

6144 6245 x

U.O.V.S. BIBLIOTEK

RDIE EKSEMPLAAR MAG ONDER
EN OMSTANDIGHEDE UIT DIE
BIBLIOTEK VERWYDER WORD NIE

University Free State



34300001920978

Universiteit Vrystaat

**A GENETIC EVALUATION OF PRODUCTION TRAITS IN
NGUNI CATTLE**

by

MICHIEL VAN NIEKERK

Dissertation submitted to the Faculty of Natural and Agricultural Sciences,
Department of Animal, Wildlife and Grassland Sciences,
University of the Free State,
In partial fulfilment of the requirements for the degree

MAGISTER SCIENTIAE AGRICULTURAE

Supervisor: Prof. F.W.C. Nesor

Co-supervisor: Prof. J.B. van Wyk

Bloemfontein, June 2003

Universiteit van die
Oranje-Vrystaat
DLOEMFONTEIN

2 - DEC 2003

UOVS SABOL BIBLIOTEEK

Acknowledgements

Immense gratitude is expressed to the following persons for their contributions without which this study would not have been possible:

Prof. F.W.C. Naser for his support, guidance and personal assistance throughout the study. Also, for many emboldening conversations which led to a more consummated grasp of animal breeding,

Prof. J.B. van Wyk for his unmitigated attention to the fundamentals of animal breeding and the study,

Dr J. van der Westhuizen for inestimable advice and constant interest in the study,

Prof. G.J. Erasmus for his valuable comments and comprehensive pertinence,

the Animal Improvement Institute of the ARC for providing the data,

the NRF for their financial support through the bursary provided,

Mr J.D. Jordaan, Mr D. Borstlap, Me. H.L. Bothma and Me. H. Breedt for their friendship and comforting advice,

David Griesel, Hanno and Minette du Preez for much needed encouragement and invaluable friendship,

my mother, father and close family. Even if God should grant me his ability to love, I cannot return the love and support that you have shown me,

colleagues from the University of the Free State for their kindness and positive comments.

Above all I thank God, from whom this study originated.

Table of contents

CHAPTER	PAGE
1 GENERAL INTRODUCTION	1
2 (CO)VARIANCE COMPONENTS AND GENETIC TRENDS FOR GROWTH TRAITS	6
2.1 Introduction	6
2.2 Material and methods	7
2.2.1 Data	7
2.2.2 Statistical analyses	8
2.3 Results and discussion	10
2.4 Conclusion	28
3 GENOTYPE X ECOLOGICAL REGION INTERACTION IN THE NGUNI BREED	29
3.1 Introduction	29
3.2 Material and methods	30
3.2.1 Data	30
3.2.1.1 Characteristics of sweetveld (region 1)	31
3.2.1.2 Characteristics of sourveld (region 2)	31
3.2.1.3 Characteristics of mixed veld (region 3)	31
3.2.2 Statistical analyses	32
3.3 Results and discussion	33
3.4 Conclusion	41

4 GENERAL CONCLUSIONS AND RECOMMENDATIONS	42
ABSTRACT	46
OPSOMMING	48
REFERENCES	50

Chapter 1

General introduction

The indigenous Nguni cattle of Africa can be classified as Sanga and belong to the humped cattle group. Sanga cattle differ from the other group of humped cattle (Zebu) with respect to the structure of the Y-chromosome as well as the shape and position of the hump. Epstein (1971) suggested that Sanga cattle are neither pure or almost pure humpless longhorn, nor pure or almost pure Zebu type, but represent a variable mixture of the pure parent stock. Historians agree that Sanga cattle must have evolved around 1600 BC in the present-day Ethiopia and Somalia from crosses between Zebu and humpless Hamitic longhorn cattle (Felius, 1985). Evidence of this possible parentage was found in Libya and the Sahara desert from rock paintings depicting Sanga-like longhorned cattle. These rock paintings are estimated to be nearly 8000 years old. Felius (1985) states that this casts new perspective on the arrival of the European humpless longhorn, the progenitor of the Hamitic longhorn previously set at about 5000 BC.

The present day Nguni has had over 1200 years to adapt to the environmental extremes of not only Southern Africa, but also Central and Eastern Africa. The breed migrated through areas rife with Nagana, East coast fever and many other endemic diseases, and has survived seasonal as well as periodic droughts (Ramsay, 1986). The migration of the progenitors of the Nguni people, together with their Sanga cattle, originated from North, Central and East Africa, crossing the Zambezi between 590 and 700 AD. The migration of Sanga cattle southwards is thought to have occurred via the following three main routes:

- 1) south westerly to Ovamboland and Botswana and later to the Western Province;
- 2) southerly to Zimbabwe, Northern Province and southern Mpumalanga, and
- 3) south easterly to Mozambique, Swaziland and KwaZulu-Natal and later along the South-Eastern coast to the Eastern Province.

Two very important periods in the history of the Nguni cattle breed were during 1947 and 1950. In 1947 the Secretary of Agriculture appointed a committee "to make a survey of the nature and

numbers of indigenous stock in this country and to report upon the desirability and means of preserving this stock". As a result the well known report of Bonsma *et al.* (1950) was published.

The recommendations of the committee were as follows:

- 1) that immediate steps be taken to arrest the deterioration of indigenous cattle in the native reserves, consequent upon the infusion of exotic blood and the use of inferior sires;
- 2) that a pure-bred herd of not less than 500 Nguni breeding stock be established with a view to investigating the potentialities of the breed with regard to growth, production and reproduction and to serve as the nucleus of Nguni stud cattle.

The Nguni had already been on the sorry road to extinction, and today we can be thankful that the recommendations of Bonsma *et al.* (1950) were heeded and implemented (Hundleby, 1986). This led to other herds being established by the Department of Bantu Affairs in the various regions in South Africa (Ramsay, 1986).

As can be seen from the above, Nguni cattle are indigenous to Africa and are adapted to African conditions. Simm *et al.* (1996) state that traits contributing towards better adaptation may include physical attributes such as litter size, coat type, ability to store body fat, some aspects of behaviour, especially maternal and grazing behaviour, and disease resistance. Reproductive success, which is recorded because of its economic importance, also provides a crude measure of adaptation and perhaps an even more crude indication of the absence of severe welfare problems. Changes in body condition may provide a measure of the adaptation of different breeds or crosses to a harsh environment. Also, survival rates of different breeds and crosses may be measured and these too may provide a crude, but absolute, measure of adaptation. (Simm *et al.*, 1996). As far as these measures of adaptation are concerned, the Nguni has a thin skin suited to moist, hot conditions (McDowell, 1972) and shorter, thicker hair than the European breeds which make them more heat tolerant than these breeds with their long woolly coats (Jenkinson *et al.*, 1973). The fertility of the Nguni, especially under extensive conditions is well documented. Lepen (1994) reported calving percentages for 1992 and 1993 of 95,6% and 96,7% for Sanga cows used in a terminal cross breeding trial at Omatjenne Research Station in Namibia. Scholtz *et al.* (1990c) reported an overall

calving percentage of 91 for early bred Nguni heifers at Loskop South experimental farm. With regard to resistance, Kostrewski (1988) showed that the Nguni carried the lowest tick numbers regardless of species of tick or season of the year. Scholtz *et al.* (1991) reported no significant influence of the productivity of Nguni cattle irrespective of being dipped or not, while Bonsmara and Hereford cattle showed a significant decline in the weaning weight of calves when not dipped. The resistance to external parasites also contributes to the resistance to tick-borne diseases. Survival rates in Nguni cattle are high and at Omatjenne Research Station in Namibia, mortality rates as low as 2.2% have been reported (Lepen, 1994). Traits other than production traits that make a contribution to efficient meat production, are calving ease and longevity.

From the above the adaptability of the breed to local, harsh conditions is clearly evident. Adaptability is certainly the first and foremost aspect in efficient meat production and plays an important role in extensive production systems. However, unlike in the EU, food production has not approached or fulfilled requirements in Africa, and to a lesser extent South Africa. This has the possible effect of breeding goals being directed towards increased production levels. Harwin (1989) reasoned that a preoccupation with high absolute production levels coaxed breeders beyond the bounds of functionally efficient cattle, and that genetic resources should be matched to the production situation. Hodges (1984) stated that those who keep breeds for profit, are narrowing the genetic base to relatively few, highly selected top-performing animals. This trend must be evaluated in the light of the known fact (Warwick & Legates, 1979) that genetic variation is one of the essential ingredients that make genetic change possible and provides the major means for adaptation to changing environmental conditions. Although such in-bred lines (high-performing lines) are suited to the exploitation of heterosis, their buffer capacity to stress is affected (Rauw *et al.*, 1998). In addition, Scholtz *et al.* (1990b) reported negative effects on fitness traits when selection for body weights (production) took place.

From the above it can be concluded that much conflict might arise when production traits are included in the selection goals. This conflict might arise because of the negative effect on fitness traits, while others might arise because of the loss in genetic diversity. With all this evidence against selection for production traits, the question as to the relevance of selection on these traits arises. Furthermore, skepticism as to the relevance of genetic parameters might also arise in a breed

as well adapted as the Nguni. A possible answer might be that where fitness traits such as fertility are high, selection on production traits may be used to improve total herd efficiency. Nonetheless, whenever the optimum point is surpassed, i.e. where animals cannot maintain high reproduction rates whilst retaining a certain production level any longer, efficiency will decline. This optimum point will unquestionably be best determined by extensive conditions in which animals are expected to reproduce and produce in the future. It must be emphasized that this is only a possibility, as such optimum levels are not known and the fact that deleterious effects, including behavioural, physiological and immunological problems, have been detected in animals selected for high production efficiency (Rauw *et al.*, 1998). It can therefore be assumed that, taken the above into account, selection goals in indigenous cattle such as the Nguni are not easy. This is supported by Gertenbach & Kars (1999) who stated that goals as in the Bartlow Combine Nguni Stud, which emphasized mainly 205-day weaning weights, cannot be ignored, nor their implementation criticized. In spite of all these misgivings to production traits, genetic parameters such as heritability estimates and genetic correlations may better direct breeders and scientists as to whether growth traits should be included in selection goals. These genetic parameters may also be used to predict breeding values more accurately, which may aid breeders in the understanding of the genetic merit of each animal. Genetic parameters may also be used to better understand and predict correlated responses as well as the response that may be realized when certain selection strategies are performed. Finally, of ultimate importance is the calculation of genetic trends using the average estimated breeding value for each year to continuously monitor whether desired progress has been made.

The fact that physical environments in which production takes place, vary widely, cannot be disputed. This leads to the fragmentation of production environments. Bijma *et al.* (2002) states that fragmentation leads to potential genotype x environment (G x E) interactions both between selection and production environments and among production environments. Bijma *et al.* (2002) also states that fragmentations will make current (existing) interactions even more extreme. Such fragmentations and consequent G x E are especially important where cattle have to produce in harsh, extensive environments (Vercoe & Frisch, 1992). In a study using Brahman and Hereford x Shorthorn cattle, changes in ambient temperature, growth (associated with the same parasite challenge) and diet supplementation were proven to be associated with G x E (Vercoe & Frisch,

1992). It was concluded that G x E can be eliminated either by completely eliminating environmental stresses or by using animals that are completely resistant to environmental stresses. Clearly the elimination of environmental stresses is not as simple with cattle production in the tropics, as with housed species like poultry and pigs. The latter, suggesting use of cattle that are resistant to environmental stresses, seems to be a viable consideration. Kolmodin *et al.* (2002b) hypothesized that the average environmental sensitivity of the population will increase when selection for high phenotypic value, in combination with a continuously improving environment, in the presence of G x E takes place. This is supported by Bijma *et al.* (2002) who state that it is clear from the field of evolutionary genetics that the environment of selection has consequences for the genetic change in environmental sensitivity. According to Falconer (1990) this has the effect of increasing the "reaction norm", which describes the slope of the graph for performance against the quality rank of the environment. Significant additive genetic variance has been found for this slope (Kolmodin *et al.*, 2002a) and environmental sensitivity can therefore be changed by artificial selection (Kirkpatrick & Bataillon, 1999, De Jong & Bijma, 2002). Consequently, it may be possible to explicitly aim at a genotype that exhibits on average the same phenotype in all environments. Kolmodin *et al.* (2002b) stated that the implications for low sensitivity could be useful for low-input agriculture and in harsh climates.

Taking the above into account, three very important conclusions can be drawn. The first is the profound effect that an existing G x E interaction may have on the selection of adaptable animals. Secondly, it shows that it is imperative to allow the environment, especially a harsh, sub-optimal environment, to have the appropriate effect on producing animals. Thirdly, it is important to select animals that have been exposed to such environmental effects as to which they are expected to perform under. Falconer & Mackay (1997) states that selection is most effective if carried out in the environment for which the improvement is sought. However, before selection programmes can take all of these factors into account, it is necessary to study whether such a G x E interaction in a population exists, as well as the possible magnitude of such an interaction. Pertinent to this is possibly the conclusion by Albers *et al.* (2002) that very strong genotype x environment interactions are very rare and are dealt with through line breeding with adapted breeding goals.

Chapter 2

(Co)variance components and genetic trends for growth traits.

2.1 Introduction

The deliberation of economically important traits is the first and foremost aspect to be considered before selection of the parents of the next generation takes place. The accurate estimation of genetic parameters for these economic traits are thus of utmost importance (Koch *et al.*, 1973). Falconer & Mackay (1997) emphasize that heritability is not only a property of the character but also of the population. It is thus unique and important for every breed, not only for constructing selection objectives, but also to predict accurate breeding values for selection. The fitting of additional random factors such as the permanent maternal environmental effect in models used to estimate such breeding values is common practice to increase the accuracy of estimates. Since selection in a beef breed such as the Nguni takes place in various environmental conditions, the inclusion of an additional random factor, i.e. herd-year-season x sire interaction seems justified, as estimates of the variance due to interaction reflect both interactions and common environmental effects and vice versa as stated by Meyer (1987).

Selection for growth is complicated by the fact that traits like birth and weaning weight are determined by the animal's own additive genetic merit as well as a maternal component, which can be separated in an additive genetic and environmental component. Statistical and computational developments make it possible to separate the additive and maternal component as well as the relationship between these two components, which is mostly negative. This is of significance, since a clearly antagonistic relationship would have consequences for the breeding program, eventually leading to the development of specialized sire and dam lines (Swalve, 1993). This may be of concern to South African indigenous cattle, as most are acknowledged as potential dam lines.

Taking the above into account, the objective of this study was to estimate the (co)variance components for growth traits of animals participating in the National Beef Cattle Performance Testing Scheme (NBPTS) for the Nguni cattle breed. Consequently heritability estimates and

genetic correlations were also estimated in an attempt to aid the prediction of selection response and correlated response when selection is based on production traits. Genetic trends were derived to observe if any genetic change had taken place.

2.2 Materials and methods

2.2.1 Data

Data from Nguni herds participating in the National Beef Cattle Performance Testing Scheme (NBPTS) from 1960 to 2001 were considered in the study. Records of birth weight (BW), weaning weight (WW), yearling weight (YW) and eighteen-month weight (EW) were used to estimate (co)variance components and genetic parameters. Incomplete records were discarded and a description of the data set, after editing, with regard to the number of records, dams, sires, herds, contemporary groups (CG) and average size of contemporary groups as well as the maximum values of contemporary groups for each trait is presented in Table 2.1. The minimum contemporary group size for all the traits were five animals. As the former Bartlow Combine Nguni Stud was the first to officially record performance of production traits in the breed, the contribution (%) of the Bartlow Combine Nguni Stud (BC) to the number of records for each trait is also shown in Table 2.1.

From Table 2.1, it is interesting to note the decrease in the number of records from WW to YW and EW. The decrease may be due to the fact that a large number of the calves are sold as weaners to feedlots and weights at yearling and/or eighteen months of age are thus not recorded. Breeders may also be more interested in the recording of WW, as this can be used to measure the efficiency of the dam as described by Van der Westhuizen & Matjuda (1999). The maternal ability is indeed important, as the breed is widely recognized as an excellent dam line. Scholtz *et al.* (1990a) state that the breed ideally suits the requirements for a dam line in terminal crossbreeding programs.

Table 2.1 Data description after editing

Trait	BW	WW	YW	EW
No. of records	26 677	23 723	10 256	7 260
No. of dams	11 223	9 673	5708	4 475
No. of sires	919	838	565	448
No. of herds	92	80	69	60
No. of CG	734	554	357	267
Avg. CG size	36	42	28	27
Max. CG size	512	511	301	239
% BC	34	37	28	27

CG – contemporary group; BC – Bartlow Combine Nguni Stud; Avg. – average value; Max. – maximum value

2.2.2 Statistical analyses

The GLM procedure of SAS (1991) was used to evaluate the different fixed effects to be included in the model. (Co)variance components as well as heritabilities were estimated using the ASREML program (Gilmour *et al.*, 1999). Log likelihood ratio tests, obtained in univariate analyses, were used to indicate the most suitable model for each trait to estimate the (co)variance components in multivariate analyses. A model was considered more suitable when a significant ($P < 0.05$) increase in the log likelihood occurred when fitting an additional random effect. Significance was assumed when minus two times the difference between the log likelihoods obtained from the different models used, was larger than the chi-square distribution with one degree of freedom (Swalve, 1993). The estimates obtained by univariate analyses were used as starting values in the multivariate analyses. In multivariate analyses another data set was used which included only herds linked with at least two other herds through sires used. This data set was also used in the bivariate analyses which were carried out to determine the covariance between the different components of the maternally influenced traits (BW and WW), as solutions from the multivariate analyses did not provide information about the covariance structure of the maternal genetic component between BW and WW. Another bivariate analysis between WW and YW was also carried out in order to gain knowledge as to a possible carry-over effect concerning the maternal genetic effect. Heterogeneous variances were tested by correcting the y-value with the standard deviation of each contemporary group, but were found to be non-significant.

In the univariate analyses, twelve different models were tested by either including or ignoring the direct effect, maternal genetic effect, permanent environmental effect of the dam, the covariance between direct and maternal effects and the effect of a herd-year-season by sire interaction (HYSxS). The models were as follows:

$$y = Xb + Z_1a + e \quad (1)$$

$$y = Xb + Z_1a + Z_3c + e \quad (2)$$

$$y = Xb + Z_1a + Z_2m + e \quad (3)$$

$$\text{with cov (a,m) = 0}$$

$$y = Xb + Z_1a + Z_4\text{HYSxS} + e \quad (4)$$

$$y = Xb + Z_1a + Z_3c + Z_4\text{HYSxS} + e \quad (5)$$

$$y = Xb + Z_1a + Z_2m + e \quad (6)$$

$$\text{with cov (a,m) = } A\sigma_{am}$$

$$y = Xb + Z_1a + Z_2m + Z_4\text{HYSxS} + e \quad (7)$$

$$\text{with cov (a,m) = 0}$$

$$y = Xb + Z_1a + Z_2m + Z_3c + e \quad (8)$$

$$\text{with cov (a,m) = 0}$$

$$y = Xb + Z_1a + Z_2m + Z_3c + e \quad (9)$$

$$\text{with cov (a,m) = } A\sigma_{am}$$

$$y = Xb + Z_1a + Z_2m + Z_4\text{HYSxS} + e \quad (10)$$

$$\text{with cov (a,m) = } A\sigma_{am}$$

$$y = Xb + Z_1a + Z_2m + Z_3c + Z_4\text{HYSxS} + e \quad (11)$$

$$\text{with cov (a,m) = 0}$$

$$y = Xb + Z_1a + Z_2m + Z_3c + Z_4\text{HYSxS} + e \quad (12)$$

$$\text{with cov (a,m) = } A\sigma_{am}$$

where

y is a vector of observations;

b is a vector of fixed effects;

a is a vector of direct additive genetic effects;

m is a vector of maternal additive genetic effects;

c is a vector of permanent environmental effects;

HYSxS is a vector of herd-year-season x sire interaction effects;

X, Z₁, Z₂, Z₃, Z₄ are incidence matrices;

e is the vector of residuals;

A is the numerator relationship matrix and

σ_{am} is the covariance between direct additive genetic and maternal additive genetic effects.

It was assumed that:

$$V(a) = A\sigma_a^2; V(m) = A\sigma_m^2; V(c) = I\sigma_c^2; V(\text{hyss}) = I\sigma_{\text{hyss}}^2; V(e) = I\sigma_e^2$$

where **I** is an identity matrix, σ_a^2 , σ_m^2 , σ_c^2 , σ_{hyss}^2 and σ_e^2 is the direct additive genetic variance, maternal additive genetic variance, permanent maternal environmental variance, HYSxS variance and environmental variance, respectively.

The models used were an extension of the six models described by Meyer (1992). In the multivariate analyses, model 11 was used to estimate the (co)variance structure of BW and WW while model 4 was used for YW and EW. Model 12 was used for both the maternally influenced traits (BW and WW) in the bivariate analyses.

Finally, genetic trends were calculated as the regression of average breeding value estimates (EBV) on year of birth. Genetic trends were separated into two time periods. The first period only contained data from Bartlow Combine Nguni Stud (BC) (1960 to 1985 for BW and WW and 1960 to 1984 for YW and EW). The second period contained data from Bartlow Combine as well as the rest of the breed (BRD) (1986 to 2000 for BW and WW and 1985 to 1999 for YW and EW).

2.3 Results and discussion

Herd-year-season, sex, age at recording (except BW) and age of dam had a significant effect ($P < 0.0001$) on the different traits measured. This agrees with results obtained by Kars *et al.* (1994) in the Bartlow Combine Nguni Stud.

The basic statistics for each trait are summarized in Table 2.2.

Table 2.2 Mean, standard deviation (SD), coefficient of variation (CV), minimum (Min) and maximum (Max) for BW, WW, YW and EW

Trait	Mean (kg)	SD (kg)	CV(%)	Min (kg)	Max (kg)
BW	25.49	3.98	12.28	13	38
WW	161.62	26.71	11.81	79	243
YW	185.97	33.28	11.23	85	290
EW	251.15	42.09	10.27	125	381

The coefficients of variation for BW, WW and YW compare well with reported values of 12.9%, 10.7% and 10.1% respectively by Van der Westhuizen (1997). The coefficient of variation for EW does, however, not correspond well with the value of 23.9% recorded by Van der Westhuizen (1997). A possible reason may be that the study conducted by Van der Westhuizen (1997) was only on the Bartlow Combine Nguni Stud. With regard to means, results obtained compared favourably with those obtained by Van der Westhuizen (1997) (26.0, 160.6, 186.4 and 254.7 kg for BW, WW, YW and EW respectively).

The log likelihoods, (co)variance components and genetic parameters for BW, WW, YW and EW as obtained by univariate analyses are presented in Tables 2.3 to 2.6.

The most complete model (Model 12) fitted BW the best, while Model 11 fitted both WW and YW the best. This model included all the components, except the covariance between the two animal effects. Model 7 fitted EW the best.

(Co)variance components and genetic parameters obtained by multivariate analyses for BW, WW, YW and EW are presented in Table 2.7.

Table 2.3 Log likelihoods, estimates of (co)variance components (kg²) and genetic parameters for BW with the “best” model in bold

Parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10	Model 11	Model 12
LogL.	-42861.1	-42801.4	-42789.6	-42691.4	-42652.8	-42745.9	-42632.6	-42776.7	-42743.4	-42616.3	-42618.8	-42613.4
σ_a^2	3.7003	3.0398	2.7300	3.3410	2.4099	4.3280	1.8647	2.7411	4.3359	2.5870	1.8999	2.6137
σ_m^2			0.6925			1.7446	0.7898	0.5342	1.5004	1.2092	0.6040	0.9848
σ_{am}						-1.5687			-1.5127	-0.6194		-0.5854
σ_c^2		0.6096			0.6365			0.1994	0.2197		0.2132	0.2160
σ_{hyss}^2				0.8178	0.8179		0.8212			0.7317	0.8196	0.7310
σ_e^2	6.4045	6.3423	6.5333	6.2299	6.3272	5.6782	6.6316	6.4759	5.6312	6.2670	6.5683	6.2114
σ_p^2	10.1048	9.9916	9.9558	10.3887	10.1915	10.1821	10.1073	9.9506	10.1744	10.1755	10.1050	10.1715
h_a^2	0.3662	0.3042	0.2742	0.3216	0.2365	0.4251	0.1845	0.2755	0.4262	0.2542	0.1880	0.2570
SE	0.0145	0.0163	0.0169	0.0151	0.018	0.0299	0.0193	0.0169	0.0298	0.0306	0.0194	0.0306
h_m^2			0.0696			0.1713	0.0781	0.0537	0.1475	0.1188	0.0598	0.0968
SE			0.0076			0.0163	0.0080	0.0106	0.0193	0.0156	0.0114	0.0181
r_{am}						-0.5709			-0.5931	-0.3502		-0.3649
c^2		0.0610			0.0625			0.0200	0.0216		0.0211	0.0212
SE		0.0071			0.0071			0.0096	0.0103		0.0098	0.0101
$\sigma_{hyss}^2 / \sigma_p^2$				0.0787	0.0803		0.0812			0.0719	0.0811	0.0719
SE				0.0062	0.0063		0.0064			0.0065	0.0064	0.0065

σ_a^2 – direct additive genetic variance; σ_m^2 – maternal additive genetic variance; σ_{am} – direct-maternal genetic covariance; σ_c^2 – permanent environmental variance; σ_{hyss}^2 – HYSxS variance; σ_e^2 – error variance; σ_p^2 – phenotypic variance; h_a^2 – direct heritability; h_m^2 – maternal heritability; r_{am} – direct-maternal genetic correlation; $c^2 = \sigma_c^2 / \sigma_p^2$; SE – standard error.

Table 2.4 Log likelihoods, estimates of (co)variance components (kg^2) and genetic parameters for WW with the “best” model in bold

Parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10	Model 11	Model 12
LogL.	-79830.5	-79452.9	-79468.5	-79632.6	-79230.3	-79432.0	-79254.6	-79420.9	-79406.1	-79250.5	-79208.8	-79220.6
σ^2_a	207.7130	124.2460	106.5530	204.2350	83.1508	154.1150	53.2746	115.1850	155.7150	73.5517	65.2354	75.1046
σ^2_m			94.1881			142.7690	101.0570	35.5787	73.8800	118.5700	40.3855	48.1020
σ_{am}						-67.0679			-53.5605	-23.6411		-10.3819
σ^2_c		83.5449			87.3360			53.9938	52.8612		54.9217	54.5421
σ^2_{hyss}				34.6123	32.4387		34.2885			31.7320	33.2337	31.9812
σ^2_e	186.5310	176.3430	189.5250	170.1780	182.6400	164.2860	201.4650	180.1820	159.3870	191.2170	191.0020	186.1560
σ^2_p	394.2440	384.1339	390.2661	409.0253	385.5655	394.1021	390.0851	384.9395	388.2827	391.4296	384.7783	385.5040
h^2_a	0.5269	0.3234	0.2730	0.4993	0.2157	0.3911	0.1366	0.2992	0.4010	0.1879	0.1695	0.1948
SE	0.0151	0.0188	0.0181	0.0156	0.0211	0.0284	0.0199	0.0191	0.0286	0.0286	0.0217	0.0288
h^2_m			0.2413			0.3623	0.2591	0.0924	0.1903	0.3029	0.1050	0.1248
SE			0.0102			0.0187	0.0101	0.0167	0.0250	0.0186	0.0174	0.0234
r_{am}						-0.4521			-0.4994	-0.2532		-0.1727
c^2		0.2175			0.2265			0.1403	0.1361		0.1427	0.1415
SE		0.0093			0.0096			0.0151	0.016		0.0155	0.0157
$\sigma^2_{hyss}/\sigma^2_p$				0.0846	0.0841		0.0879			0.0811	0.0864	0.0830
SE				0.0063	0.0063		0.0065			0.0066	0.0064	0.0067

See Table 2.3 for abbreviations.

Table 2.5 Log likelihoods, estimates of (co)variance components (kg^2) and genetic parameters for YW with the “best” model in bold

Parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10	Model 11	Model 12
LogL.	-35363.6	-35327.8	-35327.0	-35330.4	-35288.5	-35324.1	-35285.6	-35324.3	-35321.8	-35285.6	-35283.0	-35282.9
σ^2_a	182.9230	116.4280	103.2070	170.5650	77.9846	117.5420	55.0006	105.6070	118.8360	53.5717	58.7638	55.0645
σ^2_m			60.3548			86.6968	70.4147	33.8753	57.6933	68.3838	43.6980	38.3671
σ_{am}						-31.0653			-27.1634	2.3938		5.8851
σ^2_c		58.0752			65.5327			29.1752	27.7512		28.9039	29.3758
σ^2_{hyss}				25.5777	28.0706		30.0951			30.3556	29.6751	30.3495
σ^2_e	275.2500	273.3830	284.1450	271.7860	281.0570	275.5080	296.3050	278.5460	271.1010	297.0500	290.3810	292.1440
σ^2_p	458.1730	447.8862	447.7068	467.9287	452.6449	448.6815	451.8154	447.2035	448.2181	451.7549	451.4218	451.1860
h^2_a	0.3992	0.2599	0.2305	0.3645	0.1723	0.2620	0.1217	0.2361	0.2651	0.1186	0.1302	0.1220
SE	0.0272	0.0285	0.0286	0.0289	0.0320	0.0346	0.0322	0.0291	0.0348	0.0377	0.0329	0.0379
h^2_m			0.1348			0.1932	0.1558	0.0757	0.1287	0.1514	0.0968	0.0850
SE			0.0160			0.0304	0.0161	0.0291	0.0415	0.0299	0.0297	0.0399
r_{am}						-0.3077			-0.3281	0.0395		0.1280
c^2		0.1297			0.1448			0.0652	0.0619		0.0640	0.0651
SE		0.0156			0.0157			0.0277	0.0286		0.0279	0.0280
$\sigma^2_{hyss} / \sigma^2_p$				0.0547	0.0620		0.0666			0.0672	0.0657	0.0673
SE				0.0092	0.0097		0.0102			0.0109	0.0101	0.0109

See Table 2.3 for abbreviations.

Table 2.6 Log likelihoods, estimates of (co)variance components (kg^2) and genetic parameters for EW with the “best” model in bold

Parameter	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7	Model 8	Model 9	Model 10	Model 11	Model 12
LogL.	-26522.8	-26515.1	-26513.8	-26511.3	-26500.4	-26513.8	-26498.0	-26513.7	-26513.6	-26497.4	-26497.8	-26497.2
σ_a^2	225.3740	173.2930	155.7560	198.7920	119.2580	158.7910	90.8500	157.5780	160.3900	77.7976	92.8306	79.4268
σ_m^2			53.9423			60.9900	68.4628	40.8581	47.3815	45.4546	56.1309	32.0567
σ_{am}						-8.0794			-7.3486	26.5465		26.8836
σ_c^2		49.4449			60.8853			14.6928	14.5086		13.6788	14.7418
σ_{hyss}^2				27.7376	32.8408		35.2119			37.6958	35.0962	37.6708
σ_e^2	464.0450	458.9410	470.1730	471.0970	473.4260	468.3300	489.6230	466.8130	465.1860	496.3870	486.4450	493.2030
σ_p^2	689.4190	681.6789	679.8713	697.6266	686.4101	680.0316	684.1477	679.9419	680.1175	683.8815	684.1815	683.9827
h_a^2	0.3269	0.2542	0.2291	0.2850	0.1737	0.2335	0.1328	0.2318	0.2358	0.1138	0.1357	0.1161
SE	0.0334	0.0346	0.0353	0.0360	0.0391	0.0384	0.0401	0.0358	0.0387	0.0436	0.0408	0.0439
h_m^2			0.0793			0.0897	0.1001	0.0601	0.0697	0.0665	0.0820	0.0469
SE			0.0193			0.0363	0.0196	0.0371	0.0507	0.0356	0.0379	0.0492
r_{am}						-0.0821			-0.0843	0.4464		0.5328
c^2		0.0725			0.0887			0.0216	0.0213		0.0200	0.0216
SE		0.0189			0.0193			0.0356	0.0361		0.0359	0.0354
$\sigma_{hyss}^2 / \sigma_p^2$				0.0398	0.0478		0.0515			0.0551	0.0513	0.0551
SE				0.0106	0.0114		0.0119			0.0128	0.0119	0.0128

See Table 2.3 for abbreviations.

Table 2.7 Estimates of (co)variance components (kg^2) and genetic parameters obtained by multivariate analyses for BW, WW, YW and EW

Parameter	BW	WW	YW	EW
σ^2_a	4.4502	175.1190	203.6560	373.6960
σ^2_m	0.2979	1.8915	-	-
σ_{am}	-	-	-	-
σ^2_c	0.2889	26.9384	-	-
σ^2_{hyss}	3.5540	189.5020	440.5110	628.5030
σ^2_e	5.7400	146.0370	238.0590	364.0390
σ^2_p	14.3310	539.4879	882.2260	1366.2380
h^2_a	0.3105	0.3246	0.2308	0.2735
SE	0.0201	0.0204	0.0230	0.0293
h^2_m	0.0208	0.0035	-	-
SE	0.0091	0.0071	-	-
r_{am}	-	-	-	-
c^2	0.0202	0.0499	-	-
SE	0.0076	0.0069	-	-
$\sigma^2_{hyss} / \sigma^2_p$	0.2480	0.3513	0.4993	0.4600
SE	0.0104	0.0128	0.0184	0.0215

See table 2.3 for abbreviations.

An increase in the direct variance components and a reduction in the error variance components were observed for all traits, when changing from the univariate to the multivariate analyses. Similar results were observed by Bennett & Gregory (1996) when comparing univariate and multivariate analyses and also by Núñez-Domínguez *et al.* (2002) when changing from univariate to bivariate analyses. Hence, in this study as well as the study done by Núñez-Domínguez *et al.* (2002), an increase in the direct heritability estimates was evident. Eler *et al.* (1995) also reported higher estimates of direct heritabilities from multivariate analyses than from univariate analyses when BW, WW and YW were analysed. Furthermore, the increase of the direct heritability estimates, especially the large increase in WW, YW and EW, may be explained by the moderate to high and positive direct genetic correlations among the different traits (discussed later). This indicates that a large proportion of genes contributing to a specific trait, also contribute to others. Therefore, in multivariate analyses each trait is used as an additional source of information for predicting breeding values for each of the other traits included in the analyses. Breeding values obtained from

the multivariate analyses should be more accurate, due to a better connectivity among contemporary groups (Thompson & Meyer, 1986). Contributing to the increased direct heritability estimate is the reduction in the maternal genetic variance in BW and WW. Maternal heritability estimates were very low and were found to be non-significant. A possible explanation may be the lack of the inclusion of this effect in multivariate analyses for YW and EW, as bivariate analyses indicate that a partial carry-over effect exists (discussed later). A reduction in the permanent environmental variance was only observed in WW and was significant as a proportion of the phenotypic variance. This effect was non-significant in BW. Further possible causes of differences in the (co)variance structure between uni- and multivariate analyses, include the use of different data sets as well as different models used for BW, YW and EW in the multivariate compared to the univariate analyses.

The effect of including genotype by environment interaction in the model, or as in this study HYSxS, is well documented (Buchanan & Nielsen, 1979, Tess *et al.*, 1979, Bertrand *et al.*, 1985, 1987, Foulley & Henderson, 1989, Brown *et al.*, 1993a, 1993b). The inclusion of HYSxS effect is of significant importance, especially when estimating genetic parameters and subsequent breeding values as this will have an effect on the accuracy of the estimates (Neser *et al.*, 1996). This is supported by Meyer (1987) who reported that the exclusion of even a small genotype x environment interaction can lead to an overestimation of the accuracy of the sire's predicted breeding value. This is clearly evident in the reduction of the direct heritability in WW from 0.30 to 0.17 when HYSxS was included in the model (Table 2.4). This tendency was approximately the same for all the other traits. This corresponds with the results obtained by Neser *et al.* (1996) where a reduction of the direct additive genetic variance took place when HYSxS interaction was included in the analyses. This is also evident when observing the direct heritability estimates obtained by Kars *et al.* (1994) on the Bartlow Combine Nguni Stud which were 0.41, 0.29, 0.26 and 0.19 for birth, weaning, yearling and eighteen-month weight, respectively. These estimates are all well above the current estimates. Also in agreement with Neser *et al.* (1996) there is an increase in the error variance when the HYSxS interaction was included. This is true for all the traits when using the "best" model compared to a similar model without the HYSxS interaction.

A decline in the direct-maternal correlation (-0.59 to -0.36) in BW was evident when HYSxS was included in the model (Table 2.3). This is in accordance with Lee & Pollak (1997) who also found a decline (-0.29 to -0.14) when fitting a sire x year interaction. Robinson (1996) also showed that

direct-maternal correlation may be negative because of additional sire or sire x environment variation. The HYSxS variance thus explains part of the covariance (61%) and corresponding correlation (38%) between direct and maternal genetic effects.

Estimates of the HYSxS interaction variance as a proportion of the phenotypic variance was 0.07, 0.09, 0.07 and 0.05 for BW, WW, YW and EW, respectively (Tables 2.3 to 2.6). These estimates compare well with Nescer *et al.* (1996) who obtained a value of 0.08 for WW. Van der Westhuizen (1997), fitting a sire x year-season interaction, obtained values of 0.03 and 0.05 for BW and EW respectively. Lee & Pollak (1997) reported a value of 0.03 for WW, fitting a sire x year interaction. These estimates among the different traits are almost of the same order. Again this is of extreme importance in this dam line as progeny of sires may perform differently in different contemporary groups with regard to not only WW, but also BW, YW and EW.

The direct heritability estimate for BW (0.31) (Table 2.7) compares well with the weighted mean heritability of Koots *et al.* (1994a) (0.31), while the estimate for WW (0.32) is above (0.24). The estimate for YW (0.23) is lower than the weighted mean heritability of Koots *et al.* (1994a) (0.33). The direct heritability estimate for BW obtained by Van der Westhuizen (1997) (0.31), fitting a sire x year-season interaction, also compares well with this study while the estimate for EW (0.27) is higher than the estimate reported by Van der Westhuizen (1997) (0.16).

Since the multivariate analyses did not include the covariance between the two animal effects, results of univariate analyses was used to consider this relationship. A negative correlation was obtained (-0.36) between the direct and maternal component for BW. Koots *et al.* (1994b) also found the genetic correlations between direct and maternal effects for the same trait to be negative in all cases studied, with a weighted mean of -0.35 for BW. Since the environment played an integral part in the development of the breed, this negative correlation can be expected, as Falconer & Mackay (1997) state that since maternal and direct effects both contribute to fitness, negative correlations would result from natural selection. Negative relationships between the two animal effects may partially be attributed to sampling variation as found by Meyer (1992).

In this respect Robinson (1996) also illustrated that estimates of direct-maternal correlations may be negative, not only because of genetic antagonisms, but also because of additional sire or sire x year

variation or negative dam-offspring covariances. This additional sire x year variation may partially be taken into account in the present study by the inclusion of a HYSxS interaction as additional random factor.

This genetic relationship between the direct and maternal component, as well as the additive maternal component of BW, is of utmost importance, since Nguni cows have the ability to restrict the growth of the fetus (Scholtz *et al.*, 1990a) which can decrease the incidence of dystocia. Such abilities are extremely important as contributors to efficiency in beef cattle. In addition, Cartwright (1970) lists the absence of calving difficulties as an important prerequisite for specialized dam lines. Maree & Casey (1993) state that the low absolute birth weight of Sanga breeds, as well as the birth weight of cross-bred progeny which is generally below the midparent value of the parental breeds, is a clear guideline to the application of these breeds as dam lines in cross-breeding systems.

Permanent maternal environment expressed as the proportion of the phenotypic variance was 0.02 and 0.05 for BW and WW respectively (Table 2.7). The estimate for WW is lower than results obtained by Nesor *et al.* (1996, fitting a HYSxS interaction, univariate analyses) (0.15). Van der Westhuizen (1997) reported that this effect did not play a significant role in explaining variation in WW in the Bartlow Combine Nguni herd. Meyer (1992) reported a permanent maternal environmental estimate of 0.23 and stated that WW in Hereford cattle was primarily determined by this effect.

WW is the most important trait in beef production, since weaners are usually the first marketable product in the beef herd (Maree & Casey, 1993). This implicates both the direct and maternal components. Gertenbach & Kars (1999) argue that if the goal for the conservation of the Nguni breed of cattle is to retain its character as a dam line to promote maternal characteristics and fertility suitable for communal and commercial farming practices, certain traits must be retained. Such traits are, among others, those associated with maternal breeding values. This is supported by Cartwright (1970) who lists the requirement of desired milking qualities in potential dam lines. Furthermore, selection on direct breeding values for WW would place more stress on such cows if run under sub-optimal conditions, and the dam's poor mothering ability would place a ceiling on weaning weights of weaners with a high genetic potential. Such dams are not suitable for use as a dam line. (Gertenbach & Kars, 1999). Maree & Casey (1993) state that Sanga breeds produce

sufficient milk to wean heavy calves and make excellent dam lines.

Selection on maternal breeding values also seems to be coupled with some impositions. Antagonistic relationships between high milk production and several fertility traits have been observed by several authors (Hansen *et al.*, 1983, Hoekstra *et al.*, 1994, Rauw *et al.*, 1998). In beef cattle though, maternal breeding values do not only comprise milk production and an antagonistic relationship with fertility will partially depend on the accuracy with which maternal breeding values describe milk production. Nonetheless, selection on either direct or maternal breeding values separately, both seem to have their inflections.

Weaning weight can be used, as mentioned before, to calculate cow efficiency (Van der Westhuizen & Matjuda, 1999, Maree & Casey, 1993). This may be very important for a potential dam line as the improvement of efficiency in any form will increase profit. However, selection for cow efficiency could only be justified if there is no detrimental effect on fertility. This is supported by Maree & Casey (1993) who emphasize the inclusion of fertility as a true indication of productivity.

The possibility of a 'carry-over effect' (Mavrogenis *et al.*, 1978, Meyer *et al.*, 1993) from WW to YW could not be considered as maternal genetic effects and were therefore not included for YW and EW in the multivariate analyses. Univariate results did however suggest that such an effect does exist. Eler *et al.* (1995) also found a relatively high contribution of maternal effects in YW. The authors stated that the length of time from weaning to yearling is probably not sufficient for compensatory gain to buffer completely the maternal effect existing at weaning, especially for animals raised on pasture without any supplementary feeding. To clarify whether maternal effects are strictly 'carry-over' effects, Eler *et al.* (1995) performed an analysis on post weaning average daily gain (ADG) with a resulting drop in maternal heritabilities. An estimate of the maternal correlation (0.64 ± 0.10) obtained through bivariate analyses between WW and YW, shows maternal effects for YW to be partially due to a 'carry-over' effect through a part-whole relationship, since this correlation is not close to unity. This maternal correlation is lower than the estimate obtained by Meyer *et al.* (1993) who reported a high maternal correlation (0.99) between WW and YW, also from bivariate analyses.

When considering EW, selection for this trait may not be favourable as the increase in EW will increase mature weight, which, in turn will increase maintenance requirements (Kars *et al.*, 1994). Also, Muggli & Hohenboken (1984) reported higher incidence of dystocia and calf mortality as a result of selection for higher body weights. Furthermore, Cartwright (1970) lists a relatively small size as a prerequisite for specialized dam lines, whereas Maree & Casey (1993) state that small size and a relatively low mature body weight in Sanga cattle types, are considered to be an adaptational feature in terms of maintenance requirements. This is of utmost importance, since the negative effect of selection for increased body weight or growth rate on fitness, especially mature body weight, is well recorded as reviewed by Scholtz *et al.* (1990b).

Genetic correlations between direct components obtained from the multivariate analysis for BW, WW, YW and EW are presented in Table 2.8.

Genetic correlations among the different traits were all positive, ranging from moderate (0.50) to high (0.95). Estimates between WW and later weights are almost similar to those presented by Groeneveld *et al.* (1998, Afrikaner cattle) (0.86 and 0.93) and Meyer *et al.* (1993) (0.88 and 0.92) but higher than those presented by Van der Westhuizen (1997) who reported genetic correlations of BW with WW and EW, which ranged from 0.02 to 0.2. The rest of the direct genetic correlations correspond favourably with Groeneveld *et al.* (1998) and Meyer *et al.* (1993). However, these two authors did not fit a HYSxS interaction.

It is evident from the positive direct genetic correlation (0.53) between WW and BW that an increase in BW will take place when selection for WW is applied. Such practices may lead to serious problems in the long term as this may lead to a higher incidence of dystocia. Furthermore, selection on direct breeding values for WW will also lead to the unfavourable increase of EW as the direct genetic correlation of 0.90 indicates. The feasibility of increasing WW without increasing BW may look promising as the direct correlation is not close to unity. However, the almost unattainable result of maintaining EW renders such practice impractical. In addition, Cundiff *et al.* (1974) reported that fitness traits (dystocia and calf mortality) were negatively influenced in lines selected for heavier body weights. Selection for EW will in turn also lead to an increase in BW which again will lead to a higher incidence of dystocia, as the direct genetic correlation between these traits is 0.50. Van der Westhuizen (1997) reported a correlation of 0.15 between BW and EW.

The different effects fitted might be the applicable reason for the dissimilar estimates.

Table 2.8 Genetic correlations with the corresponding standard errors (SE) between direct components for BW, WW, YW and EW

Trait	WW	YW	EW
BW	0.53	0.51	0.50
SE	0.04	0.05	0.06
WW		0.95	0.90
SE		0.03	0.04
YW			0.92
SE			0.04

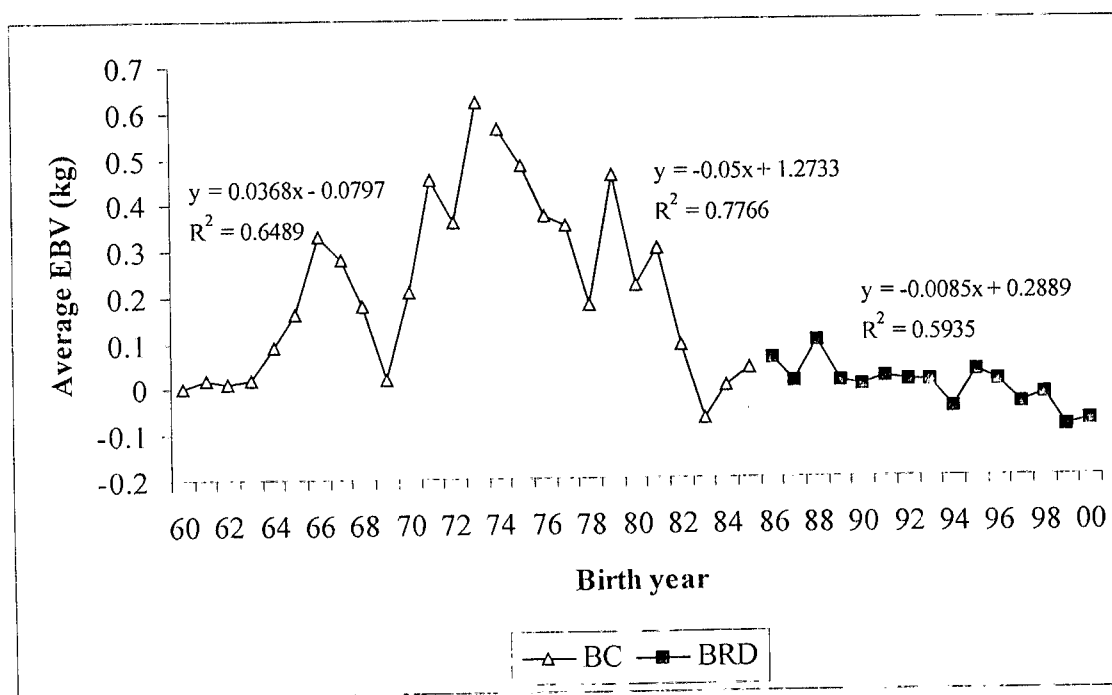
The direct genetic correlations indicate that selection for any of these growth traits will result in an increase in all the other traits. Correlated response of YW and EW when selecting for WW will be rapid as the relevant genetic correlations are close to unity. This result shows that almost the same genes that are responsible for the calf's inherent growth up to weaning are responsible for growth up to yearling and eighteen-month age. This also holds true for YW and EW. These high direct genetic correlations have several implications. The first is the inessential recording of both YW and EW, as the direct correlations between the traits show that a missing trait among one of these two will not have a significant effect on what is known about the post weaning performance of a specific animal. Although the direct correlation of WW with YW and EW is also very strong, the recording of WW together with YW or EW is essential as it is necessary for accurate breeding values of the maternal component of WW.

Bivariate analysis of maternally influenced traits (BW and WW) revealed that conflict might arise when selecting on maternal breeding values for WW, as this might have a negative effect on the dam's ability to inhibit the size of the fetus, thus increasing BW. This is illustrated by the positive, moderate genetic correlation (0.49 ± 0.08) between the maternal components. The maintenance of the dam's ability to inhibit the size of the fetus is very important for low incidence of dystocia and consequent efficient meat production. The maternal component of WW can however not be neglected as Kaps *et al.* (2000) state that maternal genetic effects influence not only growth traits, but also maturing rate. This is supported by Meyer (1995) who reported significant positive maternal effects on the maturation rate in Herefords. Such positive maternal effects on the maturing

rate of heifers will also improve efficiency in meat production. The maternal performance as measured according to the quality of offspring weaned, is also a component of fitness as illustrated by Falconer & Mackay (1997). Fortunately, however, the genetic correlation between these two maternal components is moderate, with the resultant opportunity of maintaining BW while improving WW through the maternal component, where necessary. This highlights the use of breeding values in conjunction with one another.

Although the univariate analysis showed the negative covariance between direct and maternal effects to be non-significant in WW, the bivariate analyses between BW and WW showed a negative association between all direct and maternal effects (range -0.24 to -0.71). Groeneveld *et al.* (1998) reported similar results in Afrikaner cattle. This shows that maternal abilities will decline when exclusive selection for growth on direct breeding values for WW is practised.

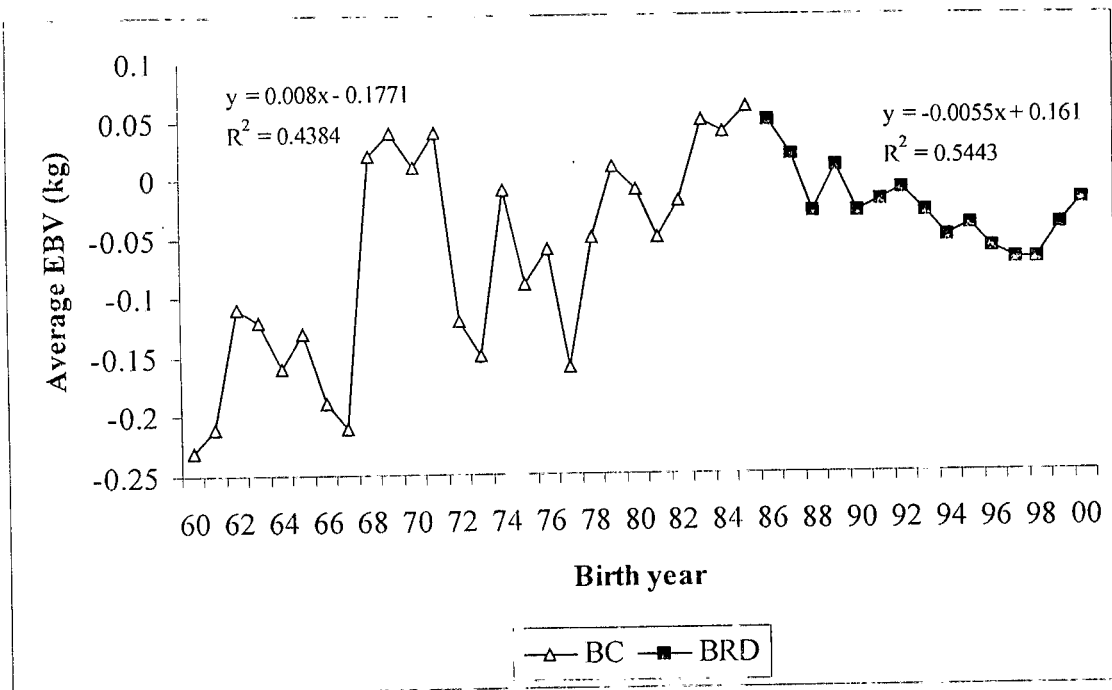
Genetic trends derived are presented in Figures 2.1 to 2.6.



BC – Bartlow Combine Nguni Stud; BRD – Breed

Figure 2.1 Annual mean direct additive breeding value estimates and genetic trend for birth weight

The direct genetic trend of the breed (BRD) for BW shows an average decrease of 0.01 kg from 1986 till 2000 (Figure 2.1). The direct trend for animals in the Bartlow Combine (BC) herd indicates that birth weight had increased from 1960 till 1973, after which it decreased again as shown by the negative trend (1974 to 1985). A possible reason is the fact that selection in the BC herd was based on type, conformation and weight at weaning and two years of age (Kars, 1993). The increase in BW may have been a correlated response from such selection. After 1970, more emphasis was placed on fertility (Kars, 1993), with a consequent decline in BW.

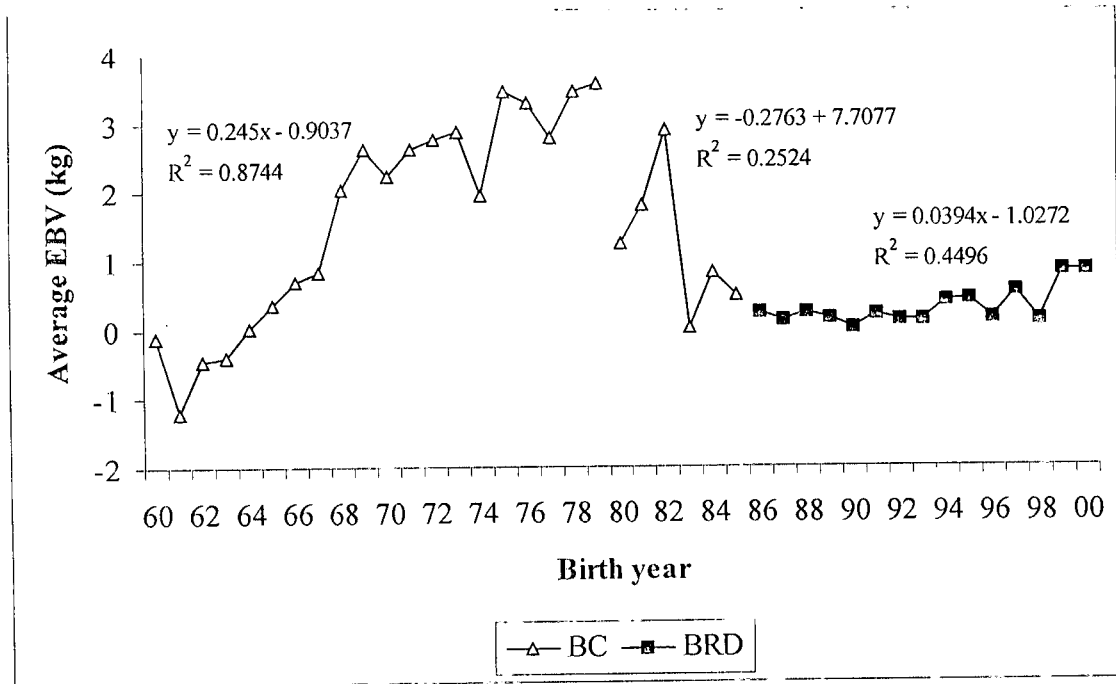


See Figure 2.1 for abbreviations.

Figure 2.2 Annual mean maternal additive breeding value estimates and genetic trend for birth weight

An annual average decrease of 0.01 kg of the maternal genetic trend for BW had taken place from 1986 till 2000 and indicates that cows had not lost their inherent ability to inhibit the growth of the fetus (Figure 2.2). It is important to sustain this trend as this may contribute to lower incidence of dystocia. A positive trend was obtained for the BC herd.

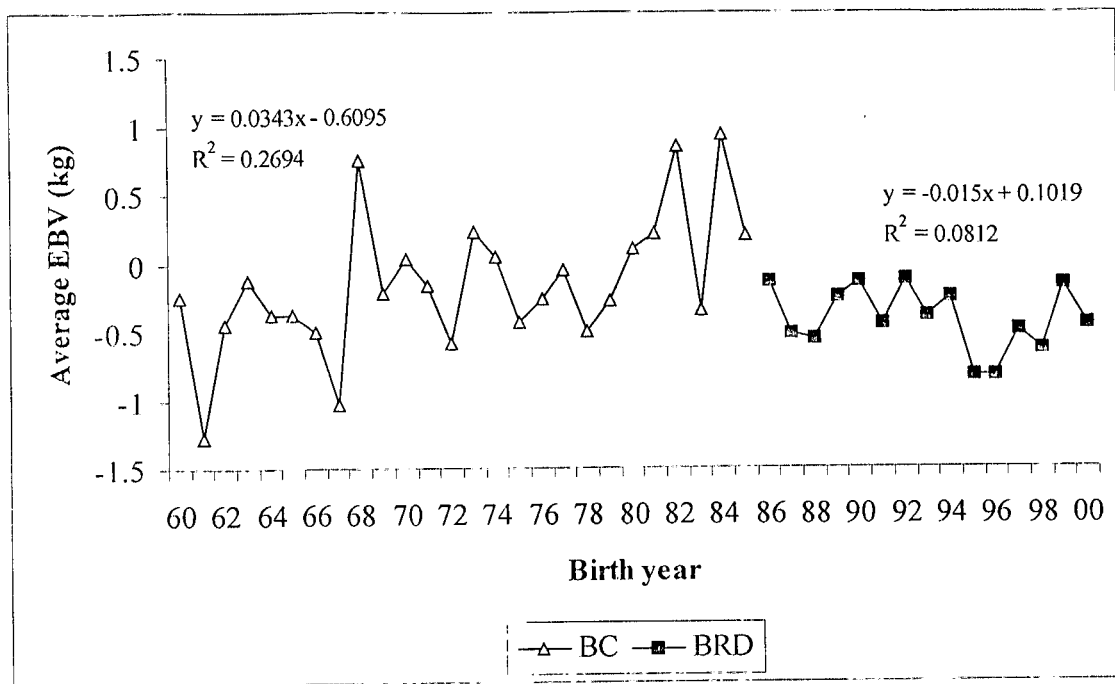
Trends for the direct and maternal components of BW in BC (Figure 2.1 and 2.2) are not in agreement with Kars (1993) who obtained a positive genetic trend for the direct component and a negative genetic trend for the maternal component. This may be attributed to the fact that a different model was fitted to estimate breeding values in this study as well as differences in the data set.



See Figure 2.1 for abbreviations.

Figure 2.3 Annual mean direct additive breeding value estimates and genetic trend for weaning weight

Figure 2.3 shows a positive trend for the direct genetic effect of WW for the breed for the period 1986 to 2000. An increase in the direct effect of WW for the BC herd was obtained till 1979, after which a decrease occurred.

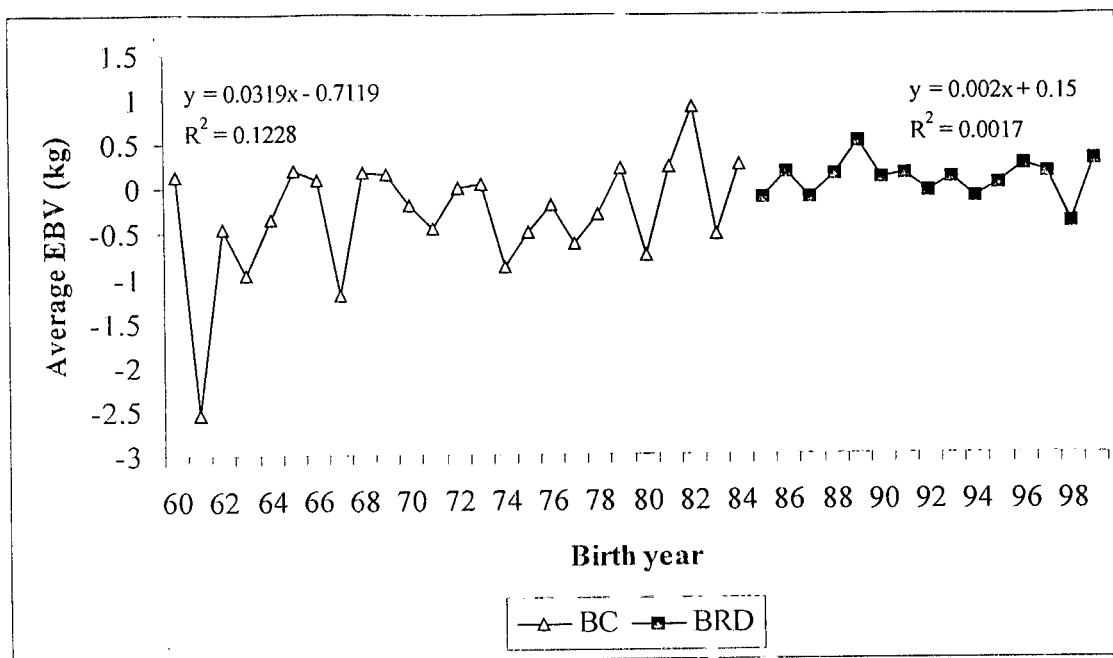


See Figure 2.1 for abbreviations.

Figure 2.4 Annual mean maternal additive breeding value estimates and genetic trend for weaning weight

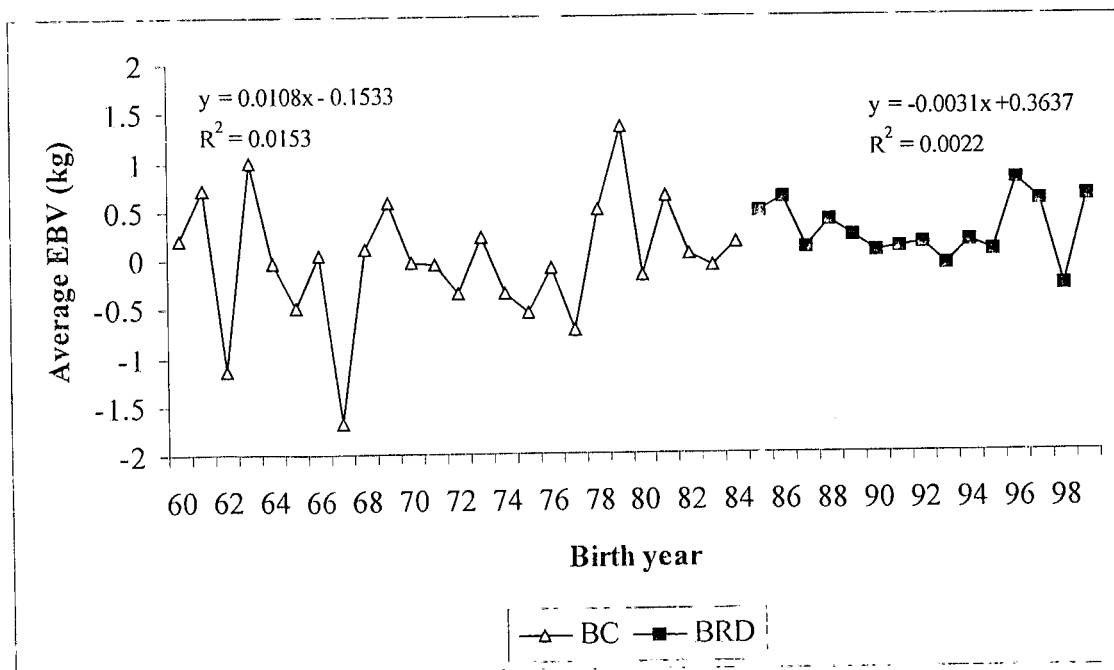
Figure 2.4 shows a slight decrease in the additive maternal genetic effect of WW for the breed. Contrary to this a positive trend was obtained for the BC herd. The decreasing mothering abilities is undesirable in a breed recognized as a dam line and may be the effect of selection on the direct breeding values for WW. This decline in the maternal effect for WW may also be one of the reasons for the decline of maternal effects for BW, as these two traits are positively correlated (0.49).

Trends for BC and WW do not compare well with Kars (1993) with relation to the direct component. The positive trend for the maternal component does, however, correspond with the positive trend of WW obtained by Kars (1993). The R-squares for the regressions of BC and BRD are very low and indicate that the regressions do not describe the annual mean additive breeding value estimates on year of birth sufficiently.



See Figure 2.1 for abbreviations.

Figure 2.5 Annual mean direct additive breeding value estimates and genetic trend for yearling weight



See Figure 2.1 for abbreviations.

Figure 2.6 Annual mean direct additive breeding value estimates and genetic trend for eighteen-month weight

The regressions for YW and EW (Figures 2.5 and 2.6) in the breed revealed minor modification indicating that there was no change in these two traits due to the direct additive genetic effect. This is very positive, because, as mentioned before, the increase of post-weaning weights is associated with many detrimental effects.

The positive direct regression of BC for YW is in correspondence with Kars (1993) while the unchanged to slightly positive direct regression of BC for EW, differs from the positive trend of Kars (1993). The R-square values for the regressions of BC and BRD for YW and EW indicate that the regressions are not accurate in describing the genetic change in BC herd or the breed.

2.3 Conclusions

Results indicate that selection when considering growth, is not as simple as might be envisaged. As the measuring of WW is often the first opportunity where selection takes place, especially in a breed considered to be a dam line, the results of selection on WW alone will be undesirable as all other weights will increase. Alternately, increasing pre-weaning growth rate while keeping mature weight (EW) the same may prove difficult to attain. Maintenance of BW will be more procurable. This is also applicable when improving the mothering ability in WW while keeping the inhibition of fetal growth, as a genetic effect of the dam, unchanged. The effect of such selection is however not yet clear and future research should focus on the effect of an increase in WW, especially the maternal component, on fitness traits, such as reproduction. The genetic correlation between the post weaning weights (YW and EW) is high and selection for one of these weights will also increase the other. No breeding value for one component or single trait associated with growth should be considered in isolation. Breeding values for production traits should be seen in conjunction with one another to accommodate undesirable effects on other traits. Lastly, genetic trends derived indicated no major change in any of the growth traits. The continuous evaluation of these trends are important to monitor genetic change, regardless of which selection goals are decided upon.

Chapter 3

Genotype x ecological region interaction in the Nguni breed.

3.1 Introduction

Nguni cattle, like most other beef producing breeds, are kept under a wide variety of extensive environments throughout South Africa. The specific differences of these environments may have a greater effect on some genotypes than others (Falconer & Mackay, 1997), that causes a change in the order of merit of a series of genotypes when measured under different environments as some genotypes may be more sensitive than others to environmental differences. Thus, genotype x environment interaction becomes important if individuals of a particular population are to be reared under different conditions. Vercoe & Frisch (1992) stressed the importance of genotype x environment interaction in extensive systems and concluded that the genotype x environment interaction when different genotypes are transferred across environments arise because genotypes differ in genetic potential and resistance to the stresses operating in the different environments. Thus, it will be of economic importance to identify any genotype x environment interaction as this will influence breeding programs with respect to the genetic progress that can be expected.

The effect of the environment on Nguni cattle in Swaziland and Zululand, especially with reference to their size, is well recorded by Bonsma *et al.* (1950). The differences in size in the different localities could generally be correlated with such environmental features as the nature of the soil and the nutritive value of the natural vegetation. Bonsma *et al.* (1950) state that these differences in environmental conditions appear to have been responsible for some interesting differences in conformation and other traits between cattle from different localities. Based on this, an interaction in this breed may be expected. Mathur (2002) stated that three very important aspects concerning the nature of interactions are the ranking order of the genotypes, the relative magnitudes of genotypic, environmental and interaction effects and the statistical significance of interaction effects.

Consequently, the aim of this study was to determine whether any genotype x environment interaction is present and if present, what the magnitude and significance of such an interaction in the Nguni breed is.

3.2 Material and methods

3.2.1 Data

Because of limitations in the data set, only weaning weight (WW) records from Nguni herds participating in the NBPTS, for the period 1960 to 2001, were used. Records from herds were allocated to one of three veld types that described the specific region in which each herd was situated. The classification of each region with respect to sweetveld (region 1), sourveld (region 2) and mixed veld (region 3) was carried out according to Tainton (1999). These three regions (environments) differs greatly with respect to soil characteristics, temperature, rainfall and subsequent quality and quantity of natural pastures for grazing (Tainton, 1999). Incomplete records were discarded and a description of the data set, after editing, with regard to the number of records, dams, sires, herds, contemporary groups (CG) and average size of contemporary groups, maximum values of contemporary groups as well the average number of progeny per sire for each region is presented in Table 3.1. The minimum contemporary group size for all the traits were five animals.

Table 3.1 Data description

Region	1 (Sweetveld)	2 (Sourveld)	3 (Mixed veld)
No. of records	2136	3984	11432
No. of dams	916	1988	4046
No. of sires	108	148	372
No. of herds	9	17	10
No. of CG	67	134	136
Avg. CG size	32	30	84
Max. CG size	156	246	511
Avg. progeny of sires	20	27	31

CG – contemporary group; Avg. – average value; Max. – maximum value

Genetic ties between herds were utilized and herds that were linked to less than two other herds through shared sires, were discarded. The number of shared sires were 13 for region 1 and 2, 23 for

region 1 and 3 and 17 for region 2 and 3. The greatest number of records was found in region 3 as the Bartlow Combine Nguni Stud, a former government herd, contributed 78% of the records in this region.

3.2.1.1 Characteristics of sweetveld (region 1)

By definition, sweetveld is veld which remains palatable and nutritious when it is mature and predominates in the arid and semi-arid areas of the central and western interior, where it mostly occurs as Karoo or climax grassveld. In the Western Cape, it occurs in the form of fynbos. In the low-lying areas in the east, it occurs mainly in the form of savanna vegetation. In the Northern Province, the northern part of the Eastern Cape and in Lesotho it occurs in the form of grassveld. Rainfall in sweetveld areas are scanty and uncertain which has an erratic effect on growth. The carrying capacity of sweetveld is normally less than that of sourveld. The cover is relatively sparse and typically a tall to moderately tall grassland. The amount of forage available for animal consumption, rather than forage quality, limits livestock production in these areas. (Tainton, 1999).

3.2.1.2 Characteristics of sourveld (region 2)

Unlike sweetveld, sourveld provides palatable material only during the growing season. Sourveld predominates in the high rainfall areas at high altitudes in the eastern and southern parts of South Africa, largely, but not entirely, as fire climax grassland. Summer temperatures are usually lower in these areas than in sweetveld areas. Rainfall is usually relatively high, and growth is more rapid and regular than in sweetveld. The carrying capacity is therefore usually higher than that of sweetveld and the grass sward is often dense. Sourveld usually provides good spring grazing, but is much less satisfactory than sweetveld in autumn. It is typically a short grassland. Animal production in these areas is normally limited by forage quality, rather than quantity. (Tainton, 1999).

3.2.1.3 Characteristics of mixed veld (region 3)

Mixed veld has characteristics which tend towards either sweetveld or sourveld, depending on whether the veld is sweet-mixed or sour-mixed. Mixed veld can thus be classified as intermediate

between sweet- and sourveld. (Tainton, 1999).

3.2.2 Statistical analyses

The different fixed effects that were to be included in the model were tested using the GLM procedure of SAS. The significant effects ($P < 0.0001$) included were herd-year-season, sex, age at recording and age of dam. Heterogeneous variances were found to be non-significant as tested by correcting the y-value with the standard deviation of each contemporary group. The method used to estimate the existence as well as the magnitude of genotype x environment interaction was the method suggested by Falconer (1952) and reviewed by Mathur (2002). Accordingly, the expression of the same trait in two environments can be considered as two different traits and the genetic correlation between them can be estimated in the same way as for any two correlated characters. Bivariate analyses of WW in the three different regions were carried out to determine the (co)variance components as well as the heritability estimates. ASREML, developed by Gilmour *et al.* (1999) was used. Those effects for which two estimates for every region were obtained were weighted using the equations of Koots *et al.* (1994a). These effects included the direct genetic effect, the permanent maternal environmental effect and the herd-year-season x sire interaction effect. For the permanent maternal environmental effect in region 2, only one estimate was obtained because of the models used. The corresponding standard errors were not weighted as the values were very similar and the average standard error of the two estimates are reported. Correlation coefficients between breeding values obtained by multivariate analysis (obtained in Chapter 2), and breeding values obtained by the respective bivariate analyses were calculated. This was done using sires with more than 29 progeny in the multivariate analyses as the accuracy of these breeding values exceed 0.84. Results presented are for these top 5% sires if ranked according to multivariate breeding values, and the rest of the sires.

Twelve different models were tested and the effects, that were either included or excluded, were the direct effect, maternal genetic effect, permanent maternal environmental effect, the covariance between the two animal effects and the effect of a herd-year-season x sire interaction (HYSxS). A more complete description of the models used is given in Chapter 2 and is the equivalent of models 4 and 5. Model 5 was used for all the regions in the bivariate analyses of Regions 1 and 3 as well as the analyses of Regions 2 and 3. For the bivariate analyses of Regions 1 and 2, model 5 was used

for Region 1 while model 4 was used for Region 2. The models were as follows:

$$y = Xb + Z_1a + Z_3\text{HYSxS} + e \quad (\text{Model 4})$$

$$y = Xb + Z_1a + Z_2c + Z_3\text{HYSxS} + e \quad (\text{Model 5})$$

where

y is a vector of observations;

b is a vector of fixed effects;

a is a vector of direct additive genetic effects;

c is a vector of permanent environmental effects;

HYSxS is a vector of herd-year-season x sire interaction effects;

X, Z_1, Z_2, Z_3 , are incidence matrices;

e is the vector of residuals;

3.3 Results and discussion

The basic statistics for each region are summarized in Table 3.2.

Table 3.2 Mean, standard deviation (SD), coefficient of variation (CV), minimum (Min) and maximum (Max) for WW in regions 1, 2 and 3

Region	Mean (kg)	SD (kg)	CV(%)	Min (kg)	Max (kg)
1 (Sweetveld)	172.99	26.46	11.13	86	243
2 (Sourveld)	162.67	29.28	12.50	80	240
3 (Mixed veld)	159.59	23.52	11.36	79	241

As can be expected, the mean WW of region 1 was the highest as sweetveld has more favourable characteristics, as pointed out earlier, than the other two regions. The coefficients of variation compare well to that of results in Chapter 2 (11.81%).

Weighted genetic parameters, using the equations by Koots *et al.* (1994a), for WW in regions 1, 2 and 3 are presented in Table 3.3.

As the inclusion of the maternal genetic effect in the models caused the parameters and/or log likelihood to not converge, the models used to analyze WW in the different regions, did not include this genetic effect. This is unfortunate as WW is a maternally influenced trait. Furthermore, as the aim of the study was to investigate possible genotype x environment interactions between the different regions, the inclusion of the maternal genetic effect is important as evidence of genotype x environment interaction in this effect has been found by Morris *et al.* (1993). This may be of specific importance to a potential dam line like the Nguni.

Table 3.3 Weighted genetic parameters with their corresponding average standard errors (SE) for WW in regions 1, 2 and 3

Parameter	Region 1 (Sweetveld)	Region 2 (Sourveld)	Region 3 (Mixed veld)
h^2_a	0.23	0.45	0.25
SE	0.07	0.04	0.03
c^2	0.26	* 0.10	0.11
SE	0.03	0.02	0.01
$\sigma^2_{hyss} / \sigma^2_p$	0.31	0.39	0.31
SE	0.03	0.03	0.01

* Unweighted (see material and methods)

h^2_a – direct heritability; $c^2 - \sigma^2_c / \sigma^2_p$, permanent maternal environmental effect as a proportion of the phenotypic variance; $\sigma^2_{hyss} / \sigma^2_p$ – herd-year-season x sire interaction effect as a proportion of the phenotypic variance; SE – standard error.

Weighted heritability estimates and parameters were calculated as some corresponding estimates from the different regions differed considerably. Weighted direct heritability estimates ranged from 0.23 to 0.45 and compare well with the results of univariate analyses of WW (range 0.14 to 0.53, Chapter 2). A value of 0.32 was obtained with multivariate analyses (Chapter 2). In addition, the direct heritability estimates of Regions 1 and 3 compared very well throughout, while the estimate of Region 2 was higher. The increase in the direct heritability is especially evident in the bivariate estimates where Region 1 and 2 were analyzed together. Here, a different model was used for Region 2 as compared to the analyses for the other regions (see material and methods). The exclusion of the permanent maternal environmental effect in this model caused a significant increase in the direct variance and subsequent heritability estimate. Weighted direct heritability

estimates where the same model was used throughout (range 0.23 to 0.25), compare well with estimates obtained by Nephawe *et al.* (1999, Bonsmara cattle) (range 0.22 to 0.36). Koots *et al.* (1994a) reported a weighted mean direct heritability of 0.24 for WW.

The permanent maternal environmental effect as a proportion of the phenotypic variance (weighted) was significant in all the regions and estimates ranged from 0.10 to 0.26. This is in agreement with estimates of univariate analyses (Chapter 2) (range 0.14 to 0.23) but somewhat higher than values obtained by Nephawe *et al.* (1999) (range 0.07 to 0.13). A possible reason for this may be the fact that Nephawe *et al.* (1999) included the maternal genetic effect which might decrease the permanent maternal environmental variance as shown in univariate analyses of WW (Chapter 2). If this is the case, it can possibly be gathered that in the analyses some difficulty arose as to the separation of the maternal genetic and maternal environmental effects. The maternal influence, irrespective of being genetic or environmental, is apparent through the permanent environmental estimates.

Estimates of the herd-year-season x sire interaction as a proportion of the phenotypic variance ranged between 0.31 and 0.39. These estimates are much higher than estimates obtained by univariate analyses (range 0.08 to 0.09, Chapter 2), but is in agreement with the value obtained in the multivariate analyses (0.35, Chapter 2). A conceivable reason may be the exclusion of the covariance between the two animal effects which caused an increase in the HYSxS interaction variance as was the case in univariate analyses. Lee & Pollak (1997) reported the same occurrence when a sire x year interaction was excluded. The interaction may therefore explain part of the direct-maternal covariance. A more plausible explanation may be a certain degree of idiosyncrasy in the data which may be difficult to estimate.

Estimates of genetic correlations between direct components obtained from bivariate analyses for WW in Regions 1, 2 and 3 are presented in Table 3.4.

Table 3.4 Genetic correlations with the corresponding standard errors (SE) between direct components of WW in Regions 1, 2 and 3

Region	2 (Sourveld)	3 (Mixed veld)
Region 1 (Sweetveld)	1.00	0.71
SE	0.33	0.19
Region 2 (Sourveld)		0.60
SE		0.34

The results (Table 3.4) indicate that no genotype x ecological region interaction between Regions 1 and 2 exists, as the direct genetic correlation for WW between these two regions is at unity. However, possible interaction exists between Regions 1 and 3, as the direct genetic correlation between these two regions is 0.71. Robertson (1959) suggests that if the genetic correlation between environments is less than 0.8, genotype x environment interaction is of biological importance. The direct genetic correlation between Regions 2 and 3 was 0.60, but was non-significant. The models used to estimate these genetic correlations included herd-year-season x sire interaction (HYSxS), also known as a contemporary group x sire interaction. The inclusion of this interaction effect is important for previously mentioned reasons, but also for reasons pointed out by Bertrand *et al.* (1985, 1987). These authors state that a genotype x environment interaction may in part be the cause of changes in sire ranking amongst contemporary groups, rather than changes in ranking of sires across the different environments. The exclusion of this interaction from the bivariate analyses may thus have caused an apparent genotype x environment interaction, which might not be the case exclusively. This is supported by Bradfield *et al.* (1997, Santa Gertrudis cattle) who reported an increase in the genetic correlation (0.63 to 0.83) between two different environments when a sire x contemporary group interaction was fitted. Similar results were reported by Nephawe *et al.* (1999) when including a HYSxS interaction. The inclusion of any sire plus interaction models does however not solve the problem of distinguishing between the heightened resemblance among half-sibs within the same herd arising from genotype x environment interaction and those arising from common environmental effects within half-sib families (Meyer, 1987). Nephawe *et al.* (1999) obtained genetic correlations non-significantly different from unity for weaning weights when a HYSxS interaction was included.

Results between Regions 1 and 2 were, at first, unexpected as logically these two regions differ more significantly from each other than any of the other pairs of regions, with regard to the environment. According to results in Table 3.4, the ranking order of animals between Regions 1 and 2 will not change with respect to the direct component of WW. In other words, the animal with the best breeding value in Region 1, will also be the animal with the best breeding value in Region 2. Bishop (1993) concluded that for environments which differ only in the quality of nutrition available, G x E interactions for weight gain in beef cattle are likely to be small and probably will not be an important factor when making selection decisions. However, where environments differ sufficiently to make adaptation to environmental stresses necessary, G x E interactions may be important factors which need to be considered when undertaking genetic improvement (Bishop, 1993). In the light of this argument, a possible explanation may be that the breed has (is) adapted to both environments to such an extent that environmental stresses are of no consequence. This statement may be questioned, as animals are not kept exclusively on natural grazing in the sourveld regions in winter, as cultivated pastures and the feeding of supplements are not uncommon. If the taking of weights in Region 2 occurred under 'artificial' environments where dipping and the feeding of supplements are practiced, results between Regions 1 and 2 are not surprising. Vercoe & Frisch (1992) concluded that G x E of small magnitude can only occur when genotypes with similar configurations of production potential and resistance to stress are compared, no matter how different the environments may be. In this regard, there is an indication of some difference in the genotypes between Regions 1 and 3, as the direct genetic correlation is 0.71 (Table 3.4). Hence, there is some divergence in genes contributing to the inherent growth of calves up to weaning between Regions 1 and 3, although there is considerable overlapping of genes. Consequently, there will be re-ranking in Region 1 when sires are selected in Region 3 and vice versa. The conclusion Vercoe & Frisch (1992) come to regarding low G x E interaction, might be explained by the fact that records for Region 3 mainly originated from one herd - the former Bartlow Combine Nguni Stud. This may cause some bias, as the genetic correlation may well be a comparison between all the herds in Region 1 with one prominent herd in Region 3 which practised specific selection strategies, especially with respect to WW (Gertenbach & Kars, 1999) - therefore being a comparison with a herd with a specific genetic merit (genotype) which may differ greatly from the rest of the breed. There are indications of differences in the production potential as well as resistance to stress between Bartlow Combine and the rest of the breed.

The issue of the contribution of one herd to most of the records in Region 3, are but one of a few factors impairing the accuracy of results obtained. These factors include the unsatisfactory linkage of herds through sires used. In this study there were only six sires with progeny in all three regions. Also, due to limitations in the data set, records from sires with progeny in a minimum of two herds which are in different regions, could not be implemented. Furthermore, the use of artificial insemination in the breed is limited which consequently restricts the number of sires with progeny in more than one region. This restricted use of A.I. is, however, common practice in all beef cattle herds in South Africa (Neser, 2002). These factors decrease the accuracy of the study as shown by the high standard errors.

Predicted breeding values of the top 5% sires with more than 29 progeny, according to multivariate analyses (Chapter 2) with their subsequent breeding values, obtained by bivariate analyses, and ranking order in each region are presented in Table 3.5. Correlation coefficients of multivariate breeding values with breeding values from the different bivariate analyses are also included.

Table 3.5 clearly shows that when these top 5% sires are selected using breeding values obtained by multivariate analyses, re-ranking will occur in the different regions. This is evident in the differing ranking order of these bulls according to bivariate breeding values in the different regions, as well as shown by the correlation coefficients. These correlation coefficients ranged from 0.51 to 0.71 and are all below the value of 0.8 as described by Robertson (1959). Consequently the multivariate breeding values are not a good predictor of the performance of the progeny of these ten bulls in the different regions.

Table 3.5 Predicted breeding values of the top 5% sires according to multivariate analyses, with their subsequent breeding values, obtained by bivariate analyses, and ranking order in each region. Correlation coefficients of multivariate breeding values with breeding values from the different bivariate analyses are also included

Sire	N	M. EBV	Rank	Region 1				Region 2				Region 3			
				1x2	Rank	1x3	Rank	1x2	Rank	2x3	Rank	1x3	Rank	2x3	Rank
A	44	27.64	1	9.76	4	17.77	1	17.16	4	12.24	6	21.10	3	13.91	3
B	58	24.70	2	14.94	1	-	-	26.43	1	17.70	2	-	-	7.29	5
C	104	22.43	3	10.17	3	-	-	18.00	3	16.37	4	-	-	6.75	6
D	92	21.00	4	-	-	15.92	3	-	-	17.68	3	21.15	2	20.31	2
E	47	20.77	5	-	-	16.17	2	-	-	18.90	1	22.87	1	22.02	1
F	30	17.38	6	6.59	5	11.26	4	11.57	5	-	-	12.59	4	-	-
G	137	17.09	7	11.53	2	-3.91	8	20.40	2	15.00	5	-5.44	8	-0.15	9
H	47	16.87	8	5.45	7	4.79	7	9.64	7	10.76	7	6.66	5	8.20	4
I	38	16.15	9	3.98	8	7.78	5	7.00	8	1.33	8	6.58	6	1.52	7
J	37	15.97	10	5.95	6	7.46	6	10.44	6	0.54	9	6.30	7	0.22	8
Correlation coefficient				0.67		0.70		0.66		0.57		0.71		0.51	

N – number of progeny; M. EBV – estimated breeding value obtained by multivariate analyses; 1x2 – estimated breeding value for the specified region obtained by bivariate analyses between regions 1 and 2; 1x3 – estimated breeding value for the specified region obtained by bivariate analyses between regions 1 and 3; 2x3 – estimated breeding value for the specified region obtained by bivariate analyses between regions 2 and 3.

Correlation coefficients between multivariate and bivariate breeding values of sires with more than 29 progeny as well as the number of sires used to calculate the correlation coefficient are presented in Table 3.6.

Table 3.6 Correlation coefficients between multivariate and bivariate breeding values of all sires with more than 29 progeny, and multivariate breeding values within the lower 95% of the ranking order. The number of sires used to calculate the correlation coefficient is also shown

	Region 1		Region 2		Region 3	
	1x2	1x3	1x2	2x3	1x3	2x3
All sires	0.80	0.77	0.80	0.80	0.80	0.81
No. of sires	79	165	79	181	165	181
Lower 95% sires	0.78	0.75	0.78	0.78	0.79	0.82
No. of sires	71	157	71	172	157	172

No. of sires – number of sires used to calculate the corresponding correlation coefficient above.

When considering all the sires with highly accurate (≥ 0.84) multivariate breeding values (Table 3.6), the correlation coefficients between multivariate and bivariate breeding values ranged from 0.77 to 0.81. These indicate that in general the multivariate breeding values are a good predictor of breeding values in the different regions and that no major re-ranking will occur in the different regions when using these breeding values. When observing the lower 95% of sires, a slight decline in the correlation coefficient is detected, but nonetheless correspond well with the correlations of all sires. Of interest though is the decrease of these correlation coefficients from the lower 95% of sires (Table 3.6) to the top 5% of sires (Table 3.5). This indicates that substantially more re-ranking will occur when selecting the top performing sires than when selecting the lower 95% of sires, using multivariate breeding values.

In this regard, Kolmodin *et al.* (2002b) reported an increase in environmental sensitivity in response to selection for high phenotypic values in the presence of G x E. Environmental sensitivity can however be changed by artificial selection as shown by Kirkpatrick & Bataillon (1999) and De Jong & Bijma (2002). This is of importance as Falconer (1990) states that stabilizing selection is expected to decrease environmental variance. This may well increase productivity through adaptability in harsh environments. Naser *et al.* (1998) also refer to the possibility of selection for

stability while SanCristobal-Gaudy *et al.* (1998) support these findings by clearly showing that this type of selection does work. Bodin *et al.* (2002) state that this clearly demonstrates the existence of some genetic mechanisms controlling phenotypic variability.

It should be mentioned that the use of the correlation coefficients as applied here between breeding values of multi- and bivariate, may be biased. These correlations may be influenced by the sample size, heritability and accuracy of the estimates of breeding values obtained by different analyses as supported by Mathur (2002).

3.4 Conclusions

No real genotype by ecological region interaction could be found between Regions 1 and 2, suggesting that there will be no ranking order change between sires in these two regions. Selection to increase weaning weight by selecting on direct breeding values in Region 1 will thus increase weaning weight in Region 2 as well. Results do however show a genotype by ecological region interaction between Regions 1 and 3 indicating that there will be a change in the ranking order of sires from Region 1 to Region 3. The high estimates of the herd-year-season x sire interaction as a proportion of the phenotypic variance in the different regions indicate that an apparent genotype x environment interaction might be the result of a re-ranking of sires between different contemporary groups. Correlation coefficients between breeding values obtained by multivariate and bivariate analyses respectively, show that no major re-ranking will occur when selection takes place on breeding values obtained by multivariate analyses which include a herd-year-season x sire interaction. Moreover, the importance of the structure of the data in genotype x environment studies was also conceived and the extended use of shared sires and artificial insemination in the breed would have increased the accuracy of the study significantly. The classification of regions or environment in such studies also needs to be more precise - not just in terms of feeding, but also at management level. This may reveal less overlapping of genes with respect to resistance to environmental stresses which might be confounded by management practices such as dipping and feeding supplements.

Chapter 4

General conclusions and recommendations

Animal breeding is concerned with the genetic improvement of animals with respect to economic important traits. The way this is done is through selection. The improvement of selection strategies is therefore the main aim of animal breeding research with respect to better accuracy and understanding. Thus, when all is said and done, knowledge obtained by research results must serve to increase profit of, in this case, meat production. Automatically this implies efficiency of production, which implies quite a few economically important traits. These traits may or may not be linked concerning the same genes that influence the expressions of more than one of these traits. In this regard, it is important to identify which economic important traits show such an overlapping of genes as to not negatively affect the most important traits which contribute to efficient meat production when selection is based on other production traits.

The Nguni breed may be classified as a dam line, as it is small framed with good maternal abilities, has a low incidence of dystocia and has high fertility. Results obtained confirm the breed's potential as a dam line, as the maternal component explained a relatively large proportion of the phenotypic variance in univariate analyses. This then gives breeders a good opportunity to improve maternal ability through selection. Such maternal traits confirm to high efficiency in meat production. Another form of measuring cow efficiency that is popular with many breeders is the ratio of calf weight (age corrected) with cow weight at weaning. This is a measure of the direct genetic component of the calf's growth as well as the maternal ability of the dam. Results in this study showed that selection strategies only emphasizing weaning weight will have undesirable effects on various other traits. Firstly, results show that maternal properties will decline which will result, in the long term, in a shifting of the breed towards characteristics not associated with a typical dam line. This is emphasized by the fact that secondly, all other weights will increase, with post weaning weights increasing more rapidly than birth weight. These two changes imply selection for an animal that will be of a larger frame, later maturing with increased maintenance requirements, decreased milk production and maternal ability and higher incidence of dystocia. Results also show that selection on the maternal component of weaning weight will cause a decrease in the ability of the dam to inhibit the growth of the fetus. This is a very important trait

causing low incidence of dystocia which is important in efficient, extensive beef breeding. This unique genetic characteristic of the dam is also important as the breed is consistent with requirements of a dam line in terminal crossbreeding with larger breeds. It has been shown that such crossbreeding programs with an adapted, low maintenance and efficient dam line may improve the efficiency of meat production considerably. Results however also show the feasibility of restricting maternal traits contributing to birth weight while selection for maternal traits at weaning are practiced. Concerning post weaning weights, i.e. 12-month weight and 18-month weight, it is recommended that with the measuring of these two seemingly identical traits, the possibility of additional measures be explored. Where the objective is to improve adaptability between these two post weaning weights, other additional recordings such as the deposition of fat and the measuring of shoulder height might play a very important role. This will give a better indication of the weight gain relationship between fat, meat and bone between these two points. This will aid breeders in selecting animals which is more in line with the breed's status as a dam line, being the selection of animals which weight gain are not only attributed to an increase in frame size, but also fat and meat. Such animals should be animals that reach puberty at a younger age and conform better to the requirements of a dam line. This might be of specific importance to yearling weight as the amount of fat at this age, compared to other animals in the same contemporary group, may be a good indication of early maturity.

The inclusion of a HYSxS interaction was shown to be significant in explaining a part of the phenotypic variance in each of the growth traits. This shows that the re-ranking of sires in different contemporary groups is indeed an important factor to keep in mind when the (co)variance structure is analyzed, as well as when breeding values are estimated. This should partially enable breeders to make more accurate selection decisions involving sires. As had been the case with many other authors, the direct additive component seemed to be overestimated when the interaction was excluded. This also held true for the covariance between the two animal effects which was less negative when the interaction was included.

Genetic trends that were derived for the different components of the growth traits did not show any major change for the breed in a fourteen- to fifteen-year period (1985,1986 to 2000). It is recommended that these genetic trends must be evaluated on a continued basis as to monitor genetic change (positive or negative) to aid future selection decisions.

Genotype x environment interaction is a function of certain genotypes being more adapted to certain environments than others. These differences in environments are not only a function of different ecological regions, but also variation in climatological factors from season to season and different years. Management practices in different herds also play a role. Therefore, by fitting a herd-year-season x sire interaction when performing bivariate analyses of weaning weight in two different ecological regions, results obtained will reveal mostly genotype x environment interaction effects caused by differences in ecological regions. Some of the genotype x environment interaction effects are therefore still entangled in the herd-year-season x sire interaction. Hence, the study specifically focused on ecological regions which is one of a few causes of genotype x environment interaction, namely genotype x ecological region interaction. Consequently, results obtained suggest that there is no genotype x ecological region interaction between sweet- and sourveld regions (Regions 1 and 2) and that there will be no re-ranking of sires with respect to weaning weight between these two regions. Results also showed that an interaction between sweet- and mixed veld regions (Regions 1 and 3) does exist and that some re-ranking of sires will occur between these two regions. Since genotype x environment interactions are also caused by differences in resistance to environmental stress and growth potential in cattle in the tropics and subtropics, these results were expected, as the difference between Regions 1 and 2, with respect to internal and external parasites, among other factors, are decreased by management practices. The fact that Regions 1 and 3 differ less in this respect makes the interaction more surprising. This might make sense when it is considered that 78% of records for Region 3 were from one herd. This implies that this herd might differ genotypically with respect to not only genes contributing to weaning weight, but also resistance to environmental stress. This was also a major factor contributing to lower accuracy in the study. Another contributing factor was the relatively few sires with progeny in all three regions. It is recommended that if more accurate results are desired, the use of shared sires and artificial insemination be introduced. This will then also make other important studies, such as studies on environmental sensitivity more viable and may aid breeders to select more adapted genotypes that are suitable for their specific environment of genotypes that are more stable across regions or environments.

Lastly, of specific importance in a breed as well adapted as the Nguni, is the selection of animals in a natural, unadulterated environment with respect to internal and external parasites and feeding supplements. Such management practices will cause an apparent absence of genotype x

environment interaction. Resisting this, breeders should use genotype x environment interaction to their favour in selecting animals which are better adapted to their environment. This may be done by rearing, measuring and selecting animals under natural stressors without minimizing the effects of the environment on animals through over-management.

Abstract

Genetic parameters may well aid the prediction of selection and correlated response when selection is based on production traits. The animal model, fitting an additional random factor such as the permanent maternal environmental effect is common practice to increase the accuracy of estimates. As selection in a beef breed such as the Nguni takes place in various environmental conditions, the inclusion of an additional random factor i.e. herd-year-season x sire interaction seems justified.

Production traits analyzed included records of birth weight (BW), weaning weight (WW), yearling weight (YW) and eighteen-month weight (EW). Herd-year-season, sex, age at recording (except BW) and age of dam had a significant effect. Herd-year-season x sire interaction (HYSxS) was included as an additional random factor. Estimates obtained by univariate analyses were used as starting values in the multivariate analyses. In multivariate analyses another data set was used which included only herds linked with at least two other herds through sires used. This data set was also used in two bivariate analyses being the analyses between the maternally influenced traits (BW and WW) and WW and YW to gain knowledge as to a possible carry-over effect of the maternal genetic effect. Genetic trends were calculated using the regression of the average breeding value estimates (EBV) on year of birth. Direct heritability estimates for BW, WW, YW and EW obtained by multivariate analyses were 0.31, 0.32, 0.23 and 0.27 respectively. Genetic correlations between direct and maternal effects for BW and WW were mostly low to moderate and negative (-0.35 to -0.59 and -0.17 to -0.50 for BW and WW respectively), while direct genetic correlations among the four growth traits were moderate to high (0.51 to 0.95). The maternal genetic correlation between BW and WW was moderate (0.49). It was concluded that selection on WW alone would be undesirable as all other weights would increase. In review, breeding values for production traits should be seen in conjunction with one another so as to take into account undesirable effects on other traits. Genetic trends derived showed no major change.

Nguni cattle, like most other beef producing breeds, are kept under a wide variety of extensive environments throughout South Africa. Based on this, a genotype x environment interaction (G x E) in this breed may be expected. Three most important aspects while considering the nature of interactions are the ranking order of the genotypes, the relative magnitudes of genotypic, environmental and interaction effects and the statistical significance of interaction effects.

Because of limitations in the data set, only weaning weight (WW) records were used. Records from herds were allocated to one of three veld types that described the specific region in which each herd was situated, i.e. sweetveld (Region 1), sourveld (Region 2) and mixed veld (Region 3). Bivariate analyses of WW in the three different regions were carried out to determine the (co)variance components and weighted direct heritability estimates obtained ranged from 0.23 to 0.45. Direct genetic correlations of Regions 2 and 3 with Region 1 were significant and were 1.00 and 0.71 respectively. This indicates that no G x E occurred between Regions 1 and 2, but indeed between Regions 1 and 3. The genetic correlation between Regions 2 and 3 (0.60) were non-significant. Correlation coefficients between breeding values of sires, obtained by multivariate analyses and the different bivariate analyses, was also calculated (range 0.77 to 0.81) indicating no major re-ranking of sires when selection is based on breeding values obtained by multivariate analyses which include a HYSxS interaction. Top performing sires showed more re-ranking.

Keywords: Nguni cattle, indigenous cattle, genetic parameters, genotype x environment interaction, herd-year-season x sire interaction, genotype x ecological region interaction, environmental sensitivity, growth traits, dam line.

Opsomming

Genetiese parameters is van kardinale belang by die voorspelling van seleksie en gekorreleerde respons wanneer seleksie vir produksie-eienskappe plaasvind. 'n Dieremodel, waarby 'n addisionele toevallige effek soos die permanente maternale effek, ingesluit word is algemeen om die akkuraatheid van beraamings te verhoog. Aangesien seleksie by vleisbeeste soos die Nguni-ras, in verskillende omgewingstoestande plaasvind, blyk die insluiting van 'n addisionele toevallige effek nl. kudde-jaar-seisoen x vaar interaksie geregverdig te wees.

Produksie-eienskappe wat gebruik is het ingesluit geboortegewig (BW), speengewig (WW), 12-maande gewig (YW) en 18-maande gewig (EW). Kudde-jaar-seisoen, geslag, ouderdom by meting (behalwe BW) en ouderdom van die moeder het almal 'n betekenisvolle effek gehad. Kudde-jaar-seisoen x vaar interaksie (HYSxS) is as 'n addisionele toevallige effek ingesluit. Enkeleienskap ontledings sowel as twee twee-eienskapontledings is uitgevoer en het BW en WW (eienskappe met maternale invloed) ingesluit asook WW en YW (om die moontlikheid van 'n oordrag-effek van die maternale komponent vas te stel). Enkeleienskapwaardes is as beginwaardes in 'n veelvoudige eienskapontleding gebruik om die (ko)variëansie-komponente van en/of tussen die verskillende eienskappe te beraam. Genetiese tendense is bereken deur die regressie van die gemiddelde teelwaardeberamings op jaar van geboorte. Direkte oorerflikhede vir BW, WW, YW en EW verkry deur veelvoudige-eienskapontleding was onderskeidelik 0.31, 0.32, 0.23 en 0.27. Genetiese korrelasies tussen die direkte- en maternale effek vir BW en WW was laag tot medium en negatief (-0.35 tot -0.59 en -0.17 en -0.50 vir BW en WW onderskeidelik), terwyl die direkte genetiese korrelasies tussen die vier eienskappe medium tot hoog was (0.51 tot 0.95). Die maternale genetiese korrelasies tussen BW en WW was medium (0.49). Daar is tot die gevolgtrekking gekom dat seleksie vir WW alleen ongewens sal wees aangesien alle ander gewigte ook sal toeneem. Ten slotte behoort teelwaardes vir produksie-eienskappe in afhanklikheid met mekaar beskou te word om sodoende rekening te hou met die ongewenste effek op ander eienskappe. Genetiese tendense het geen noemenswaardige verandering getoon nie.

Nguni-beeste, soos meeste ander vleisbeeste, word onder 'n wye verskeidenheid omgewings aangehou regdeur Suid-Afrika. Gebaseer hierop kan 'n moontlike genotipiese omgewingsinteraksie

(G x E) in die ras dus verwag word. Drie belangrike faktore moet oorweeg word wanneer die effek van interaksies bestudeer word, nl. die rangorde van die genotipes, die relatiewe omvang van genotipiese-, omgewings- en interaksie-effekte asook die statistiese betekenisvolheid van die interaksie-effekte.

As gevolg van beperkinge ten opsigte van die datastel, kon slegs WW-rekords gebruik word. Rekords van kuddes is toegewys aan een van drie veldtipes wat die spesifieke omgewing waarin elke kudde produseer beskryf, nl. Soetveld (Streek 1), Suurveld (Streek 2) en Gemengde veld (Streek 3). Twee-eienskapontledings van WW in die drie verskillende streke is gedoen om die (ko)variansie-komponente te beraam. Geweegde direkte oorerflikheidsberamings hierdeur verkry het gestrek van 0.23 tot 0.45. Direkte genetiese korrelasies van Streke 2 en 3 met Streek 1 was betekenisvol en was onderskeidelik 1.00 en 0.71. Hierdie resultate dui aan dat daar geen G x E tussen Streke 1 en 2 bestaan nie, maar wel tussen Streke 1 en 3. Die direkte genetiese korrelasie tussen Streke 2 en 3 (0.60) was nie betekenisvol nie. Korrelasie-koëffisiënte tussen teelwaardes van vaars, afkomstig van veelvoudige-eienskapontleding en die verskillende dubbeleienskapontledings, is ook bereken (omvang 0.77 tot 0.81) en dui aan dat geen wesenlike herrangskikking van vaars sal voorkom nie wanneer seleksie gebaseer word op teelwaardes verkry van veelvoudige-eienskapontleding, wat 'n HYSxS interaksie insluit. Die toppresterende vaars het 'n meer drastiese herrangskikking getoon.

References

- Albers, G.A.A., Broekman, K., Visscher, J., Buddiger, N. & Maatman, R., 2002. Role of genotype x environment interactions in applied breeding programs. 7th Wrld Congr. Genet. Appl. Livest. Prod. August 19-23, Montpellier, France. CD-ROM communication No. 25-35.
- Bennett, G.L. & Gregory, K.E., 1996. Genetic (co)variances among birth weight, 200-day weight, and postweaning gain in composites and parental breeds of beef cattle. *J. Anim. Sci.* 74, 2598-2611.
- Bertrand, J.K., Berger, P.J. & Willham, R.L., 1985. Sire x environment interaction in beef cattle weaning weight field data. *J. Anim. Sci.* 60, 1396-1402.
- Bertrand, J.K., Hough, J.D. & Benyshek, L.L., 1987. Sire x environment interaction and genetic correlations of sire progeny performance across regions in dam-adjusted field data. *J. Anim. Sci.* 64, 77-82.
- Bijma, P., Meuwissen, T.H.E. & Woolliams, J.A., 2002. Design of sustainable breeding programs in developed countries. 7th Wrld Congr. Genet. Appl. Livest. Prod. August 19-23, Montpellier, France. CD-ROM communication No. 25-35.
- Bishop, S.C., 1993. Grassland performance of Hereford cattle selected for rate and efficiency of lean gain on a concentrate diet. *Anim. Prod.* 56, 311-319.
- Bodin, L., Robert-Granié, C., Larzul, C., Allain, D., Bolet, G., Elsen, J.M., Garreau, H., de Rochambeau, H., Ros, M. & SanCristobal, M., 2002. Twelve remarks on canalization in livestock production. 7th Wrld Congr. Genet. Appl. Livest. Prod. August 19-23, Montpellier, France. CD-ROM communication No. 25-35.
- Bonsma, F.N., Bisschop, J.H.R., Barnard, W.G., Van Rensburg, J.A., Duvenhage, J.J., Van Wyk, H.P.D. & Watermeyer, F., 1950. Nguni cattle. *Bull. Dept. Agric.* No. 311.
- Bradfield, M.J., Graser, H-U. & Johnston, D.J., 1997. Investigation of genotype x production environment interaction for weaning weight in the Santa Gertrudis breed in Australia. *Aust. J. Agric. Res.* 48, 1-5.
- Brown, M.A., Tharel, L.M., Brown, A.H. Jr., Jackson, W.G. & Meisner, J.R., 1993a. Genotype x environment interactions in preweaning traits of pure-bred and reciprocal cross Angus and Brahman calves on common Bermudagrass and endophyte-infected Tall Fescue Pastures. *J. Anim. Sci.* 71, 326-333.

- Brown, M.A., Brown, A.H. Jr., Jackson, W.G. & Meisner, J.R., 1993b. Genotype x environment interaction in postweaning performance to yearling in Angus, Brahman and reciprocal cross calves. *J. Anim. Sci.* 71, 3273-3279.
- Buchanan, D.S. & Nielsen, M.K., 1979. Sire by environment interaction in beef cattle field data. *J. Anim. Sci.* 48, 307-312.
- Cartwright, T.C., 1970. Selection criteria for beef cattle for the future. *J. Anim. Sci.* 30, 706-711.
- Cundiff, L.V., Gregory, K.E. & Koch, R.M., 1974. Effects of heterosis on reproduction in Herefords, Angus and Shorthorn cattle. *J. Anim. Sci.* 38, 711-727.
- De Jong, G. & Bijma, P., 2002. Selection and phenotypic plasticity in evolutionary biology and animal breeding. *Livest. Prod. Sci.* 78, 195-214.
- Eler, J.P., Van Vleck, L.D., Ferraz, J.B.S. & Lôbo, R.B., 1995. Estimation of variances due to direct and maternal effects for growth traits of Nelore Cattle. *J. Anim. Sci.* 73, 3253-3258.
- Epstein, H., 1971. The origin of the domestic animals of Africa 1. Africana Publ. Corp., New York.
- Falconer, D.S., 1952. The problem of environment and selection. *Amer. Nat.* 86, 293-298.
- Falconer, D.S., 1990. Selection in different environments: effects on environmental sensitivity (reaction norm) and on mean performance. *Genet. Res.* 56, 57-70.
- Falconer, D.S. & Mackay, T.F.C., 1997. Introduction to quantitative genetics. Longman, England.
- Felius, M., 1985. Genus Bos – Cattle breeds of the world. Published by MSD AGVET.
- Foulley, J.L. & Henderson, C.R., 1989. A simple model to deal with sire by treatment interaction when sires are related. *J. Dairy Sci.* 72, 167-172.
- Gertenbach, W.D. & Kars, A.A., 1999. Toward the conservation of the indigenous cattle of Kwazulu-Natal. *S. Afr. J. Anim. Sci.* 29, 55-63.
- Gilmour, A.R., Cullis, B.R., Welham, S.J. & Thompson, R., 1999. ASREML Reference Manual. NSW Agriculture Biometric Bulletin No.3 NSW Agriculture, Orange Agricultural Institute, Forest Road, Orange 2800 NSW, Australia.
- Groeneveld, E., Mostert, B.E. & Rust, T., 1998. The covariance structure of growth traits in the Afrikaner beef population. *Livest. Prod. Sci.* 55, 99-107.
- Hansen, L.B., Freeman, A.E. & Berger, P.J., 1983. Yield and fertility relationships in dairy cattle. *J. Dairy Sci.* 66, 293-305.
- Harwin, G.O., 1989. Strategies for beef production in South Africa – a selection of lectures. Edited by Professor Arthur Lishman, Stock Owners Co-operative Limited.
- Hodges, J., 1984. Conservation of animal genetic resources. *Livest. Prod. Sci.* 11, 1-22.

- Hoekstra, J., Van der Lugt, A.W., Van der Werf, J.H.J. & Ouweltjes, W., 1994. Genetic and phenotypic parameters for milk production and fertility traits in upgraded dairy cattle. *Livest. Prod. Sci.* 40, 225-232.
- Hundleby, J.A.B., 1986. The Nguni Breed – Origin and progress. Nguni information day. Ciskei. June. Unpublished.
- Jenkinson, D., McEwan, J. & Nay, T., 1973. The sweat glands and hair follicles of Asian, African and South American cattle. *Aust. J. Biol. Sci.* 26, 259-275.
- Kaps, M., Herring, W.O. & Lamberson, W.R., 2000. Genetic and environmental parameters for traits derived from the Brody growth curve and their relationships with weaning weight in Angus cattle. *J. Anim. Sci.* 78, 1436-1442.
- Kars, A.A., 1993. A genetic analysis of the Bartlow Combine Nguni Cattle Stud. Ph.D. (Agric) thesis. University of the Free State, Bloemfontein.
- Kars, A.A., Erasmus, G.J. & Van der Westhuizen, J., 1994. Variance component and heritability estimates for growth traits in the Nguni cattle stud at Bartlow Combine. *S. Afr. J. Anim. Sci.* 25, 129-132.
- Kirkpatrick, M. & Bataillon, T., 1999. Artificial selection on phenotypically plastic traits. *Genet. Res.* 74, 265-270.
- Koch, R.M., Cundiff, L.V., Gregory, K.E. & Dickerson, G.E., 1973. Genetic and phenotypic relations associated with preweaning and post-weaning growth of Hereford bulls and heifers. *J. Anim. Sci.* 35, 327-335.
- Kolmodin, R., Strandberg, E., Madsen, P., Jensen, J. & Jorjani, H., 2002a. Genotype by environment interaction in Nordic dairy cattle studies by use of reaction norms. *Acta Agric. Scand., Sect. A.* 52, 1-24.
- Kolmodin, R., Strandberg, E., Jorjani, H. & Danell, B., 2002b. Selection in presence of genotype by environment interaction may increase environmental sensitivity. 7th Wrlld Congr. Genet. Appl. Livest. Prod. August 19-23, Montpellier, France. CD-ROM communication No. 25-35.
- Koots, K.R., Gibson, J.P., Smith, C. & Wilton, J.W., 1994a. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. *Anim. Breed. Abstr.* 62, 309-338.

- Koots, K.R., Gibson, J.P. & Wilton, J.W., 1994b. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. *Anim. Breed. Abstr.* 62, 825-853.
- Kostrewski, M., 1988. Potential of selection for tick resistance in Nguni cattle. SASAP developing areas branch symposium. Univ. of Fort Hare, Ciskei.
- Lee, C. & Pollak, E.J., 1997. Relationship between sire x year interactions and direct-maternal genetic correlation for weaning weight of Simmental cattle. *J. Anim. Sci.* 75, 68-75.
- Lepen, J.M., 1994. The performance of indigenous Sanga/Nguni cattle in Namibia. TVL Nguni club symposium, Pietersburg. November.
- Maree, C. & Casey, C.H., 1993. *Livestock production systems: principles and practice*. Brooklyn: Agric developmental foundation.
- Mathur, P.K., 2002. Methods for estimation and use of genotype-environment interactions. 7th Wrlld Congr. Genet. Appl. Livest. Prod. August 19-23, Montpellier, France. CD-ROM communication No. 25-35.
- Mavrogenis, A.P., Dillard, E.U. & Robinson, O.W., 1978. Genetic analysis of post-weaning performance of Hereford bulls. *J. Anim. Sci.* 47, 1004-1013.
- McDowell, R.E., 1972. *Improvements of livestock production in warm climates*. W.H. Freeman and Company, San Francisco.
- Meyer, K., 1987. Estimates of variance due to sire x herd interactions and environmental covariances between paternal half-sibs for first lactation dairy production. *Livest. Prod. Sci.* 17, 95-114.
- Meyer, K., 1992. Variance components due to direct and maternal effects for growth traits in Australian beef cattle. *Livest. Prod. Sci.* 31, 179-204.
- Meyer, K., Carrick, M.J. & Donnelly, B.J.P., 1993. Genetic parameters for growth traits of Australian beef cattle from a multibreed selection experiment. *J. Anim. Sci.* 71, 2614-2622.
- Meyer, K., 1995. Estimates of genetic parameters for mature weight of Australian beef cows and its relationship to early growth and skeletal measures. *Livest. Prod. Sci.* 44, 125-137.
- Morris, C.A., Baker, R.L., Hickey, S.M., Johnson, D.L., Cullen, N.G. & Wilson, J.A., 1993. Evidence of genotype by environment interaction for reproductive and maternal traits in beef cattle. *Anim. Prod.* 56, 69-83.
- Muggli, N. & Hohenboken, W., 1984. Inheritance of maternal immunoglobulin G1 concentration by the bovine neonate. *J. Anim. Sci.* 59, 39-48.

- Núñez-Domínguez, R., Ramirez-Valverde, R., Ruíz-Flores, A. & Domínguez-Viveros, J., 2002. Univariate vs bivariate analyses of weaning and 18-months weights in Tropicarne cattle. 7th Wrld Congr. Genet. Appl. Livest. Prod. August 19-23, Montpellier, France. CD-ROM communication No. 25-35.
- Nephawe, K.A., Naser, F.W.C., Roux, C.Z., Theron, H.E. & Erasmus, G.J., 1999. Sire x ecological region interactions in Bonsmara cattle. *S. Afr. J. Anim. Sci.* 29, 189-201.
- Naser, F.W.C., Erasmus, G.J., Van Wyk, J.B. & Van Deventer, C.S., 1998. Quantifying herd-year-season x sire interaction in Bonsmara cattle. *S. Afr. J. Anim. Sci.* 28, 167-172.
- Naser, F.W.C., Konstantinov, K.V. & Erasmus, G.J., 1996. The inclusion of herd-year-season by sire interaction in the estimation of genetic parameters in Bonsmara cattle. *S. Afr. J. Anim. Sci.* 26, 75-78.
- Naser, F.W.C., 2002. A preliminary investigation into the use of cluster analyses in genotype x environment interaction studies in beef cattle. 7th Wrld Congr. Genet. Appl. Livest. Prod. August 19-23, Montpellier, France. CD-ROM communication No. 25-35.
- Ramsay, K.A., 1986. The role of the Department of Development Aid and the self-governing states in the early development and the future of the Nguni as a competitive indigenous breed of cattle. Nguni information day, June. Unpublished.
- Rauw, W.M., Kanis, E., Noordhuizen-Stassen, E.N. & Grommers, F.J., 1998. Undesirable side effects of selection for high production efficiency in farm animals: a review. *Livest. Prod. Sci.* 56, 15-33.
- Robertson, A., 1959. The sampling variance of genetic correlation coefficient. *Biometrics* 15, 469-485.
- Robinson, D.L., 1996. Models which might explain negative correlations between direct and maternal genetic effects. *Livest. Prod. Sci.* 45, 111-122.
- SanCristobal-Gaudy, M., Elsen, J.M., Bodin, L., Chevalet, C., 1998. Prediction of the response to a selection for canalisation of a continuous trait in animal breeding. *Genet. Sel. Evol.* 30, 423-451.
- SAS, 1991. SAS / STAT User's guide, Release 6.03 Edition. Statistical Analysis System Institute, Inc, Cary, NC.
- Scholtz, M.M, Roux, C.Z. & Lombard, P.E., 1990a. Breeding strategies for beef cattle in the subtropics and tropics: Terminal crossbreeding. Proc. 4th Wrld Congr. Appl. Anim. Genet. Edinburgh, 361-364.

- Scholtz, M.M., Roux, C.Z. & Schoeman, S.J., 1990b. An investigation into the consequences of selection for growth, size and efficiency. *S. Afr. J. Anim. Sci.* , 20, 169-173.
- Scholtz, M.M., Lombard, P.E. & Enslin, C.B., 1990c. A note on the early calving of beef heifers. *S. Afr. J. Anim. Sci.* 21, 206-209.
- Scholtz, M.M., Spickett, A.M., Lombard, P.E. & Enslin, C.B., 1991. The effect of tick infestation on the productivity of cows of three breeds of cattle. *Onderstepoort J. Vet. Res.* 58, 71-74.
- Simm, G., Conington, J., Bishop, S.C., Dwyer, C.M. & Pattinson, S., 1996. Genetic selection for extensive conditions. *Appl. Anim. Behaviour Sci.* 49, 47-59.
- Swalve, H.H., 1993. Estimation of direct and maternal (co)variance components for growth traits in Australian Simmental beef cattle. *J. Anim. Breed. Genet.* 110, 241-252.
- Tainton, N., 1999. Veld management in South Africa. University of Natal press. Scottsville.
- Tess, M.W., Kress, D.D., Burfening, P.J. & Friedrich, R.L., 1979. Sire by environment interaction in Simmental-sired calves. *J. Anim. Sci.* 49, 964-971.
- Thompson, R. & Meyer, K., 1986. A review of theoretical aspects in the estimation of breeding values for multi-trait selection. *Livest. Prod. Sci.* 15, 299-312
- Van der Westhuizen, J., 1997. Performance factors influencing total herd efficiency in beef cattle. Ph.D. (Agric) thesis. University of the Free State, Bloemfontein.
- Van der Westhuizen, J. & Matjuda, L.E., 1999. Beef breeding in South Africa. Agricultural Research Council, Animal Improvement Institute, Irene.
- Vercoe, J.E. & Frisch, J.E., 1992. Genotype (breed) and environment interaction with particular reference to cattle in the tropics. *Aust. J. Anim. Sci.* 5, 401-409.
- Warwick, E.J. & Legates, J.E., 1979. Breeding and improvement of farm animals. McGraw-Hill Book Company, New York.

UNIVERSITY LIBRARY