

**EFFECT OF SELECTION AT WEANING ON GENETIC
PARAMETERS OF WEIGHT GAIN FOR CENTRALIZED AND
ON FARM TEST FOR BEEF BULLS**

By

**Mashiloane Majela Lesley
(B Sc. Agric)**

Mini dissertation submitted to the discipline of Animal Production in the
school of Agricultural and Environmental Science of the Faculty of Health,
Science and Agriculture of University of Limpopo in partial fulfillment of
the requirements for the degree

**Master of Science in Agriculture
(Quantitative Animal Breeding and Genetics)**

2007

Supervisor: Dr D. Norris

Co-supervisors

Dr A. Maiwashe

Dr K. A. Nephawe

Prof J.W. Ng'ambi

Dr M.S. Malatje

Declaration

I Majela Lesley Mashiloane (First author) hereby declare that the information contained in this document was self originated and compiled and that all sources of reference utilized were duly acknowledged. This document has never been presented for the current or any other degree by the author or any other person at this or any other university.

.....

.....

Signature

Date

Acknowledgements

Execution of this study was carried out through financial backing by THRIP (Technology and Human Resource for Industry Project) and NRF (National Research Foundation). The author would like to thank the South African Angus Breeders Society for the data utilized in this study and the Agricultural Research Council (ARC) for their technical training and facilities used for the integral part of this project. Special acknowledgements to supervisors Norris D., Nephawe K.A. Maiwashe A., Ng'ambi J.W. and Malatje M.S. for their invaluable inputs and efforts which made this project what it turned out to be.

Conception of this study was made possible with aid from the team of researchers from Best linear Unbiased Prediction (BLUP) section of the Livestock Business Division of the Agricultural Research Council which included Theron H.E., Nephawe K.A., Maiwashe A., Banga C. and van der Westhuizen R.R.

Dedication

This manuscript is dedicated to my late uncle **Nkotsane Rufus Mashiloane[†] (1961-2006)** who passed away weeks after the onset of this project. The legacy he left me is the words that keep me going in hard and trying times “monsters that we fear most are monster we create” and it shall live with me forever. **O robale ka khutšo Mokone.**

TABLE OF CONTENTS

Chapter	Page
Declaration	I
Acknowledgements	II
Dedication	III
Abstract	IV
Table of contents	V
List of tables	VI
List of appendices	VII
General Introduction	1
2 Review of literature	6
2.1. South African Beef cattle Improvement Scheme	7
2.2. Estimates of genetic parameters for ADG of performance tested bulls	9
2.3. Environmental factors affecting post-weaning ADG in test stations	10
2.4. The relationship between pre-weaning and post-weaning performance	11
2.5. Effect of pre-weaning information on the genetic analysis of post-weaning traits	13
2.6. Summary	16
3. Materials and Methods	17
3.1. Data Description	17
3.2. Statistical Analysis	20
3.2.1. Preliminary Analysis	20
3.2.2. Estimation of (co)variance components and genetic parameters	20

4. Results and Discussion	25
4.1. Summary Statistics	25
4.2. Fixed Effect Modeling Results	26
4.3. (Co)variance components	27
4.4. Variance Ratios and Genetic correlations	29
4.5. Estimated Breeding Value Rank Correlations	34
5. Conclusions and Recommendations	38
5.1. Conclusions	38
5.1. Recommendations	39
6. References	40

Abstract

The objectives of this study were to evaluate the effect of pre-weaning selection on estimates of genetic parameters for post-weaning average daily gain in Phases C (ADG-C) and D (ADG-D) and to estimate genetic relationships between average daily gain in the two phases. Performance records of the South African Angus cattle breed was used in the analysis. (Co)variance components and genetic parameters for weaning (WWT), AGD-C and ADG-D were estimated by REML procedures fitting three different models (Models 1, 2 and 3) that differed in how they integrated sequential selection in the analysis of post-weaning traits. Model 1 was a univariate model of WWT, ADG-C and ADG-D. Model 2 was a two trait model of WWT and either ADG-C or ADG-D. Model 3 was a three trait model of WWT, ADG-C and ADG-D. Estimates of heritability for ADG-C were 0.39 ± 0.08 , 0.42 ± 0.06 and 0.44 ± 0.01 from Model 1, 2 and 3 respectively. Corresponding estimates of heritability for ADG-D were 0.18 ± 0.021 , 0.19 ± 0.021 and 0.21 ± 0.02 respectively. An estimate of genetic correlation between ADG-C and ADG-D was $0.58 \pm$ and it suggested that the two traits may not necessarily be under the same genetic control. Rank correlations for all bulls based on ADG-C estimated breeding values (EBV's) were 0.92, 0.83 and 0.94 for Model 1 vs. Model 2, Model 1 vs. Model 3 and Model 2 vs. Model 3 respectively. Corresponding ADG-D EBV's rank correlations were 0.88, 0.84 and 0.93. Rank correlations for top and bottom 1%, 5% and 10% were lower than those for all bulls in both ADG-C and ADG-D. Low rank correlations showed that the difference in magnitude of genetic parameters from different models was enough to alter bull rankings based on EBV's of ADG-C and ADG-D. Hence it was concluded

that inclusion of pre-weaning information in genetic analysis for post-weaning average daily gain is necessary to account for selection at weaning.

TABLE OF CONTENTS

Chapter	Page
Declaration	I
Acknowledgements	II
Dedication	III
Abstract	IV
Table of contents	V
List of tables	VI
List of appendices	VII
General Introduction	1
2 Review of literature	6
2.1. South African Beef cattle Improvement Scheme	7
2.2. Estimates of genetic parameters for ADG of performance tested bulls	9
2.3. Environmental factors affecting post-weaning ADG in test stations	10
2.4. The relationship between pre-weaning and post-weaning performance	11
2.5. Effect of pre-weaning information on the genetic analysis of post-weaning traits	13
2.6. Summary	16
3. Materials and Methods	17
3.1. Data Description	17
3.2. Statistical Analysis	20
3.2.1. Preliminary Analysis	20
3.2.2. Estimation of (co)variance components and genetic parameters	20

4. Results and Discussion	25
4.1. Summary Statistics	25
4.2. Fixed Effect Modeling Results	26
4.3. (Co)variance components	27
4.4. Variance Ratios and Genetic correlations	29
4.5. Estimated Breeding Value Rank Correlations	34
5. Conclusions and Recommendations	38
5.1. Conclusions	38
5.1. Recommendations	39
6. References	40

List of tables

Table	Page
1. Characteristics of the data structure	19
2. Summary statistics for traits and covariates	25
3. Analysis of variance for fixed effects	26
4. (Co)variance components for weaning weight and average daily gain in Phase C (ADG-C) and Phase D (ADG-D)	28
5. Variance ratios and genetic correlations for weaning weight (WWT) and Average daily gain in Phase C (ADG-C) and Phase D (ADG-D)	30
6. Rank correlations based on EBV for ADG-C from different models	35
7. Rank correlations based on EBV for ADG-D from different models	36

List of appendices

Appendix	Page
1. Testing phases of the South African National Beef Cattle Improvement Scheme	52

Chapter 1

General Introduction

Genetic evaluation of beef cattle dates back to the early days of the art of animal improvement. As early as 1944, Dickerson and Hazel studied the relative merits of performance and progeny testing as a basis for selection for improvement (Harris and Newman, 1994). In the beef cattle industry, the practice of performance testing is aimed at providing the industry with objective performance information on individual animals in order to improve the biological and economic efficiency of beef production.

In South Africa, the National Beef Cattle Improvement Scheme (NBCIS) administered by the Agricultural Research Council (ARC) is tasked with the responsibility of providing beef cattle performance information to beef producers. The scheme comprises of five phases to cover the entire production cycle i.e. Phase A, B, C, D and E. The first two phases (Phases A and B) are the evaluation of the cow herd, Phase C is the standardized central growth test of young beef bulls, Phase D is the on-farm growth test of young beef bulls, while Phase E is the feedlot recording and slaughter phase.

Selection of elite breeding bulls is done at Phases C and D based on performance in postweaning traits. Sire selection aided by test station records increases selection intensity (within breed) and hence increased genetic gain in traits of interest (Cain and Wilson, 1983). In Phase C, weekly measurements of weight gain and feed intake are recorded, while body measurements such as shoulder height, body length and scrotal

circumference are recorded at the end of test. Similar measurements recorded in Phase C are also taken in Phase D, with the exception of feed intake.

The literature reveal that proper bull selection is the most rapid way to change genetic composition of a herd of cattle (Kriese *et al.*, 1991) and thus emphasis should be on performance testing with concentration on bull selection (Tawah *et al.*, 1994). It is therefore not surprising that most of genetic progress in beef cattle is associated with postweaning growth and this is in line with the objectives of beef improvement (Koch *et al.*, 1995).

Knowledge of genetic parameters for economically important traits in beef cattle is required for estimation of breeding values and development of breeding objectives. Estimates of genetic parameters are currently obtained using the best linear unbiased prediction (BLUP) procedure developed by Henderson (1975). BLUP was introduced to the South African beef cattle industry on a national level in 1994 when univariate models were used to predict breeding values for traits measured in Phases A and B (Bradfield *et al.*, 2000).

The assumptions and properties of BLUP require that the unknown (co)variance components be substituted with the most accurate estimates available (Woodward *et al.*, 1992). Schaeffer *et al.* (1997); Kaps *et al.* (1999) and Long *et al.* (1991), state that selection of animals could influence genetic parameters estimated from their performance records. The main assumption when estimating genetic parameters from linear models is that there is random sampling of data, however Long *et al.* (1991) and Van der Werf and

Thompson (1992), indicated that this assumption is usually violated when field data is used because it includes records of selected animals.

A common management practice in South Africa is to cull poor performing and functionally inefficient animals at weaning before further testing in Phase C or D (Bradfield *et al.*, 2000) this constitute an intense level of sequential selection. Sequential selection has been indicated to have major effects on genetic parameter estimates and thus it requires specific statistical treatment (Schaeffer *et al.* 1997). The effects can be accounted for by including records on which prior selection was based (Henderson. (1986), Bulmer *et al.* (1971) and Thompson and Meyer (1986)).

In the past it was a common practice in genetic evaluation programs that traits of interest are the only traits that were included in the model of analysis for (co)variance estimation (Henderson, 1984). This practice may lead to the exclusion of the records from the early stage at which selection took place thus not incorporating the effect of selection in the analysis. Exclusion of selection records may affect the accuracy of (co)variance estimates and hence the breeding values that are derived from these estimates. Thus, there are two approaches to genetic evaluation of post-weaning traits, viz. single trait models (STM) and multiple trait models (MTM). These linear models differ on how they incorporate sequential selection in the analysis. Multiple trait models (MTM) introduce records from a stage at which prior selection was conducted and they also combine information on sequential and correlated traits to predict the genetic merit of animals for many traits

simultaneously (Tier and Meyer, 2003). Single trait models of postweaning traits do not take into consideration any preweaning or selection information (Bradfield *et al.*, 2000).

Given that these models could be indiscriminately used to estimate post-weaning genetic parameters (including Phases C and D), the current study will assess the difference of estimates and their accuracy from these different linear models. If the accuracy of breeding values estimated for use as selection tools for bulls is compromised, there will be a slow genetic progress. Satoh *et al.* (2002) indicated that maximal response of traits to selection depends on the accuracy of genetic parameters used in estimation of breeding values. Knowledge of the magnitude of the effect of selection on estimates of breeding values would be useful in assessing procedures for genetic evaluations (Long *et al.* 1991).

The aim of the current study was to assess the effect of pre-weaning selection on the estimates of subsequent genetic parameters for post-weaning traits (ADG) at centralized and on-farm growth tests of young beef bulls in South Africa. The specific objectives were to:

1. Establish if including or excluding pre-weaning information has an effect on estimates of genetic parameters for average daily gain on the centralized growth test (Phase C) of beef bulls.

2. Establish if including or excluding pre-weaning information has an effect on estimates of genetic parameters for average daily gain on the on-farm growth test (Phase D) of beef bulls.

3. Estimate genetic correlation between average daily gain in Phase C and Phase D.

4. Evaluate the effect of including or excluding pre-weaning information in genetic evaluation of post-weaning ADG by assessing rank changes based on the calculated estimates of breeding values (EBV's).

Chapter 2

Literature review

Growth traits have received considerable attention in beef cattle genetic improvement programs. The quest for high growth rate is motivated by an effort by the beef cattle industry to produce animals that attain heavy weights at market ages. Furthermore, high growth rate is associated with increased returns over short periods of time (Beltran *et al.*, 1992). The literature also reveal that the most rapid way to genetically change a herd of cattle is by proper bull selection and selecting bulls that are genetically superior in growth through national cattle evaluation programs could double genetic change as compared to within herd selection (Beltran *et al.*, 1992). Consequently, bull testing station records are an aid to sire selection and breed utilization (Cain and Wilson, 1983).

The main indicator of growth rate in bull testing stations is average daily gain (ADG) and it is used as a criterion for selection of bulls with genetic superiority for growth. However, prior to testing of bulls, there is an intense level of sequential selection at weaning. Schaeffer *et al.* (1997) indicated that sequential selection can have effects on analysis for genetic parameters of subsequent traits. Thus to obtain accurate estimates of genetic parameters, information on which selection decisions were based on at weaning should be incorporated into the analysis of post-weaning traits.

This chapter presents a review of literature on the South African National Beef Cattle Improvement Scheme (NBCIS), estimates of genetic parameters for weaning weight and post-weaning test performance, the relationship between pre-weaning and post-weaning

performance and the impact of pre-weaning information in genetic analysis of post-weaning traits.

2.1 The South African National Beef Cattle Improvement Scheme (NBCIS)

In South Africa, the National Beef Cattle Improvement Scheme (NBCIS) administered by the Agricultural Research Council (ARC) is tasked with the responsibility of providing beef producers with objective performance information in order to improve the biological and economic efficiency of beef production through genetic improvement and improved management practices (Bergh, 1999). The scheme comprises five Phases, namely A, B, C, D and E (Appendix 1). Phases A and B are on farm pre-weaning test phases which come as basic requirements and are compulsory for all beef farmers participating in the NBCIS. In Phases C (centralized test) and D (on farm test) bulls are tested for post-weaning performance (including growth and fertility) and these phases are optional. Phase E (slaughter phase) entails evaluation of carcass characteristics.

Bull testing in the NBCIS is thus performed through the two alternative phases i.e. Phase C (centralised test) and Phase D (on farm test). The two phases differ with certain technical and management aspects but the principles of testing are basically similar. These differences in test management practices, lead to a state at which Phase C (with standardized test conditions) environment becomes considerably more optimal for genetic expression than Phase D. Due to these differences Phase C has received more attention as the procedures of the test allows for maximal expression of genetic capacity due to optimized environmental conditions.

Central testing of beef bulls (Phase C) has developed into an important component of genetic improvement programs for beef cattle (Schenkel *et al.*, 2004; Scholtz *et al.*, 1998; Archer *et al.*, 1999). The main aim is to compare beef bulls fairly under a uniform management and environmental conditions (Schenkel *et al.*, 2004; Nephawe *et al.*, 2006). Records that are collected in this phase are weekly body weights and individual feed intake, whilst body measurements such as body length and scrotum circumference, ultrasonic scans, functional appearance scoring and condition scoring are only recorded at end of test. Noteworthy is that Phase C is the only test phase from which data on feed conversion ratio of individual bulls can be derived. Registered bulls (usually of above average performance at weaning and pre-weaning stages) from participating farmers aged between 151 to 250 days are eligible for central testing. The test runs for 84 days after a 28 days pre-test adaptation period. The test length of this phase was not the same over the years. Improvement of facilities and management, reduced the days required to make meaningful observations and the test length was reduced from 112 to 84 days in 1999. Further details on the Phase C testing requirements and procedures are available in NBCIS Guidelines (NBCIS, 2005).

Phase D is similar to Phase C but with less standardized environmental conditions. Phase D has always received more bulls than Phase C and this may be due to less stringent admission requirements (Bergh, 1999). Registered or grade bull calves sired by registered bulls together with bulls that meet the requirements of the performance testing scheme are eligible to enter Phase D. In this phase, the requirement is that bulls should be below 365 days of age at start of test and variation of age within a test group should not exceed

100 days. As compared to Phase C, the test duration of this phase is longer, with ranges between 21 to 90 (depending on growth rate and test procedure) for pre-test adaptation and 84 to 270 for the test period. Similar measurements collected in Phase C are also recorded in Phase D, with the exception of feed intake. Tick counts are also recorded in Phase D, although optional.

At completion of test at either Phase C or D, body weights data are used to calculate average daily gain (ADG) for each individual bull. Bergh (1999) reported the mean ADG for the South African Angus breed of 1804 g/day in Phase C, whilst Bradfield *et al.* (2000) reported 980 g/day for Phase D in the same breed.

2.2 Estimates of genetic parameters for ADG of performance tested bulls

The literature indicates that heritability estimates of ADG in test stations are moderate to high. Koots *et al.*, (1994a) reported a weighted average estimate of 0.31 for ADG for different breeds, all or most of which, may be from centralized tests (Phase C). The heritability estimates from Phase C are higher than those from Phase D perhaps because conditions in Phase C are more standardized and conducive for expression of individual genetic differences than is the case in Phase D. Bradfield *et al.* (2000) reported heritability estimates for ADG of 0.47 and 0.28 in Phase C and D respectively, for South African Angus breed. These results may be suggestive that ADG in the different phases is genetically not necessarily the same trait. Information on the magnitude of genetic association between ADG in the two phases is however limited.

2.3 Environmental factors affecting post-weaning ADG in test stations

The main aim of a central performance test is to compare bulls fairly under uniform management and environmental conditions (Schenkel *et al.*, 2004; Nephawe *et al.*, 2006). However, individual bull performance in central test stations depends upon several pre-weaning and post-weaning genetic and environmental factors (Cain and Wilson, 1983). Therefore, in order to select genetically superior bulls from within and among central test stations it is necessary to determine the influence of environmental factors on test performance. Environmental factors that influence test performance include test station, age of the bull at the start of test and herd of origin (Liu and Makarechian, 1993)

2.3.1. Test station

Despite the fact that management and nutrition are standardized in central testing centers, there is always some test center specific environmental factors which are generally unique to each test station. Self (1972) investigated test center specific factors such as housing facilities, diet and climate and reported significant difference in gain among different stations.

2.3.2. Age of bull

It is expected that during the ascending phase (before maturity) along the growth curve, older animals will have bigger weights and consequently their average daily gain will tend to be positively influenced. Liu and Makarechian (1993) indicated that age of a bull has significant effect ($P < 0.001$) on the starting weight of the bulls. In the latter study, start of test weight accounted for 4.3 to 8.2 % of variation in subsequent weights and less

than 4.6 % of variation in relative growth rate. Given the accepted age ranges in NBCIS in Phases C and D, there is a huge variation in ages of bulls that are tested for post-weaning performance. This variation in age may lead to older animals having an advantage over younger ones in terms of growth.

2.3.3. Herd of origin

The herd from which the bulls were weaned before undergoing the test may also influence test performance. Several studies indicated that the herd of origin has an important effect on the performance of bulls on test despite pre-test adaptation periods (Collins-Lusweti and Curran, 1985; Tong *et al.*, 1986; Amal & Crow, 1987; Mantovani *et al.*, 1999; Liu & Makarechian, 1993; Schenkel *et al.*, 2002; Schenkel *et al.*, 2004 and Nephawe *et al.*, 2006).

The literature also indicates that this effect should be modeled as a herd of origin by year effect (De Rose *et al.*, 1988; Schenkel *et al.*, 2004; Nephawe *et al.*, 2006). De Rose *et al.* (1988) indicated that the across herd-year (HY) component constitutes those effects that are generally consistent within a given HY but that may vary between herd-years. Nutritional plane, health, housing, climatic influences and management factors would be included in this category. For post-weaning ADG in a centralized environment, Nephawe *et al.* (2006) and Schenkel *et al.* (2004) reported the variance ratios for HY of 0.09 ± 0.01 and 0.08 ± 0.01 respectively. The results further suggested the need for proper accounting for HY in genetic evaluation for growth performance in bull testing programs.

2.4 The relationship between pre-weaning and post-weaning performance

Weaning weight is a valuable indicator trait for pre-weaning performance. The age at which calves are weaned can vary depending on the management systems of the farmer. The accepted age for NBCIS is 151 to 250 days though 205 days is the recommended age. As such, 205 days is also used in adjusting the weaning weights for the differences in environmental factors to which the calves have been exposed. Early growth rate of an animal, in particular till weaning, is determined not only by its own genetic ability but also by the maternal environment (Meyer, 1992). Thus the weight does not only indicate the genetic ability of the calf but also the mothering ability of the dam.

The first opportunity where selection takes place in beef cattle is usually at weaning (Van Niekerk *et al.*, 2004; Bradfield *et al.*, 2000). It has been indicated by Khombe *et al.* (1995) that weaning weight is the most appropriate selection criteria for improving growth traits as such it has become one of the major selection objectives in many improvement schemes. Heritability estimates of weaning weight are relatively low to moderate across breeds but still improvement in this trait has been continuously attained in almost every breed. Koots *et al.* (1994a) in his review article reported a weighted heritability of 0.24 for various beef breeds. Bradfield *et al.* (2000) reported a heritability estimate of 0.29 for South African Angus breed.

Weaning weight has been used in selection criterion for improving growth traits in beef cattle, probably because it is positively correlated with most if not all of post-weaning growth traits. Harris and Newman, (1994) indicated that lack of proper knowledge about

genetic correlations may be one of the obstacles in the way of genetic progress by selection. Thus for within breed selection to be effective it is necessary to have a selection objective clearly defined and the knowledge of genetic parameters relevant to the selection objective (Bishop, 1991). Moderate to high correlations between growth traits suggest that growth measures particularly weight, are influenced by a similar set of genes and selection for one weight measure is likely to increase weight at other stages (Maiwashe *et al.*, 2002).

The literature shows that selection for higher weaning weight in young bulls could also improve ADG. Koots *et al.* (1994b) reported a weighted estimate of genetic correlation between weaning weight and post-weaning ADG of 0.24. Recently genetic correlation estimates of 0.63 (± 0.05), 0.44 (± 0.05) and 0.47 (± 0.06) were reported by Bradfield *et al.* (2000); Schenkel *et al.* (2004) and Nephawe *et al.* (2006) respectively. The latter three estimates were based on ADG from centralized tests (Phase C). Bradfield *et al.* (2000) reported a correlation estimate of 0.44 between weaning weight and ADG in Phase D for South African Angus breed and 0.30 for Bonsmara breed. Maiwashe *et al.* (2002) reported a correlation estimate of 0.26 between weaning weight and ADG in Phase D for the Bonsmara.

2.5 Effect of pre-weaning information on the genetic analysis of post-weaning traits

Increasing the efficiency of beef production systems by genetic means rests primarily on selection within breeds to enhance critical characters (Ahunu *et al.*, 1997). Schaeffer *et al.* (1997) indicated that selection causes problems for estimating genetic parameters and

breeding values. Test records of Phase C and Phase D are data on bulls that have undergone an intense performance based selection at weaning stages of rearing. Thus it could be hypothesized that if selection that occurred at weaning before testing in bull testing phases is not properly accounted for, it could have an influence on the subsequent genetic analysis for post-weaning performance.

Several researchers (Henderson, 1975; Polak and Quaas, 1981; Goffinet, 1983; Im *et al.*, 1988 and Fernando and Gianola, 1989) considered the theoretical effects of within generation selection on predictions of breeding values and suggested inclusion of all records of prior selections, use of multiple trait models and restricted maximum likelihood procedures (REML) as alternative ways to minimize these effects. As a suggested solution to rid the analysis of the effects of selection inclusion of all records of prior selections can be done using multivariate models. Kaps *et al.* (1999) also indicated that culling or selection in field data can be accounted for by considering traits of interest in a multiple trait model together with some genetically correlated traits measured earlier in life less subjected to selective reporting. De Rose *et al.* (1988b), Schenkel *et al.* (2004) and Nephawe *et al.* (2006) also indicated that a two trait animal model, incorporating pre-weaning and test performance would account for pre-test environmental carry over effect on test performance.

Multivariate models have proven to have the ability to overcome the effects of selection (Schaeffer *et al.*, 1997). There are two distinct advantages of multivariate analysis (Villanueva *et al.*, 1993). First is the ability to consider all traits simultaneously, which

increases the accuracy and consequently response to selection and the second the ability to avoid or reduce bias due to selection on a correlated trait in evaluations by integrating correlations between traits. In selection for multiple traits, multivariate best linear unbiased prediction using an animal model has been proposed as the optimum procedure for genetic evaluation (Henderson and Quaas, 1976; Villanueva *et al.*, 1993).

On the other hand, univariate linear models are simpler and less computationally demanding as compared to multivariate analysis. Although univariate analysis uses all available pedigree information to calculate genetic parameters, it does not account for sequential selection, nor does it use the correlations between traits (Bradfield *et al.*, 2000). Univariate BLUP can give biased estimates of breeding values because correlation between traits is not accounted for (Villanueva *et al.*, 1993). In the past, it was a common practice in genetic evaluations that traits of interest were the only traits fitted into the model of analysis for (co)variance estimation (Henderson, 1984). Thus, records from the early stage at which selection took place were excluded and consequently the effect of selection was not incorporated in the analysis. The accuracy of (co)variance estimates was affected and hence the breeding values that were calculated from these estimates were biased.

2.6 Summary

Testing of beef bulls in Phase C and Phase D is an integral part of the South African beef cattle industry. However, there is intense selection that occurs at weaning before bulls are tested for post-weaning performance. Selection at this stage may have an effect on parameters estimated for post-weaning traits measured in testing phases of bulls. To deal with the effect, multiple trait models have been recommended. Although selection has been shown by several researchers to have effect on genetic parameters, emphasis has not been given to quantification of this effect.

Chapter 3

Materials and Methods

3.1. Data description

Records of South African Angus cattle participating in the National Beef Cattle Improvement Scheme (NBCIS), born between 1975 and 2005, were obtained from the Integrated Registration and Genetic Information System (INTERGIS) of South Africa. In the five testing phase programme of the NBCIS (Appendix 1), Phase C and D are the bull testing phases. Bulls entering Phase C must be registered with the breeder's society concerned and must be aged between 151 and 250 days. Bulls must also have participated in phases A1 (birth phase) and A2 (weaning phase). In Phase C, bulls are fed individually *ad libitum*. A uniform diet comprising at least 20 percent roughage is fed to all bulls tested. Health management is maximized and standardized across tests and is effected through immunization (against anthrax, black quarter, lumpy skin disease, and infectious rhinotracheitis (IBR) two weeks prior to arrival at the testing centre) before entry and regular spray-dipping. Records of individual feed intake and body weights are taken on a weekly basis. Body measurements such as scrotum circumference, body length and height as well as ultrasonic scans are taken at the end of the test. A minimum number of 10 bull calves in a test group is necessary for Phase C test to be considered valid. Currently, there are 10 central bull-testing centres with a total capacity for testing 3,180 bulls per year. Five of these centres are privately owned and five are owned by the ARC.

In Phase D, registerable, recordable or grade bull calves sired by registered bulls together with bulls that meet the requirements of the performance testing programme are eligible

for testing. In this phase, bulls of the same breed from one or more breeders participating in the NBCIS are tested on the farm of a member or at a central venue for post-weaning growth and efficiency. Contrary to Phase C, bulls tested in Phase D are not individually fed and therefore individual feed intake is not recorded. Two weekly weights and body measurements similar to those in Phase C are recorded. A Phase D test is only regarded as official or supervised by the Animal Improvement Institute (AII) of the ARC if there are at least 10 bulls per breed in a test group. A detailed description of bull testing phases is available in the NBCIS Guidelines (NBCIS, 2005).

Traits considered in the current study were weaning weight (WWT) and average daily gain in Phases C (ADG-C) and D (ADG-D). The total number of animals in the original data set was 78 392. Only 1 441 and 6 676 of the bulls were tested in Phases C and D, respectively. The weaning contemporary group was defined by the weaning herd, weaning date and management index code and the test contemporary was a concatenation of test centre, test member and test year. The herd of origin by year group was defined by weaning herd and year of weaning. ADG was calculated as the difference between final and initial weight in kilograms divided by test length in days. The data were edited as follows: (1) records from a weaning contemporary group with less than 5 animals were excluded (2) contemporary groups with less than 2 sires were eliminated (3) observations beyond three standard deviations from the mean were excluded. The final data set included 45 259 animals with WWT, 4360 with ADG-D and 1118 with ADG-C.

To account for genetic relationships among animals, a 3 ancestral generation pedigree (n = 66 274) were created using the Animal Breeders Toolkit (ABTK; Golden *et al.*, 1992). Pedigree integrity checks were conducted to ensure that animals were born after their parents. Table 4 provides the summary of the data after editing.

Table 1 Characteristics of the data structure

Description	N
Animals in the pedigree	66 274
Animals with weaning weight	45 259
Animals with ADG from Phase C	1 118
Animals with ADG from Phase D	4 360
Dams	16 759
Sires	4 031
Weaning contemporary groups	2 551
Phase C test groups	209
Phase D test groups	224
Phase C Weaning herd-year groups	353
Phase D weaning herd-year groups	322

3.2 Statistical analysis

3.2.1. Preliminary analysis

The PROC MEANS procedure of the Statistical Analysis System (SAS, 2004) was used to compute descriptive statistics for the traits (i.e. weaning weight, average daily gain in Phases C and D) and covariables (i.e. dam age, weaning age and test age). The GLM (generalized linear models) procedure of SAS was used to determine fixed effects affecting traits of interest in the analysis. The fixed effects considered for weaning weight were weaning contemporary group, sex of the calf and covariates of age of dam at birth of calf and age of calf at weaning. For ADG, the fixed effects considered were test group and covariates age of dam and age of bull at the end of test.

3.2.2. Estimation of (co)variance components and genetic parameters

The following equations were used to obtain estimates of (co)variance components and genetic parameters of the traits:

$$\mathbf{WWT}_{ijk} = C_k + S_l + b_1X_1 + b_2X_1^2 + b_3X_2 + b_4X_2^2 + G_i + D_j + e_{ijk} \quad (\mathbf{T1})$$

$$\mathbf{ADG-C}_{ijkl} = T_k + b_1X_1 + b_2X_1^2 + b_3X_2 + b_4X_2^2 + G_i + HY_1 + e_{ijkl} \quad (\mathbf{T2})$$

$$\mathbf{ADG-D}_{ijkl} = T_k + b_1X_1 + b_2X_1^2 + b_3X_2 + b_4X_2^2 + G_i + HY_1 + e_{ijkl} \quad (\mathbf{T3})$$

where \mathbf{WWT}_{ijk} , $\mathbf{ADG-C}_{ijkl}$ and $\mathbf{ADG-D}_{ijkl}$ are weaning weight, average daily gain in Phases C and D, respectively; C_k is the fixed effect of the k^{th} weaning contemporary group; S_l is the fixed effect of l^{th} sex class; b_1 and b_2 are the linear and quadratic

regressions on age of the calf at measurement respectively, b_3 and b_4 are the linear and quadratic regressions on age of dam at birth respectively; G_i is the random direct genetic effect of the i^{th} animal; D_j is the random dam effect of the j^{th} dam (including both maternal genetic and permanent environmental effect of the dam); HY_l is the random effect of the l^{th} weaning herd-year and e_{ijkl} is the random residual effect.

For weaning weight, in addition to random direct genetic effects of the animal and random residual effects, dam effect was also fitted as random to account for differences in dam environment (affection and rearing ability) and mothering ability (constituted mainly by capacity for milk production). Meyer, (1992) indicated that fitting the dam environment and maternal additive genetic effect does not only help in estimation of variation due to the two, but also increases the accuracy of estimation of (co)variances. However, in the current study a random dam effect was fitted in the place of maternal additive and permanent environmental effects for weaning weight to create a more sparse system of equations to enhance the analysis (Schenkel *et al.*, 2004 and Nephawe *et al.*, 2006).

To account for heterogeneous differences in HY, the effect can be fitted as either fixed or random (Rust *et al.*, 2004). In the current study, the HY effect was fitted as random because the data had many HY classes with few animals which would have resulted in inaccurate estimates of the fixed HY effects. Furthermore, genetic evaluation for postweaning traits would likely involve an even larger proportion of small HY groups,

which would make fitting HY as a fixed effect unfeasible (Schenkel *et al.*, 2004). Thus it was fitted as random and this also enabled for calculation of variance due to HY effects.

The Variance Component Estimation-Restricted Maximum Likelihood (VCE-REML) Version 5.0 program of Kovač and Groeneveld (2003) was used to estimate (co)variance components and genetic parameters using three different models (i.e. **Models 1, 2 and 3**). Each model represented an approach with which information about prior selection is incorporated or not incorporated in the genetic parameter estimation. Model 1 (univariate model), represented an approach in which sequential selection is not taken into consideration in genetic analysis. For completeness, Model 1 also included a single-trait analysis of weaning weight. Models 2 and 3 represented approaches which consider sequential selection by incorporating pre-weaning information. Model 3 does not only incorporate preweaning information but also provides information on a correlated trait on the same phase of growth. Model 2 was a two-trait model of WWT and either ADG-C or ADG-D. Model 3 was a three-trait model including WWT, ADG-C and ADG-D, this model was also used to estimate genetic correlation between ADG-C and ADG-D.

The (co)variance components estimated were then subsequently used to estimate breeding values for ADG-C and ADG-D using the Prediction and Estimation Program (PEST) of Groeneveld *et al.* (2001). Spearman's rank correlations were computed among the three sets of breeding values (from Models 1, 2 and 3) for ADG-C and ADG-D for different samples of bulls: all bulls in the data set, top and bottom 1%, 5% and 10% of all

the bulls. The rank correlations were used to establish if there were rank changes amongst the top selected candidates.

The most comprehensive multivariate animal model (Model 3) for analysis of WWT, ADG-C, and ADG-D in matrix notation was as follows:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{X}_3 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \\ \mathbf{b}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{Z}_2 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{Z}_3 \end{bmatrix} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{a}_3 \end{bmatrix} + \begin{bmatrix} \mathbf{W}_1 & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} \end{bmatrix} \begin{bmatrix} \mathbf{c}_1 \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix} \\ + \begin{bmatrix} \mathbf{0} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{H}_1 & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{H}_2 \end{bmatrix} \begin{bmatrix} \mathbf{0} \\ \mathbf{f}_1 \\ \mathbf{f}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \end{bmatrix}$$

Where:

y_1 , y_2 and y_3 are vectors observations of WWT, ADG-C and ADG-D, respectively; \mathbf{X} is an incidence matrix that relates observations to fixed effects; \mathbf{b}_1 , \mathbf{b}_2 and \mathbf{b}_3 are vectors of fixed effects for WWT, ADG-C and ADG-D respectively; \mathbf{Z} is an incidence matrix relating observations to random direct genetic effects; \mathbf{a}_1 , \mathbf{a}_2 , and \mathbf{a}_3 are vectors of random direct genetic effects for WWT, ADG-C and ADG-D respectively; \mathbf{W} is an incidence matrix relating observations to random dam effects; \mathbf{c}_1 is a vector of random dam effects for weaning weight; \mathbf{H} is an incidence matrix relating observations to random herd of origin by year effects; \mathbf{f}_1 and \mathbf{f}_2 are vectors of random HY effects for ADG-C and ADG-D respectively and \mathbf{e}_1 , \mathbf{e}_2 and \mathbf{e}_3 are vectors of random residual effects for WWT, ADG-C and ADG-D respectively.

The first and second moments were as follows;

$$\mathbf{E} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{a}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \mathbf{E} \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \mathbf{E}[\mathbf{c}_1] = \mathbf{0} \text{ and } \mathbf{E} \begin{bmatrix} \mathbf{f}_1 \\ \mathbf{f}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix}$$

$$\mathbf{Var} \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \\ \mathbf{e}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma_{e1}^2 & \mathbf{I}\sigma_{e1,e2} & \mathbf{I}\sigma_{e1,e3} \\ \mathbf{I}\sigma_{e2,e1} & \mathbf{I}\sigma_{e2}^2 & \mathbf{I}\sigma_{e2,e3} \\ \mathbf{I}\sigma_{e3,e1} & \mathbf{I}\sigma_{e3,e2} & \mathbf{I}\sigma_{e3}^2 \end{bmatrix}$$

$$\mathbf{Var} \begin{bmatrix} \mathbf{a}_1 \\ \mathbf{a}_2 \\ \mathbf{a}_3 \end{bmatrix} = \mathbf{G} \otimes \mathbf{A} \quad \text{where } \mathbf{G} = \begin{bmatrix} \sigma_{a1}^2 & \sigma_{a1,a2} & \sigma_{a1,a3} \\ \sigma_{a2,a1} & \sigma_{a2}^2 & \sigma_{a2,a3} \\ \sigma_{a3,a2} & \sigma_{a3,a2} & \sigma_{a3}^2 \end{bmatrix}$$

\mathbf{A} is the numerator relationship matrix and \otimes is the kronecker product notation.

$$\mathbf{Var} \begin{bmatrix} \mathbf{f}_1 \\ \mathbf{f}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma_{d1}^2 & \mathbf{I}\sigma_{d1,d2} \\ \mathbf{I}\sigma_{d2,d1} & \mathbf{I}\sigma_{d2}^2 \end{bmatrix} \quad \mathbf{Var}[\mathbf{c}_1] = \mathbf{I}\sigma_{c1}^2$$

Chapter 4

Results and Discussion

4.1 Summary statistics

The descriptive statistics of the data are presented in Table 2. Results show that the average for WWT, ADG-C and ADG-D are 219 kg, 1711 g/day and 1083 g/day respectively. These results indicate that bulls in Phase D grow at a lower rate than those participating in Phase C. The possible explanation for these results is the lower plane of nutrition in Phase D in comparison to that in Phase C. Bergh and Gerhard (1999) reported averages of 215 kg and 1804 g/day for WWT and ADG-C respectively for the South African Angus breed.

Table 2 Summary statistics for traits and covariates¹.

Variable	N	Mean	SD	Min	Max
WWT (kg)	45429	219	40	100	330
ADG-C (g/day)	1118	1711	253	1035	2440
ADG-D (g/day)	4360	1083	359	214	2205
AGE-W (days)	45429	212	27	150	281
AGE-C (days)	1118	363	34	264	462
AGE-D (days)	4360	415	57	244	586
Dam Age (months)	45429	66	32	22	226

¹WWT=weaning weight, ADG-C= average daily gain Phase C, ADG-D=average daily gain Phase D, AGE-W=weaning age, AGE-C=age at end of Phase C test, AGE-D=age at end of Phase D test and Dam Age = age of dam at birth of the calf.

4.2. Analysis of fixed effects

The analysis of variance was carried out to investigate which non-genetic effects to include in the models for WWT, ADG-C and ADG-D; the results are presented in Table 3.

Table 3 Analysis of variance for fixed effects.

Trait	Effect					
	CG	Sex	Age	Age ²	Damage	Damage ²
WWT	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.1924
ADG-C	<0.0001	--	<0.0001	<0.0001	0.0957	0.0366
ADG-D	<0.0001	--	<0.0001	<0.0001	0.0008	0.0069

CG=contemporary group, Sex= sex of the animal, Age and Age² = linear and quadratic effects of age, Damage and Damage² = linear and quadratic effects of damage. Figures in the table are the p-values or Pr > F values.

Weaning weight differed considerably ($P < 0.0001$) between the male and female calves. The effect of CG was highly important ($P < 0.0001$) for all the traits. Maiwashe *et al.* (2002) also reported a highly significant contemporary group effect for all traits considered including ADG-D in Bonsmara breed. The covariate of age (both linear and quadratic) also influenced ($P < 0.0001$) all the traits. Linear and quadratic regressions of age were reported as important ($P < 0.0001$) for postweaning ADG from phases C and D by Van der Westhuizen *et al.* (2004) in Bonsmara. The effect of age of dam on WWT was adequately modeled by a linear regression while the second-order polynomial (linear and quadratic regression) provided a better fit for ADG-C and ADG-D.

However, only the linear regression of dam age was found to be significant for ADG by Van der Westhuizen *et al.* (2004). Contrary to the significant effect of age of dam (linear and quadratic) on ADG-D in the current study, Maiwashe *et al.* (2002) reported a non-significant effect of age of dam (linear and quadratic) for ADG-D but significant effect on other postweaning test traits (i.e. shoulder height, body length and scrotal circumference).

4.3 (Co) variance components

(Co)variance components for WWT, ADG-C and ADG-D are presented in Table 4. The phenotypic variance for ADG-C showed clear increasing trend from the simple (model 1) to the comprehensive model (model 3). There was however not a clear trend in the phenotypic variances for ADG-D and WWT among the three models. The additive genetic variance for weaning weight was almost stable across models while that for average daily gain in both phases increased from Model 1 to Model 3. The residual variance for average daily gain in both phases decreased from Model 1 to Model 3. The variance due to the dam effect for weaning weight remained relatively similar across the three models. This result was expected given that the dam effect was assumed to be uncorrelated to any other random effects in the model in Chapter 3. There was no apparent trend in magnitude of the variance due to the effect HY across models.

Table 4. (Co)variance components for WWT, ADG-C and ADG-D

Effect ¹	Models									
	Model 1			Model 2		Model 3				
	WWT	ADG-C	ADG-D	WWT	ADG-C	WWT	ADG-D	WWT	ADG-C	ADG-D
A	141	12800	4785	141.4	494 14240	141.4	451.9 5169	146.6	576 15360	485 5353 5546
D	131	-	-	131.2	-	131.2	-	130.9	-	-
HY	-	3014	2697	-	2314	-	2743	-	3957	-1812 2128
E	354	17150	18700	330.1	719.4 17020	330.1	316 18610	336.1	701.7 16050	308 307.9 18350
P	625	32960	26190	603.4	1214 33580	603.4	767.9 26520	613.6	1278 35370	793 4184 26030

A= direct additive genetic (co) variance, D= dam (co)variance, HY= herd of origin (co)variance, E= residual (co)variance and P= phenotypic (co)variance.

4.4 Variance ratios and genetic correlations

Variance ratios and genetic correlations for WWT, ADG-C and ADG-D are presented in Table 5. The heritability estimates for weaning weight were relatively similar across models i.e. 0.22, 0.23 and 0.24 for Models 1, 2 and 3 respectively. Heritability estimates for ADG-C were 0.39, 0.42 and 0.44 from Models 1, 2 and 3 respectively. The estimates of heritability for ADG-D were 0.18, 0.19 and 0.21 from Models 1, 2 and 3 respectively. These results indicate that there was a slight increase in heritability estimates for average daily gain in both phases from Model 1 to Model 3.

Considering the comprehensive model (Model 3), the variance ratio for dam effect for WWT was 0.21 and the variance ratios for HY were 0.11 and 0.08 for ADG-C and ADG-D respectively. The genetic correlation between WWT and ADG-C was 0.38 and between WWT and ADG-D was 0.53. Genetic correlation between ADG-C and ADG-D was 0.58. The correlation between HY for ADG-C and ADG-D was negative and moderate (-0.62) but associated with a high standard error ($se = 0.7$) and thus not significantly different from zero.

Table 5 Variance ratios and genetic correlations WWT, ADG-C and ADGD

Effect	Models									
	Model 1			Model 2				Model 3		
	WWT	ADG-C	ADG-D	WWT	ADG-C	WWT	ADG-D	WWT	ADG-C	ADG-D
h^2	0.22 (0.004)	0.39 (0.08)	0.18 (0.021)	0.23 (0.011)	0.34 (0.026)	0.23(0.011)	0.53 (0.059)	0.24 (0.01)	0.38 (0.016)	0.53 (0.056)
					0.42 (0.06)		0.19 (0.021)		0.44 (0.05)	0.58 (0.11) 0.21 (0.02)
d^2	0.20 (0.009)	-	-	0.22(0.008)	-	0.22(0.008)	-	0.21 (0.01)	-	-
hy^2	-	0.09(0.033)	0.10 (0.019)	-	0.07(0.022)	-	0.10 (0.022)	-	0.11 (0.03)	-0.62 (0.7) 0.08(0.015)
e^2	0.57 (0.008)	0.52 (0.075)	0.71 (0.027)	0.54 (0.02)	0.30 (0.042)	0.54(0.02)	0.12 (0.019)	0.54 (0.03)	0.30 (0.04)	0.12 (0.018)
					0.50 (0.08)		0.70 (0.02)		0.45 (0.05)	0.04(0.0001) 0.70 (0.022)

h^2 = heritability; d^2 = dam variance ratio; hy^2 = herd of origin by year variance ratio and e^2 = residual variance ratio. Variance ratios are figures in bold font while the regular font figures are correlations.

While variance ratios and genetic correlations are relatively similar across models, estimates from the comprehensive model are associated with lower standard error and hence more accurate. Thus estimates from the comprehensive model are compared with estimates from other similar studies. The heritability estimate of weaning weight in the current study is 0.24 ± 0.01 . Bradfield *et al.* (2000) reported a slightly higher heritability estimate of 0.29 ± 0.001 for WWT in South African Angus breed while Meyer *et al.* (1993) reported an estimate of 0.22 for Aberdeen Angus. Koots *et al.* (1994a) reported a weighted average estimate of heritability of 0.24. The estimate of heritability obtained in the current study is within range of estimates from studies by Sand and Lemaster (1997), Schenkel *et al.* (2004), Nephawe *et al.* (2006), Van der Westhuizen *et al.* (2004), Bradfield *et al.* (2000), Meyer, 1993 and Maiwashe *et al.* (2002) which reported 0.30 (for mixed breeds), 0.36 (for mixed breeds), 0.22 (for Bonsmara), 0.24 (for Bonsmara) 0.15 (for Bonsmara), 0.23 (for Hereford) and 0.29 (for Bonsmara) respectively.

The variance ratio for the dam effect of 0.21 ± 0.01 obtained in the current study is comparable with estimates reported by Nephawe *et al.* (2006) and Schenkel *et al.* (2004). It should be noted that the proportion of the phenotypic variation for WWT accounted for by the dam effect was similar to that due to direct genetic effect. Meyer, (1992) also found an important effect of the dam environment and maternal genetic effect on weaning weight.

Heritability estimates in the current study (from comprehensive model) for ADG were 0.44 ± 0.05 and 0.21 ± 0.02 for Phases C and D respectively. These estimates were comparable with those in the literature. Bradfield *et al.* (2000) reported slightly higher heritability estimates of 0.47 ± 0.001 and 0.28 ± 0.001 for ADG-C and ADG-D respectively for the South African Angus breed. The slight difference in the estimates could be due to the difference in the models fitted. For example, in the current study the effect of herd of origin by year was included in the model. De Rose *et al.* (1988) reported an estimate of 0.46 ± 0.10 for ADG measured under intensive growth tests for Aberdeen Angus. Koots *et al.* (1994a) reported a weighted estimate of 0.31 for different breeds at centralised tests. Estimates for ADG-C were also comparable with estimates in the study by Gregory *et al.* (1995) which are 0.35 ± 0.009 (all breeds), 0.33 ± 0.10 (pure breeds), and 0.48 ± 0.17 (composite breeds). Other estimates in the literature are 0.45 ± 0.01 , 0.34 ± 0.03 , 0.31 ± 0.03 , 0.37 ± 0.01 and 0.22 by Sand and Lemaster (1997), Schenkel *et al.* (2004), Nephawe *et al.* (2006), Van der Westhuizen *et al.* (2004) and Bradfield *et al.* (2000). Heritability estimates for ADG-D were also comparable with an estimate of 0.19 reported by Maiwashe *et al.* (2002) for the Bonsmara breed. Heritability estimate for ADG-D were generally lower compared to that of ADG-C. This could be due to less standardized conditions in Phase D which might limit the expression of the genetic potential for growth.

Genetic correlations between weaning weight and average daily gain were 0.38 ± 0.02 and 0.53 ± 0.06 for ADG-C and ADG-D respectively. Higher estimates of genetic correlations between WWT and ADG-D as compared to ADG-C suggest that there are more genes in

common influencing ADG-D and WWT than is the case with ADG-C. Contrary to this result, Bradfield *et al.* (2000) reported genetic correlations between WWT and ADG-C and ADG-D of 0.63 and 0.44 respectively. Weighted estimate of genetic correlation between WWT and ADG-C of 0.24 has been reported in the literature (Koots *et al.*, 1994b). Other estimates for genetic correlations between WWT and ADG-C are 0.43, 0.28, 0.47* and 0.49* by Nephawe *et al.* (2006), Van der Westhuizen *et al.* (2004) and De Rose *et al.* (1988)*. For ADG-D, correlations with WWT were estimated at 0.42 and 0.26 by Bradfield *et al.* (2000) and Maiwashe *et al.* (2002) respectively in Bonsmara breed. Moderate to high genetic correlations between WWT and postweaning ADG from different phases indicated that selection at weaning is important for correlated response in post weaning growth performance in South African Angus breed. Genetic correlation between ADG-C and ADG-D was estimated to be 0.58. Bradfield *et al.* (2000) reported an estimate of 0.43 and 0.78 for South African Angus and Bonsmara respectively.

Proportion of variance due to HY effect was estimated to be 0.11 and 0.08 for ADG-C and ADG-D respectively. An estimate for ADG-C is comparable with estimates available in the literature. Schenkel *et al.* (2004) analyzed 25 315 bulls of different breeds in Canada and reported a HY contribution to variation for ADG-C of 0.08. Nephawe *et al.* (2006) reported a HY variance ratio of 0.09 for Bonsmara. Sizable effect of HY on average daily gain was also reported in studies by Collins-Lusweti & Curran (1985), Tong *et al.* (1986), Amal & Crow (1987), Mantovani *et al.* (1999), Liu & Makarechian (1993) and Schenkel *et al.* (2002).

Information on the effect of HY on Phase D average daily gain is not available in the literature. However, the HY effect ratio estimates for ADG-C and ADG-D in the current study suggest that the effect is quantitatively not different between the two phases. The correlation between HY for ADG-C and ADG-D obtained in the current study was -0.62 ± 0.70 and not significant.

4.5 Rank Correlations of Estimated Breeding Values

Rank correlations of the estimated breeding values (EBV's) obtained from different models are presented in Tables 6 and 7 for ADG-C and ADG-D respectively. Correlations between the EBV's for ADG from different models were generally low for both phases. Estimates of correlations were higher for all bulls as compared to other proportions (e.g. top 10%, 1% etc). The correlations between EBV from Models 1 and 2 and correlations between Models 2 and 3 were generally higher than those between Models 1 and 3 for both phases. The correlation estimates were not very different between the two phases.

Table 6 Rank correlations based on EBV for ADG-C from different models

Models	Bull Rank Correlations							
	No of bulls	All	10% Best	10% Worst	5% Best	5% Worst	1% Best	1% Worst
Model 1 vs. Model 2	1118	0.92	0.67	0.59	0.68	0.72	0.44	0.74
Model 1 vs. Model 3	1118	0.83	0.53	0.43	0.57	0.61	0.35	0.32
Model 2 vs. Model 3	1118	0.94	0.69	0.68	0.78	0.68	0.54	0.61

Table 7 Rank correlations based on EBV for ADG-D from different models

Models	Bull Rank Correlation							
	No of bulls	All	10% Best	10% Worst	5% Best	5% Worst	1% Best	1% Worst
Model 1 vs. Model 2	4360	0.88	0.69	0.49	0.67	0.30	0.55	0.20
Model 1 vs. Model 3	4360	0.84	0.66	0.45	0.61	0.28	0.54	0.23
Model 2 vs. Model 3	4360	0.93	0.77	0.65	0.74	0.66	0.78	0.56

The rank correlations are generally low thus indicating differences in bull ranking when preweaning information is not included in the analysis of postweaning average daily gain. The differences in bull ranking indicate that preweaning selection information is crucial in genetic analysis for postweaning average daily gain in bull testing phases. There is an intense level of selection at weaning to which bulls are subjected before testing in phases C and D (Bradfield *et al.*, 2000). Schaeffer *et al.* (1997) indicated that selection causes problems for estimating genetic parameters and breeding values.

Results of the current analysis suggest that selection at weaning could have a sizeable effect on the subsequent genetic evaluation for postweaning growth performance if it is not properly accounted for. The difference in estimated genetic parameters from the different models was due to the difference in how the three models incorporate preweaning selection information in the analysis of postweaning ADG. The difference may seem small, but could have huge implications in the genetic evaluation program. Schenkel and Schaeffer, (2000) indicated that accurate estimates of variance components are needed for prediction of genetic values of livestock with the lowest possible prediction error. Furthermore the reliability of genetic parameters may become a limiting factor for their successful application in selection programs (Fuerst-Waltl *et al.*, 1997).

Chapter 5

Conclusions and Recommendations

5.1 Conclusions

Selection at weaning has an effect on genetic evaluation of post-weaning average daily gain on bulls from central tests. Results from the current study demonstrated sizeable differences in genetic parameters when pre-weaning selection information was included or excluded in the genetic analysis of average daily gain. Ranking of bulls based on EBVs was also different when pre-weaning information was included or excluded in genetic analysis for ADG-C and ADG-D. Therefore inclusion of pre-weaning information is necessary in genetic analysis for ADG-C and ADG-D.

There is a moderate genetic correlation between ADG-C and ADG-D but this correlation was significantly different from unity suggesting that although many of the genes for ADG-C and ADG-D are common, they two are not necessarily the same trait. Estimates of genetic correlation between weaning weight and average daily gain in Phases C and Phase D suggest that selection at weaning is a useful tool for correlated response of post-weaning average daily gain. ADG-C has a higher heritability estimate as compared to ADG-D. Thus selection of bulls for post-weaning growth through centralised bull testing will yield more genetic progress than would selection through on farm bull testing. HY influenced average daily gain in both centralized and on farm bull tests despite the pretest adaptation periods. The negative genetic correlation between HY in Phase C and Phase D was difficult to interpret because of high standard error associated with it.

5.2 Recommendations

Genetic analysis of post-weaning average daily gain should incorporate pre-weaning information through fitting a multiple trait model to account for sequential selection that occurred at weaning before bulls were tested. Herd of origin by year effect should be included in the genetic evaluation model for post-weaning average daily gain. Results from the current study suggest that average daily gain in Phase C and Phase D are not necessarily under the same additive genetic control and therefore further research aimed at verifying these findings is needed.

Chapter 6

References

Ahunu, B.K., Arthur, P.F. and Kissiedu, H.W.A., 1997. Genetic and phenotypic parameters for birth and weaning weights of purebred and crossbred Ndama and West African Shorthorn cattle. *Livestock Production Science* 51, 165-171.

Amal, S. and Crow, G.H., 1987. Herd of origin effects on the performance of station tested beef bulls. *Canadian Journal of Animal Science* 67, 349-358.

Archer, J.A., Richardson, E.C., Herd, R.M. and Arthur, P.F., 1999. Potential for selection to improve efficiency of feed use in beef cattle: a review. *Australian Journal of Agricultural Research* 50, 147-161.

Beltran, J.J., Butts, W.T., Olson, T.A. and Koger, M., 1992. Growth patterns of two lines of Angus cattle selected using predicted growth parameters. *Journal of Animal Science* 70, 734-741.

Bergh, L., 1999. The National Beef Cattle Performance Testing Scheme. *Beef Breeding in South Africa* pp. 81-92. Agricultural Research Council, Animal Improvement Institute, Irene, South Africa.

Bergh, L. and Gerhard, R., 1999. Introduction of beef cattle breeds participating in National Beef Cattle Performance Testing Scheme. *Beef Breeding in South Africa* pp. 115-118. Agricultural Research Council, Animal Improvement Institute, Irene, South Africa.

Bishop, S.C., 1991. Phenotypic and genetic variation in body weight, food intake, and energy utilization in Hereford cattle. II. Effects of age and length of performance test. *Livestock Production Science* 30, 19-31.

Bradfield, M.J., Mostert, B.E., Exley, C.A.J., Jordan, F. and Berg, L., 2000. Estimates of genetic parameters for traits measured in Phase A, C and D of the South African Performance Testing Scheme. *South African Journal of Animal Science* 30, 8-10.

Bulmer, M.G., 1971. The effect of selection on genetic variability. *American Naturalist* 105, 201-211.

Cain, M.F. and Wilson, L.L., 1983. Factors influencing individual bull performance in central test stations. *Journal of Animal Science* 57, 1059-1066.

Collins-Lusweti, E. and Curran, M.K., 1985. A note on environmental factors affecting beef cattle performance tests. *Animal Production* 41, 131-134.

Dickerson, G. E. and Hazel, L.N., 1944. Effectiveness of selection on progeny performance as a supplement to earlier culling in livestock. *Journal of Agricultural Research* 69, 459-464.

De Rose, E.P., Wilton, J.W., and Schaeffer, L.R., 1988. Estimation of variance components for traits measured on station tested bulls. *Journal of Animal Science* 66, 626-634.

Fernando, R.L. and Gianola, D., 1989. Statistical inferences in populations undergoing selection and non-random mating. In: *Advances in statistical methods for genetic improvement of livestock*. Springer-Verlag, New York.

Fuerst-Waltl, B., Essl, A. and Solkner, J., 1997. Nonlinear genetic relationships between traits and their implications on the estimation of genetic parameters. *Journal of Animal Science* 75, 3119-3125.

Goffinet, B., 1983. Selection on selected records. *Genetics, Selection and Evolution* 15, 91-99.

Groeneveld, E., 2001. Prediction and Estimation Program User's guide and reference manual. Marienskee, Germany

Harris, D.L. and Newman, S., 1994. Breeding for profit: Synergism between genetic improvement and livestock production. *Journal of Animal Science* 72, 2178-2200.

Henderson, C.R., 1975. Best linear unbiased estimation and prediction under selection models. *Biometrics* 31, 423-447.

Henderson, C.R., 1984. Applications of linear models in animal breeding. University of Guelph. Canada.

Henderson, C.R., 1986. Recent developments in variance and covariance estimation. *Journal of Animal Science* 63, 3118-3128.

Henderson, C.R. and Quass, R.L., 1976. Multiple trait evaluation using relative's records. *Journal of Animal Science* 43, 1188-1187.

Im, S., Fernando, R.L. and Gianola, D., 1989. Likelihood inferences in animal breeding under selection: a missing data theory view point. *Genetics, Selection and Evolution* 21, 399-406.

Kaps, M., Herring, W.O. and Lamberson, W.R., 1999. Genetic and environmental parameters for mature weight in angus cattle. *Journal of animal Science* 77, 569-574.

Khombe, C.T., Hayes, J.F., Cue, R.I. and Wade, K.M., 1995. Estimation of direct and maternal additive genetic effects for weaning weight in Mashona cattle of Zimbabwe using an individual animal model. *Animal Science* 60, 41-48.

Kriese, L.A., Bertrand, J.K. and Benyshek, L.L., 1991. Age adjustment factors, Heritabilities and genetic correlations for scrotal circumference and related growth traits in Hereford and Brangus bulls. *Journal of Animal Science* 69, 478-489.

Koch, R.M., Cundiff, L.V. and Gregory, K.E., 1995. Direct and maternal genetic responses to selection for weaning or yearling weight or for yearling weight and muscle score in Hereford cattle. *Journal of Animal Science* 73, 2951-2958.

Koots, K.R., Gibson, J.P., Smith, C. and Wilton, J.W., 1994a. Analysis of published genetic parameter estimates for beef production traits. 1. Heritability. *Animal Breeding Abstracts* 62, 311-338.

Koots, K.R., Gibson, J.P., Smith, C. and Wilton, J.W., 1994b. Analysis of published genetic parameter estimates for beef production traits. Phenotypic and genetic correlations. *Animal Breeding Abstracts* 62, 825-853.

Kovac, M. and Groeneveld, E., 2003. VCE-5 User's guide and reference manual

version 5.1, Marienskee, Germany

Liu, M. F. and Makarechian, M., 1993. Optimum test period and associations between

standard growth rate in station tested beef bulls. *Journal of Animal Breeding and*

Genetics 110, 312-317.

Long, T.E., Johnson, R.K. and Keele, J.W., 1991. Effects of selection of data on

estimates of breeding values by three methods for litter size, backfat and average

daily gain in swine. *Journal of Animal* 69, 2787-2794.

Lowman, B.G., Hunter, E.A., Hinks, C.E. and Lewis, M., 1994. Effect of breed type,

sex and method of rearing on lifetime performance and carcass composition in a

20-month beef system: effects of winter feeding treatments. *Animal Production*

58, 347-355.

Maiwashe, A.N., Bradfield, M.J., Theron, H.E. and Van Wyk, J.P., 2002. Genetic

parameter estimates for body measurements and growth traits in South African

Bonsmara cattle. *Livestock Production Science* 75, 293-300.

Mantovani, R., Contiero, B., Gallo, L., Carnier, P., Cassandro, M. and Bittande, G.,

1999. The effect of herd of origin on selection of Chianina, Marchigiana, and Romagnola performance tested young bulls. *Zootecnica Nutrizione Animale* 25, 109-121.

Meyer, K. 1992. Variance components due to direct and maternal effects for growth traits of Australian beef cattle. *Livestock Production Science* 31, 179-204.

Meyer, K. 1993. Estimates of direct and maternal correlations among growth traits in Australian beef cattle. *Livestock Production Science* 38, 91-105.

NBCIS, 2005. National Beef Cattle Improvement Scheme guidelines, Version 200.1, ARC-Animal Improvement Institute, Irene, Pretoria.

Nephawe, K.A., Maiwashe, A. and Theron, H.E., 2006. The effect of herd of origin by year on postweaning traits of young beef bulls at centralised testing centres in South Africa. *South African Journal of Animal Science* 36, 33-39.

Pollak, E.J. and Quass, R.L., 1981. Monte Carlo study of genetic evaluations using sequentially selected records. *Journal of Animal Science* 69, 2787-2794.

Rust, T., Van der Westhuizen, J., Schoeman., S.J. and Van Wyk, J.B., 2004.

Variance components estimation for reproductive merit of beef cattle using linear and non-linear models. South African Journal of Animal Science 34, 59-61.

SAS Institute Inc, 2004, SAS 9.1.2 User's guide, Cary, NC: SAS Institute Inc.

Satoh, M., Hicks, C., Ishii, K. and Furukawa., T., 2002. Choice of statistical model for estimating genetic parameters using restricted maximum likelihood. Journal of Animal Breeding and Genetics 119, 285-296.

Sand, R.S. and Lemaster, J.W., 1997. Selecting beef bulls. AS 22, Department of Animal Science, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida.

Schaeffer, L.R., Schenkel, F.S. and Fries, L.A., 1997. Selection bias on animal model evaluation. Journal of Animal Science 75: 2344-2352.

Schenkel, F.S., Miller, S.P., Jamrozik, J. and Wilton, J.W., 2002. Two step random regression analyses of weight gain of station tested beef bulls. Journal of Animal Science 80, 1497-1507.

Schenkel, F.S., Miller, S.P. and Wilton, J.W., 2004. Herd of origin effect on weight gain of station-tested beef bulls. *Livestock Production Science* 86, 93-103.

Schenkel, F.S. and Schaeffer, L.R., 2000. Effects of nonrandom parental selection on estimation of variance components. *Journal of Animal Breeding and Genetics* 117, 225-239.

Scholtz, M.M., Jürgens, Y., Bergh, L. Van der Westhuizen, J. and Bosman, D.J., 1998. The importance of feed efficiency in the selection of beef cattle in South Africa. In proceedings of the 6th World Congress on Genetics Applied to livestock production, Volume 25, pp. 89-92.

Self, H.L., 1972. Environmental implications in economy of gain in feedlot cattle. *Journal of Animal Science* 35, 148-154.

Tawah, C.L., Rege, J.E.O., Mbah, D.A. and Oumate, H., 1994. Genetic evaluation of birth and weaning weight of Gudali and two-breed synthetic Wakwa beef populations under selection in Cameroon: genetic and phenotypic trends. *Animal Production* 58, 25-34.

- Tier, B. and Meyer, K., 2004.** Approximating prediction error covariances among additive genetic effects within animals in multiple-trait and random regression models. *Journal of Animal Breeding and Genetics* 121, 77-89.
- Thompson, R. and Meyer, K., 1986.** A review of theoretical aspects in the estimation of breeding values for multitrait selection. *Livestock Production Science* 15, 299-313.
- Tong, A.K.W., Newman, J.A. and Rahnefeld., 1986.** Pretest herd effects on station performance test. *Canadian Journal of Animal Science* 66, 925-935.
- Van Niekerk, M., Nesser, F.W.C. and Van Wyk, J.B., 2004.** (Co)variance components for growth traits in the Nguni cattle breed. *South African Journal of Animal Science* 34, 113-115.
- Van der Werf, J.H.J. and Thompson, R., 1992.** Variance decomposition in the estimation of genetic variance with selected data. *Journal of Animal Science* 70, 2975-2985.

Van der Westhuizen, R.R., Van der Westhuizen, J. and Schoeman, S.J., 2004.

Genetic variance components for residual feed intake and feed conversion ratio and their correlations with other production traits in beef bulls. South African journal of Animal Science 34, 257-264.

Villanueva, B., Wray, N.R. and Thompson, R., 1993. Prediction of asymptotic rate of

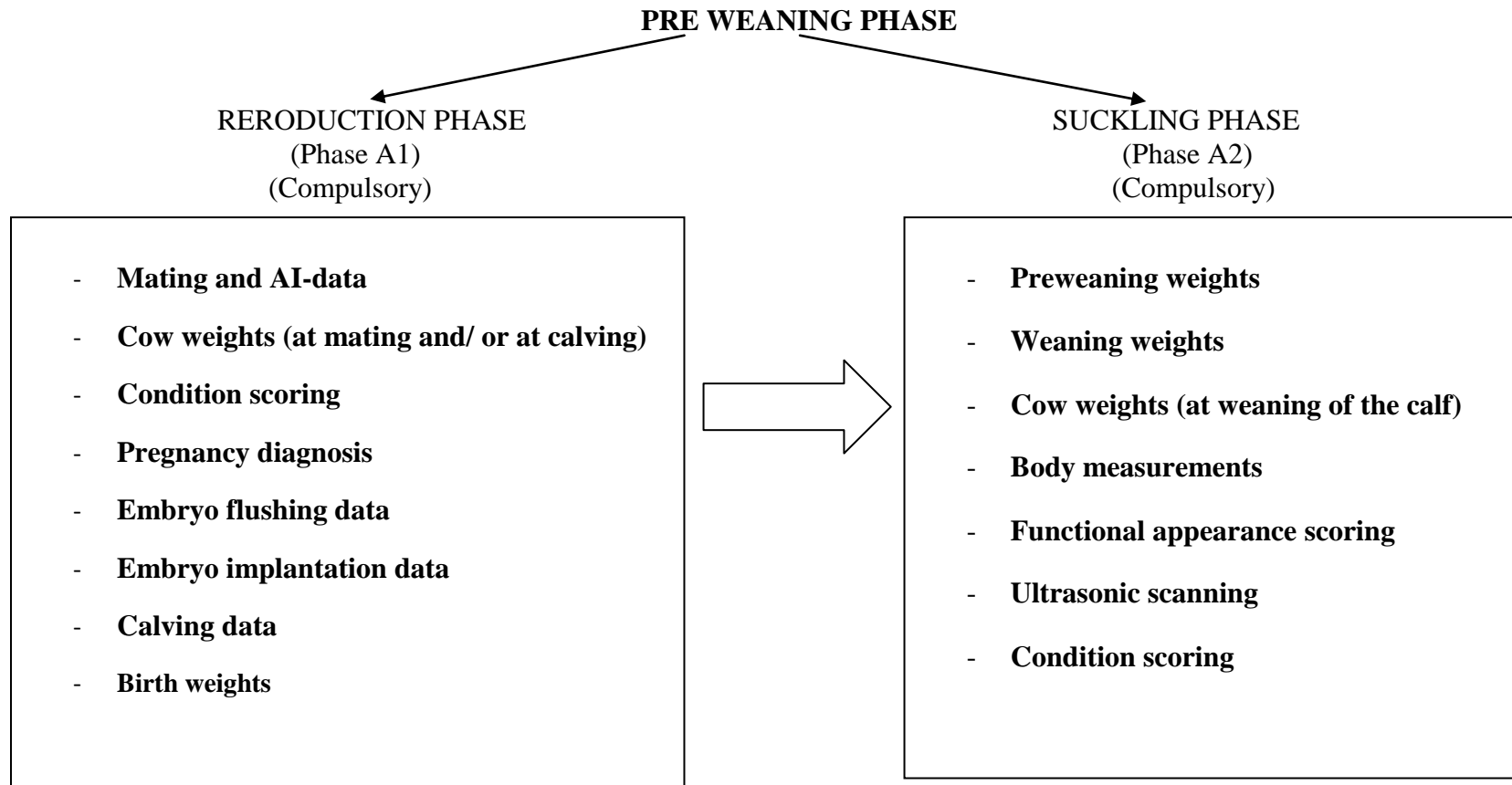
response from selection on multiple traits using univariate and multivariate best linear unbiased predictors. Animal Production 57, 1-13.

Woodward, B.W., Pollak, E.J. and Quass, R.L., 1992. Parameter estimation for carcass

traits including growth information of Simmental beef cattle using restricted maximum likelihood with a multiple-trait model.

Appendix 1

Testing phases of the South African National Beef Cattle Improvement Scheme. (Adapted from NBCIS, 2005)



POST WEANING PHASE

