significant ($P < 0.01$) improvement between models. The estimate for sire \times herd-year-season interaction of 6% was within ranges of 2 to 13%, as reported in the literature (Notter *et al.*, 1992; Naser, 1996; Bradfield *et al.*, 1997; Meyer, 1997; Nephawe, 1998; Berweger *et al.*, 1999; Doderhoff *et al.*, 1999).

The estimate of the correlation between direct and maternal genetic effects, ignoring sire \times herd-year-season interaction, was highly negative (-0.54), compared to -0.34 when sire \times herd-year-season interaction was considered. A similar result was observed by Doderhoff *et al.* (1999) in Angus cattle. It was interesting to note that the phenotypic variance remained constant, while the error variance increased. As pointed out by Lee and Pollak (1997), this interaction may be either a true interaction, perhaps caused by different environmental factors associated with different years, or the effect is confounded with other unidentified sources of covariation between progeny records in the same year. These authors suggested that before changing models to address the sire \times herd-year-season interaction, the nature of the effect needs to be defined. Thus Model 6, excluding the sire \times herd-year-season interaction, was regarded as the operational model of choice in subsequent analyses.

3.3.3 Average daily gain

The estimates of (co)variance components and genetic parameters for average daily gain are summarised in Table 3.5. The estimates of σ_a^2 were consistently higher in those models excluding the permanent environmental effect. The inclusion of the permanent environmental effect reduced the estimates of σ_e^2 in Models 2 and 5, with little or no effect on the σ_p^2 . The maternal additive genetic effect σ_m^2 was almost zero as shown by Models 3 and 5.

The estimate of h_a^2 was fairly consistent across all the models fitted. This shows that the fitting of only the direct additive effect (Model 1) does not lead to the overestimation of the genetic component. Fitting Model 2 showed some presence of the permanent environmental effect (6%). However, the presence of the permanent environmental effect was cause for

concern in view of the fact that the amount of information available to obtain an estimate of the permanent environmental effect, was limited (i.e. an average of 1.2 progeny per dam, see Table 2.1). Since Models 3 to 6 show no evidence of maternal genetic effect on this traits, only Models 1 and 2 were compared. The log likelihood shows that the difference between these two models is statistically non-significant. Thus, Model 1 will be fitted.

Table 3.5: Estimates of (co)variance components (g/day)² and genetic parameters for average daily gain using different models

Parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ_a^2	3660.46	3356.37	3867.23	4071.53	3356.49	4086.76
σ_m^2			0.0035	65.72	0.0083	122.03
σ_{am}				-474.22		-674.20
σ_c^2		1245.60			1245.59	1573.90
σ_e^2	17618.50	16641.80	17449.60	17631.80	16642.10	16184.00
σ_p^2	21280.00	21240.00	21320.00	21240.00	21240.00	21290.00
σ_e^2/σ_p^2	0.83	0.78	0.82	0.83	0.78	0.76
SE	± 0.04	± 0.05	± 0.05	± 0.05	± 0.05	± 0.03
σ_{am}/σ_p^2				-0.02		-0.03
SE				± 0.04		± 0.04
h_c^2		0.06			0.06	0.07
SE		± 0.04			± 0.04	± 0.04
r_{am}				-0.92		-0.96
h_a^2	0.17	0.16	0.18	0.19	0.16	0.19
SE	± 0.04	± 0.04	± 0.05	± 0.00	± 0.04	± 0.01
h_m^2			0.00	0.00	0.00	0.01
SE			± 0.03		± 0.00	± 0.00002
LogL	-18983.3	-18982.1	-18983.4	-18982.8	-18982.1	-18980.6
ΔLogL	-1.2	0				

See Table 3.1 for abbreviations

The estimate of h_a^2 reported in this study was comparable to other studies (Mavrogenis *et al.*, 1978; DeNise and Torabi, 1989; Stalhammer and Philipsson, 1997; Prinsloo *et al.*, 1998). Koots *et al.* (1994) reported a weighted mean heritability of 0.31 for post-weaning gain. On the contrary, higher heritability estimates of 0.40 to 0.65 were reported in literature (Kennedy and Henderson, 1975; Eriksson *et al.*, 1979; Wilton and McWhir, 1985; Bourdon and Brinks, 1986; DeNise and Ray, 1987; De Rose *et al.*, 1988; Miglior

et al., 1994). Lower heritability estimates are expected for gains made on pasture or high roughage rations compared to those for gains made on high levels of concentrate feeding. This may be due to the inadequacy of the energy intake from low-energy rations to permit full expression of genetic differences, or the increased importance of random or chance environmental variables under extensive conditions (Koots *et al.*, 1994). Hence, the heritability estimate of 0.44 from intensive central tests reported for the same breed (Scholtz and Van der Westhuizen, 1998).

The correlations between direct and maternal effects were very high (i.e. -0.92 and -0.96 for Models 4 and 6, respectively). This may be spurious correlations since Model 3 showed that maternal additive effects were negligible for average daily gain. These results are in agreement with the findings of Meyer (1992) who reported a high positive correlation of about 0.91 for final weight while the maternal genetic effect was zero. Generally, the correlation between direct and maternal effects increases as h_m^2 decreases. Waldron *et al.* (1993) indicated that the strong r_{am} might be the result of the model used rather than a biological effect.

3.3.4 Final weight

The estimates of (co)variance components and genetic parameters for final weight are presented in Table 3.6. The estimate of h_a^2 was 0.20 from Model 1. This figure changed slightly when other random effects were considered. The permanent environmental effect was almost as important (88%) as the direct additive genetic effect in Model 2. In contrast, the contribution of the maternal genetic effect was minimal at 5% for Model 3 and zero for Model 6. These results indicate that some presence of maternal additive effects is probably a cross-substitution effect. However, the reverse was true for Meyer (1993), who found that the h_m^2 (0.09) was more important than h_c^2 (0.05) in Hereford cattle.

Table 3.6: Estimates of (co)variance components (in kg^2) and genetic parameters for final weight using different models

Parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ_a^2	166.52	129.79	144.52	142.93	137.56	138.89
σ_m^2			40.35	36.65	0.59	0.87
σ_{am}				4.56		-8.52
σ_c^2		112.79			112.33	117.42
σ_e^2	668.81	587.29	650.08	650.91	587.23	581.77
σ_P^2	835.30	829.90	834.90	835.1	829.80	830.40
σ_e^2/σ_P^2	0.80	0.71	0.78	0.78	0.71	0.70
SE	± 0.05	± 0.05	± 0.05	± 0.05	± 0.05	± 0.03
σ_{am}/σ_P^2				0.01		-0.01
SE				± 0.05		± 0.0004
h_c^2		0.14			0.14	0.14
SE		± 0.04			± 0.04	± 0.04
r_{am}				0.60		-0.77
h_a^2	0.20	0.16	0.17	0.17	0.16	0.17
SE	± 0.05	± 0.04	± 0.05	± 0.05	± 0.04	± 0.007
h_m^2			0.05	0.04	0.00	0.00
SE			± 0.03	± 0.05		
$LogL$	-13467.5	-13459.9	-13466.1	-13466.1	-13459.9	-13459.7
$\Delta LogL$	-7.6***	0				

See Table 3.1 for abbreviations

Rutledge *et al.* (1972) working with mice, found no evidence of post-natal maternal effects on 42 to 82-day gain, and thus ascribed the persistence of maternal effects on post-weaning weight to differences acquired prior to 42 days or weaning. Meyer (1993) found a high correlation between weaning and yearling permanent environmental effects. This indicates that a large proportion of the maternal effects observed at yearling is a carry-over effect of the maternal influence at weaning.

Heritability estimates from the 'best' model (2) were considerably lower than those reported in other studies (Ojala, 1984; Nelsen *et al.*, 1986; DeNise and Ray, 1987; Miglior *et al.*, 1994). Most of these studies were conducted under more standardized conditions of high nutritional regimes compared to this study. Mavrogenis *et al.* (1978) indicated that higher heritability estimates found in studies conducted under intensive conditions were

due to a reduction in the environmental variance. Estimates of heritability as high as from 0.4 to 0.61, were also reported in the literature (Brinks *et al.*, 1962; Swiger *et al.*, 1963; Mavrogenis *et al.*, 1978; Bourdon and Brinks, 1986).

3.3.5 Scrotal circumference

The estimates of (co)variance components and genetic parameters for scrotal circumference are presented in Table 3.7. The fitting of a simple animal model is very common in studies concerning scrotal circumference. The approach used in this study was to include additional random components of the maternal effects, leading to the fitting of six different models. There was a decline in σ_a^2 from Models 1 to 6. The decline was more pronounced in Models 2 and 5, where the permanent environmental effect was considered.

The direct heritability estimate was highest in Model 1 (0.44). Model 2 shows that the fitting of only the direct additive effect overestimates the direct genetic component. From Models 3 to 6, the maternal genetic effect was not important for scrotal circumference. The high estimate (0.12) for h_c^2 in Model 2 shows that the permanent environmental effect is important for this trait. Thus Model 2 proves to be the 'best' model describing variation in the data set. This was in sharp contrast to the results of Van Marle-Köster *et al.* (1999) who found no effect of permanent environment on yearling scrotal circumference. These authors, however, reported small permanent environmental effect (0.03) for weaning scrotal circumference for Hereford cattle.

Considering Model 1, the direct heritability estimate was comparable to the weighted average of heritabilities of 0.51 and 0.53 reported by Koots *et al.* (1994) and De Rose *et al.* (1988), respectively. Neely *et al.* (1982) reported a similar estimate of 0.44. The estimate of direct additive heritability from Model 2 (0.37) agrees with 0.38 reported by Latimer *et al.* (1982). In general, heritability estimates in literature ranged from 0.36 to 0.78 (Coulter and Foote, 1979; Knights *et al.*, 1984; Bourdon and Brinks, 1986; Nelsen *et al.*, 1986; Smith *et al.*, 1989; Kriese *et al.*, 1991*b*; Meyer, 1991; Miglior *et al.*, 1994; Evans *et al.*, 1999). The

Table 3.7: Estimates of (co)variance components (in mm^2) and genetic parameters for scrotal circumference using different models

Parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ_a^2	217.00	182.59	194.36	194.30	183.83	191.52
σ_m^2			22.39	21.97	0.001	4.72
σ_{am}				0.57		-16.55
σ_c^2		59.84			62.82	67.40
σ_e^2	280.79	249.48	278.48	278.74	245.78	244.81
σ_p^2	497.80	491.90	495.20	495.60	492.4	491.90
σ_e^2/σ_p^2	0.56	0.51	0.56	0.56	0.50	0.50
SE	± 0.06	± 0.06	± 0.06	± 0.06	± 0.06	± 0.06
σ_{am}/σ_p^2				0.001		-0.03
SE				± 0.05		± 0.005
h_c^2		0.12			0.13	0.14
SE		± 0.04			± 0.04	± 0.05
r_{am}				0.88		-0.55
h_a^2	0.44	0.37	0.39	0.39	0.38	0.39
SE	± 0.06	± 0.06	± 0.06	± 0.07	± 0.06	± 0.07
h_m^2			0.05	0.04	0.00	0.01
SE			± 0.03	± 0.05	± 0.03	± 0.04
LogL	-12489.9	-12484.7	-12488.9	-12488.9	-12484.7	-12484.4
ΔLogL	-5.2***	0				

See Table 3.1 for abbreviations

heritability estimate of 0.37 from Model 2 indicates that selection for scrotal circumference should result in considerable genetic progress.

3.3.6 Shoulder height

The estimates of (co)variance components and genetic parameters for shoulder height are summarized in Table 3.8. The results from Models 3 through 6 shows that the maternal genetic effect is not important for shoulder height. The heritability estimate for the direct additive effect from Model 2 was lower than in Model 1 where it was overestimated. The estimate of 7% for the permanent environmental effect was quite substantial to necessitate its inclusion in the model. However, given the few numbers of progeny per dam in this

study, it is suspected that the effect of the permanent environmental effect might be an artifact of the data structure. In addition, considering changes in the log likelihood, Model 2 is also significantly different from Model 1 and therefore Model 2 is the operational model of choice.

Table 3.8: Estimates of (co)variance components (in mm^2) and genetic parameters for shoulder height using different models

Parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ_a^2	260.79	227.55	244.67	224.38	227.54	176.73
σ_m^2			13.30	3.58	0.002	0.78
σ_{am}				26.97		7.75
σ_c^2		47.34			47.34	46.15
σ_e^2	381.31	361.04	382.05	384.89	361.04	394.70
σ_P^2	642.10	636.00	640.00	638.8	635.90	626.1
σ_e^2/σ_P^2	0.59	0.57	0.60	0.60	0.57	0.63
SE	± 0.06	± 0.06	± 0.06	± 0.06		± 0.03
σ_{am}^2/σ_P^2					0.04	0.01
SE						± 0.0005
h_c^2		0.07			0.07	0.07
SE		± 0.04			± 0.04	± 0.04
r_{am}				0.92		0.66
h_a^2	0.41	0.36	0.38	0.35	0.36	0.28
SE	± 0.06	± 0.06	± 0.07		± 0.06	± 0.01
h_m^2			0.02	0.01	0.00	0.001
SE			± 0.03		± 0.00	± 0.0001
LogL	-12937.3	-12935.3	-12937.0	-12936.7	-12935.3	-12936.0
ΔLogL	-2.0**	0				

See Table 3.1 for abbreviations

Kriese *et al.* (1991b) found different results whereby the maternal additive effect (0.19) was the only maternal influence on shoulder height. The direct heritability estimate of 0.41 from Model 1 was within the ranges of 0.27 to 0.77 reported in the literature (Neville *et al.*, 1978; Sasaki *et al.*, 1982; De Rose *et al.*, 1988; Kriese *et al.*, 1991b; Koots *et al.*, 1994; Miglior *et al.*, 1994; Van Marle-Köster *et al.*, 1999). Bullock *et al.* (1993) reported an estimate of 0.59 for yearling hip height in Polled Hereford cattle. Literature estimates of hip and wither height in dairy cattle of various ages, ranged from 0.34 to 0.77 (Phillipsson,

1976; Ali *et al.*, 1984).

3.3.7 Body length

The estimates of (co)variance components and genetic parameters for body length are summarized in Table 3.9. According to the log likelihood values, Model 2 was found to be significantly different from the simplest model (Model 1). These results show that the heritability estimate for the direct additive effect was low ($h_a^2 = 0.15$). However, this estimate was not unexpected because it is difficult to measure this trait accurately. Similar estimates of heritability of 0.14 for h_a^2 and lower permanent environmental effects (0.04) at yearling were reported in Hereford cattle by Van Marle-Köster *et al.* (1999).

Table 3.9: Estimates of (co)variance components (in mm^2) and genetic parameters for body length using different models

Parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ_a^2	252.81	206.95	207.59	199.61	206.82	196.54
σ_m^2			59.49	30.04	0.23	1.72
σ_{am}				35.33		15.46
σ_c^2		141.58			141.40	129.89
σ_e^2	1176.63	1074.30	1159.34	1161.93	1074.32	1079.33
σ_P^2	1429.00	1423.00	1426.00	1427.00	1423.00	1423.00
σ_e^2/σ_P^2	0.82	0.76	0.81	0.81	0.76	0.76
SE	± 0.05	± 0.05	± 0.04	± 0.05	± 0.05	± 0.03
σ_{am}/σ_P^2				0.02		0.01
SE				± 0.04		± 0.0004
h_c^2		0.10			0.10	0.09
SE		± 0.04			± 0.04	± 0.04
r_{am}				0.46		0.84
h_a^2	0.18	0.15	0.15	0.14	0.15	0.14
SE	± 0.05	± 0.04	± 0.05	± 0.05	± 0.04	± 0.01
h_m^2			0.04	0.02	0.00	0.00
SE			± 0.03	± 0.04		
LogL	-14390.7	-14386.7	-14389.6	-14389.4	-14386.7	-14386.7
ΔLogL	-4.0**	0				

See Table 3.1 for abbreviations

The high positive correlation between direct and maternal genetic effects was of less concern since there was almost no maternal genetic influence in this trait as shown in Models 4 and 6. This result suggests that this correlation may be spurious.

3.4 Conclusions

In general, heritability estimates reported in this study were in agreement with estimates found in the literature. The heritability estimates for both direct and maternal genetic components for BW and WW were adequate to lead to significant improvements through selection in these traits. However, the highly negative genetic correlation between the direct and maternal genetic effects would make simultaneous improvement through selection difficult, particularly for weaning weight where the total heritability (h_T^2) was found to be low.

Attempts to reduce the negative correlation between direct and maternal genetic effects by fitting an additional random effect, namely, the sire \times herd-year-season interaction, confirms the possibility of the bias associated with strong negative direct-maternal correlation in field data. However, this did not improve h_T^2 , rather it made it worse. Since the nature of this interaction is not understood as indicated by Lee and Pollak (1997), fitting of a sire \times herd-year-season interaction in models for routine estimation of EBVs for these traits cannot be considered at the moment.

High heritability estimates for scrotal circumference and body height clearly indicate that significant progress can be achieved through selection for these traits. The high genetic correlation between scrotal circumference and pregnancy rate in cows (Toelle and Robison, 1985) is an indication that scrotal circumference may be useful as an alternative selection criterion in selection for fertility in both male and female calves. Lower heritability estimates found in average daily gain and final weight indicate that selection for growth (as expressed by average daily gain and final weight) under low nutritional regimes, will still

be possible, but might not be as fast as it could be expected under good environmental conditions. Furthermore, the lower heritability estimate reported for body length is an indication that direct selection for this trait may be slower than for body height.

Chapter 4

Additive genetic relationships among body measurements and growth traits

4.1 Introduction

The progress made when selecting for two or more characteristics depends in large part on the actual intensity of selection, the heritabilities of and the genetic correlations between these characteristics. Selection for a particular trait in one direction is likely to be accompanied by a decline or improvement in other genetically correlated traits. For example, genes that increase growth rate increase both stature and weight (Falconer, 1989). Genetic correlations between characters can arise by two mechanisms (Falconer, 1989):

- pleiotropy - the property of a gene whereby it affects two or more traits, so that if the gene is segregating it causes simultaneous variation in the characters it affects.
- linkage - the phenomenon where inheritance at two or more loci is non-independent due to linkage i.e. some combination of alleles are more likely to be inherited together

than others.

While pleiotropy is responsible for permanent genetic associations, linkage causes temporary (transient) genetic relationships between traits. Genetic correlations may be estimated between the same measurement on different animals or between different measurements on the same individual (Robertson, 1959; Yamada, 1962). The former approach is considered in studies investigating genotype \times environment interactions. For the purpose of this study, genetic correlations between different measurements in the same individual were considered.

The estimation of genetic correlation is an extremely demanding enterprise, requiring substantially larger sample sizes than are necessary in univariate analysis. This is largely due to the fact that a number of covariances between traits have to be estimated. Furthermore, the inclusion of a nonzero covariance between additive direct and maternal genetic effects is likely to considerably increase the computing time, because it reduces the sparsity of the MME coefficient matrix, so that the inversion or factorization in REML algorithm becomes prohibitive (Chapuis *et al.*, 1996). However, developments in computing power and statistical modeling have enabled the fitting of more complicated multivariate models. These multivariate analyses produce estimates that are unbiased by selection when all the information related to selection is included (Ducos *et al.*, 1993).

The purpose of this study was to estimate (co)variance components and genetic correlations among body measurements and some growth traits fitting multivariate models in Bonsmara bull calves participating in post-weaning growth tests.

4.2 Materials and methods

4.2.1 Data

The data for this study have already been described in Chapter 3. Traits considered were scrotal circumference, body length, shoulder height, birth weight, weaning weight, final weight and average daily gain on test.

4.2.2 Statistical analyses

A series of multivariate analyses were used to cover the full range of covariances amongst traits. This was due to the fact that the package used could not allow simultaneous estimations of (co)variance components for all the traits. The first multivariate model included 8 traits i.e. direct and maternal genetic effects for birth and weaning weight, final weight, scrotal circumference, body length and shoulder height. Series of 4-trait models were also run to cover the covariances between average daily gain and all other traits considered in this study. It was, therefore, possible that more than one value exist for some estimates, in which case the (co)variance components and ratios were pooled, weighting each estimate by the inverse of its sampling variance (SE^2) (Koots *et al.*, 1994) as follows:

$$h_{pooled}^2 = \frac{\sum_{i=1}^n h_i^2 / (SE_{h_i^2})^2}{\sum_{i=1}^n 1 / (SE_{h_i^2})^2}$$

Models 'best' fitting the data were identified in Chapter 3 from univariate analyses. Though permanent environmental effects were important for some post-weaning traits such as final weight, scrotal circumference and body length, a simple model fitting only the direct genetic effect and the residual was considered for these traits in multivariate analyses. The fitting of a simple model for all post-weaning traits was due to the computational limitation imposed by the data set. However, Model 6 was fitted for both birth and weaning weights.

The models were fitted in ASREML which uses the Average Information Algorithm and a multivariate animal model to obtain estimates of the (co)variance components (Gilmour *et al.*, 1996).

4.3 Results and discussions

4.3.1 Heritability estimates

Heritability estimates from both univariate (Chapter 3) and multivariate models are given in Table 4.1. Estimates of heritability from univariate analyses were comparable to those from multivariate analyses with some few exceptions. These findings were consistent with those of Meyer (1993) who found that selection bias had little influence on heritability estimates.

Table 4.1: Heritability estimates from univariate and multivariate analyses for body measurements and growth traits

Trait	Analyses	
	Univariate	Multivariate
Birth Direct	0.32±0.05	0.31±0.05
Birth Maternal	0.13±0.04	0.10±0.03
Wean Direct	0.25±0.04	0.29±0.05
Wean Maternal	0.18±0.04	0.04±0.02
ADG	0.17±0.04	0.19±0.04
FW	0.20±0.05	0.30±0.05
BL	0.18±0.05	0.27±0.05
SL	0.41±0.06	0.42±0.05
SC	0.44±0.06	0.46±0.06

The most pronounced effect of fitting multivariate models was in the maternal heritability (h_m^2) for weaning weight, which dropped from 18% to 4% (Table 4.1). The heritability estimates for body length and final weight were drastically increased from 18% to 27% and 18% to 30%, respectively, from univariate to multivariate analyses. The birth maternal

was also slightly reduced but remained within ranges reported in literature i.e. from 13% to 10%. Heritability estimates for these traits suggest that these traits should respond to selection though the response might be slow for post-weaning growth rate (ADG) and body length.

4.3.2 Genetic correlations

Scrotal circumference and other traits. Additive genetic correlations between SC and weight traits, and other body measurements were moderate (Table 4.2). The correlation between SC and WW direct was 0.22 ± 0.11 . However, a high standard error associated with this estimate suggests that this correlation could even be zero. Similar estimates of 0.08 and 0.14 were reported in Hereford and Limousin cattle by Kriese *et al.* (1991b) and Keeton *et al.* (1996), respectively. However, Kriese *et al.* (1991b) found a higher value of 0.34 in Brangus cattle. It therefore seems that selection for bulls with large SC will not hamper the pre-weaning growth potential of their progeny.

Scrotal circumference in young bulls is regarded as a potentially useful indicator of reproductive potential in beef cattle (Bourdon and Brinks, 1986). Toelle and Robison (1985) found that SC was highly correlated with age at puberty of their female half sibs. In the present study, the correlation (0.38 ± 0.13) of SC with maternal performance of the calves for weaning weight was favourable and moderately positive (Table 4.2). This result was consistent with that of Kriese *et al.* (1991b), who reported a value of 0.22. This is further consolidation of the importance of SC as a selection criterion for both reproductive and maternal performance in female animals. However, Keeton *et al.* (1996) reported a negative correlation of -0.22 between these same traits. Therefore, bulls with large SC will generally produce daughters with enhanced maternal performance at weaning.

The positive correlations between SC and both direct and maternal genetic effects was not surprising, because the direct-maternal correlation for weaning weight from multivariate analyses was lowly negative with high standard error (-0.12 ± 0.15) suggesting

Table 4.2: Heritability estimates (diagonal) and genetic correlations between body measurements and growth traits (off-diagonal)

Trait	BW		WW		ADG	FW	SC	BL	SH
	Direct	Maternal	Direct	Maternal					
BW Dir	0.31±0.05	0.24±0.16	0.45±0.09	-	0.28±0.13	0.45±0.10	0.25±0.10	0.35±0.11	0.38±0.10
BW Mat		0.10±0.03	-	0.30±0.16	0.36±0.19	0.26±0.13	-0.22±0.15	0.09±0.15	0.29±0.13
WW Dir			0.29±0.05	-0.12±0.15	0.26±0.15	0.71±0.07	0.22±0.11	0.60±0.09	0.54±0.10
WW Mat				0.04±0.02	0.03±0.17	0.45±0.13	0.38±0.13	0.32±0.14	0.21±0.13
ADG					0.19±0.04	0.67±0.08	0.10±0.13	0.55±0.11	0.40±0.11
FW						0.30±0.05	0.37±0.10	0.83±0.05	0.72±0.06
SC							0.46±0.06	0.28±0.11	0.08±0.10
BL								0.27±0.05	0.76±0.06
SH									0.42±0.05

independence between these two traits. The direct-maternal correlation for weaning weight was considerably different from the strong negative correlation found in univariate analyses (-0.54). Though proper explanation cannot be advanced for this reduction, it seems that the inclusion of other traits might have provided more information for the estimation of this component. Low direct-maternal correlations have also been reported by Meyer (1993).

The direct-maternal correlation for birth weight was -0.24 ± 0.16 . The correlation between SC and birth direct genetic effects of 0.25 ± 0.10 and that between SC and birth maternal of -0.22 ± 0.15 indicate that selection for SC might lead to increased birth weight and a decline in prenatal maternal performance of the progeny. Knights *et al.* (1984) reported a low, but positive correlation between birth weight and SC. Contrasting results were, however, reported by Nelsen *et al.* (1986) who found a correlation of almost zero between SC and birth weight (-0.04). Van Marle-Köster *et al.* (1999) found that SC was highly negatively (-0.65) correlated with birth weight in Hereford cattle.

The highest correlation between SC and growth traits was for final weight (0.37 ± 0.05). This correlation was comparable to earlier findings by Bourdon and Brinks (1986) in Hereford and Nelsen *et al.* (1986) who reported a value of 0.44. A slightly higher correlation of 0.52 between SC and 305d weight was found by Neely *et al.* (1982). This result suggest that selection for bulls with large SC may lead to progeny that are fast growing.

Post-weaning gain on test (ADG) was lowly correlated to SC (0.10 ± 0.13). Evidence of a low correlation between these traits have also been reported by Kriese *et al.* (1991b) and Miglior *et al.* (1994) in Brangus and Limousin, respectively. Moderately positive but higher estimate of 0.37 was found in Hereford (Bourdon and Brinks, 1986). Thus, selection for scrotal circumference should result in little or no response in post-weaning gain.

Genetic correlation between SC and body length was low (0.28 ± 0.11) while that for shoulder height was almost zero (0.08 ± 0.10). The high standard error associated with the estimate for the correlation between SC and shoulder height is an indication that no

genetic relationship exists between these two traits. Therefore, selection for SC should not be accompanied by a correlated response in shoulder height while a tendency towards longer animals should be expected from this selection. The findings of Van Marle-Köster *et al.* (1999) were consistent with the results of this study. In their study, the genetic correlation between scrotal circumference and body length at yearling was 0.21 and -0.01 for SC and hip height at yearling. Low correlation between SC and hip height was also reported in other studies (Nelsen *et al.*, 1986; Miglior *et al.*, 1994). However, Bourdon and Brinks (1986) reported a genetic correlation between SC and hip height at 365d of 0.42.

Body length and other traits. Genetic relationship between body length and other traits ranged from low to high i.e. 0.09 ± 0.15 to 0.83 ± 0.05 . The lowest correlation (0.09 ± 0.15) was between body length and birth weight maternal. Therefore, selecting for long-bodied bulls will not affect the prenatal maternal performance of their daughters. However, the moderate correlation between body length and birth weight direct of 0.35 ± 0.11 indicates that long-bodied bulls will sire calves that have superior prenatal growth.

Strong positive correlations between body length and direct weaning and final weights indicate that the growth potential of calves from birth to end of test will be enhanced by selecting for bulls with long bodies. Body length was also found to be positively correlated with post-weaning gain and maternal performance at weaning. These results show that longer bulls tend to grow faster and sire daughters with good maternal performance. These results suggest that weaning weight direct, final weight and average daily gain could be used to improve body length by indirectly selecting on them, since body length is lowly heritable.

Shoulder height and other traits. Shoulder height was found to be highly correlated with body length (0.76 ± 0.06). Correlations between shoulder height and other traits are consistently similar to those of body length and other traits, hence a high correlation

between these two traits. However, the correlation between shoulder height and growth traits were low to high with the highest correlation found between shoulder height and final weight.

Shoulder height was found to be positively and favourably correlated with both birth weight direct and maternal genetic effects. The correlation for shoulder height and direct weaning weight was high (0.54 ± 0.10). In the contrary, the correlation between shoulder height and maternal weaning weight was low (0.21 ± 0.13). Therefore, selecting for shoulder height should result in improvements in body length, final weight and weaning weight direct. In addition, shoulder height should be easy to measure where there is no weigh-bridge. Contrary to these findings, Kriese *et al.* (1991b) reported a moderate, negative genetic correlation between maternal weaning weight and hip height.

Growth traits. The major concern is, however, on the effect of weight traits that are expressed early in life on other economically important traits measured late in life such as final weight and average daily gain. Generally, the genetic correlation between growth traits were moderate to high.

Though ADG was found to be correlated to other growth traits, the highest correlation was with final weight (0.67 ± 0.08) as expected. This correlation was comparable to the estimate of 0.44 reported by Miglior *et al.* (1994). However, the correlation between these two traits was not unexpected due to the fact that final weight is a component of ADG and thus there is auto-correlation between them. It is therefore apparent that animals with high growth rates on test tend to have high final weights at the end of the test.

The correlation between post-weaning growth rate (ADG) and direct weaning weight was 0.26 ± 0.15 . A similar estimate of 0.27 ± 0.20 was reported in bulls by Koch *et al.* (1974). Bennett and Gregory (1996) reported a higher estimate (0.56) between 168d gain and direct weaning weight. Chapman *et al.* (1969) and Chavraux and Bailey (1977) reported a positive response in weaning weight of the progeny from selection on post-weaning gain of the

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sires. The correlation between growth rate and maternal weaning weight was almost zero (0.03 ± 0.17). Selection for bulls with high post-weaning growth rate should result in calves that are constantly heavier at weaning with little or no effect on maternal performance of daughters at weaning. The moderate correlation between post-weaning growth rate and maternal birth weight (0.36 ± 0.19) suggest that selection for growth rate will improve the prenatal maternal performance.

As was expected, a positive but unfavourable genetic correlation was found between direct birth weight and final weight (0.45 ± 0.10). Van Marle-Köster *et al.* (1999) also reported a positive but slightly higher correlation between birth weight and yearling weight (0.50). A correlation of 0.45 ± 0.09 was found for direct birth weight and direct weaning weight, indicating a positive relationship between pre- and post-natal direct genetic effects.

4.4 Conclusions

Estimates of heritability found in this study indicate that sufficient additive genetic variance exists in these traits, which should therefore respond to selection. However, slower progress should be expected in post-weaning ADG and body length.

Generally, genetic correlations between body measurements and growth traits were favourably positive. The positive correlation between scrotal circumference and maternal weaning weight suggests that selection for scrotal circumference could lead to improved maternal performance of the daughters of such bulls.

It was important to note that the genetic correlation between scrotal circumference and post-weaning growth rate (ADG) was almost zero, implying selecting for bulls with large scrotal circumference should not interfere with the post-weaning growth rate of their progeny. A positive correlation between scrotal circumference and body length with no correlation with shoulder height is desirable. Selection for scrotal circumference should be advantageous because it can lead to long animals without any concomitant change in

height. However, the high correlation between body length and shoulder height proposes that selection for either of these traits will result in an increase in the other and selection for these two traits should be practiced with caution. Moderate to high correlations between growth traits suggest that growth measures, particularly weight, are influenced by similar genes and selection for one weight traits is likely to increase weight at other stages.

Therefore, the results of this study shows that simultaneous selection for body measurements and growth traits is feasible. The practical implications of these results are that body measurements may be useful as selection criteria for performance traits in those scenarios where weight measures might not be feasible.

Chapter 5

General conclusions and recommendations

Response to selection has always been a major concern to animal breeders. Though response depends on many factors, the heritability of a trait primarily determines whether it is at all possible to genetically improve a particular trait or not. However, variable heritability estimates have been reported in literature due to factors such as breed, sex and data structure.

The results of this study have revealed that body measurements are highly heritable though the heritability of body length was low. The heritability estimates for growth traits was generally low to moderate. Generally, changing the size or shape of the animals may be achieved easily. Selection for growth traits will, however, be slower as opposed to those animals that are evaluated under good nutritional regime.

Selection for a trait is always followed by a correlated response in genetically correlated traits. Thus, the practical importance of body measurements regarding their relationship to performance traits is a major concern. The results of this study show that correlations between body measurements and performance traits were positive and favorable

though a low negative correlation was found between scrotal circumference and maternal birth weight. Correlations close to zero were also found between scrotal circumference and post-weaning ADG. It was interesting to note that no significant genetic relationship (multivariate analyses) was found between direct and maternal weaning weight. Therefore, selection for direct weaning weight is likely not to affect the maternal performance of the individual. These results suggest that selection for most of the traits will not hamper the maternal performance of the daughters.

The positive correlation between body length and post weaning growth rate indicates that selection for body length will lead to animals that grow faster. However, the high positive correlation between body length and shoulder height may be problematic since selection for long-bodied bulls will be accompanied by increase in the height of the animal. Therefore, weighting factors should be used between these two traits.

Selection for large animals at the end of the test will positively enhance maternal performance at weaning in progeny. Post-weaning growth rate was found to be uncorrelated to maternal weaning performance. Thus, selection for fast growing bulls will not affect the maternal performance of their daughters.

It could therefore be concluded from the favorable correlations between body measurements and performance traits that simultaneous selection for both traits may not lead to undesirable results. Furthermore, rapid progress may be achieved in individual traits by considering fewer traits with high heritabilities. However, further research needs to be conducted to evaluate which of those traits considered in this study are of economic importance so that an appropriate selection index can be developed.

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