GENOTYPE X ENVIRONMENT INTERACTION IN AFRIKANER CATTLE

by

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ABSTRACT

A line x environment interaction study with grade Afrikaner cattle was established at Matopos Research Station, Zimbabwe, in 1956. From a grade pool of 200 cows, two selection lines of 100 cows were reared in different management environments. The non-supplemented (NS) line relied on the range throughout the year and was mated to calve with the onset of the rains (December to February). The supplemented (S) line was offered protein-rich supplements during the dry season and mated to calve prior to the onset of the rains (October to December). Bull selection based on weight at weaning was to develop lines adapted to their respective environments.

After approximately 2 generations of selection, lines were sub-divided into 4 sub-lines, consisting of 75 cows each. One sub-line remained within each environment as a control; the remaining sub-lines were interchanged between environments. Bulls were selected within control lines, while replacement heifers were generated within sub-line. Heifers were selected on weight at mating and replacement rates were dictated by the sub-line with the least number of suitable animals (>265kg). Data collected over a 40-year period representing 6 generations of selection were analyzed to determine a) genetic and environmental factors influencing calf growth and survival and cow fertility, b) direct and correlated responses to selection and c) presence and importance of genotype x environment interactions.

Productivity in the S environment, in terms of calf growth and cow fertility, was superior compared with the NS environment. While there were no differences in birth weight, calves born early in the S environment were estimated to be 90kg (33%) heavier at 18 months than calves born late in the NS environment. The performance of calf growth from birth to 18 months in this study has emphasized the importance of matching animal physiological status with seasonal changes in the sub-tropics. Given the significant and consistent detrimental effects of previous lactation status of the cow on fertility and calf growth, it is recommended that this effect be considered in routine evaluations.

The high generation intervals (6.7 and 5.5 years pre- and post-crossover) reflect the cow age at first calving (4 and 3 years respectively for the two periods). Direct cumulative selection differentials for weaning weight were very low (0.08 and 0.05 standard deviation units/generation for the S and NS lines respectively). The correlated cumulative selection differentials for pre-weaning weight gain were negative for the pre-crossover period and positive for the post-crossover period, and together with the low direct cumulative selection differentials suggest that significant attention was paid to secondary characteristics. Consequently, selection responses were low (2.35±0.045 and 2.22±0.047kg/generation for weaning weight for the S and NS lines respectively). All correlated direct genetic trends were positive and linear, while maternal genetic trends were very low and negative for the S line.

Direct and maternal (in parenthesis) heritability estimates for weights at birth, weaning and 18-months were 0.39±0.03 (0.14±0.02), 0.19±0.03 (0.21±0.04) and 0.36±0.06 (0.15±0.04) respectively. Apart from the non-significant direct-maternal genetic correlation for birth weight, other correlations were all moderately negative (-0.35 to –0.57). With the exception of correlations with birth weight which were variable and often close to zero, direct and maternal genetic correlations among traits were high, particularly for traits measured at ages close to each other

The average incidence of calving success (CS: including abortions at term and stillbirths) was 68%. Heritability and repeatability (in parenthesis) estimates for CS and calving date (CD: with a 21 day penalty for censored records) were 0.08±0.02 (0.10±0.02) and 0.09±0.02 (0.17±0.02) respectively. Service sire was important for both traits, but only accounted for <2% of the total phenotypic variation. Favourable genetic trends were shown for both traits (1.2±0.14% and 0.8±0.13%/generation for CS for the S and NS lines respectively, and -0.8±0.09 days/generation for both lines for CD). The genetic correlation between CS and CD was high (-0.95) and the correlation of sires' estimated breeding values (EBV) indicated that a one-day improvement in CD EBV is associated with a 1% increase in CS EBV. However, correlation estimates of sires' EBV between measures of fertility and growth were all unfavourable, but not-significantly different from zero.

There were no indications of line x environment interaction for all the growth traits. A significant interaction was, however, manifested for CS and was due to the markedly poorer performance of the S line cows in the NS environment. While no sire x environment interactions were manifested, significant sire x year interactions were found for all the growth traits and for CS, which serves to highlight the tremendous seasonal differences experienced in the sub-tropics. Therefore there is a need to consider selection for genotypic stability, particularly for the more extensive farming environments.

This study revealed that concomitant genetic improvements in both growth and fertility were attainable. It is recommended that fertility and calf survival be included in routine breed evaluations. There is however an urgent need to implement data collection strategies to ensure that all calving activities are comprehensively recorded, not least the adequate definition of contemporary groups.

Keywords: Afrikaner cattle, sub-tropics, growth, fertility, survival, genetic parameters, selection response, genotype x environment interaction.

OPSOMMING

‘n Lyn x omgewing-interaksiestudie met graad-Afrikanerbeeste is in 1956 by Matopos Navorsingstasie, Zimbabwe, onderneem. Vanuit ‘n poel van 200 koeie is twee seleksielyne van 100 koeie elk in verskillende bestuursomgewings grootgemaak. Die lyn wat geen byvoeding ontvang het nie (NS) was dwarsdeur die jaar op weiding alleen aangewese en is gepaar om met die aanvang van die reënseisoen (Desember tot Februarie) te kalf. Die lyn wat byvoeding ontvang het (S) het proteïenryke aanvullings gedurende die droë seisoen ontvang en is gepaar om voor die aanvang van die reëns (Oktober tot Desember) te kalf. Bulseleksie gebaseer op gewig met speen is gemik op ontwikkeling van lyne wat by hul spesifieke omgewings aangepas sou wees.

Na ongeveer twee generasies van seleksie is lyne onderverdeel in 4 sub-lyne wat uit 75 koeie elk bestaan het. Een sub-lyn het in elke omgewing as kontrole gebly. Die oorblywende sublyne is tussen die omgewings verdeel. Bulle is uit die kontrolelyne geselekteer, terwyl vervangingsverse uit die sublyne gekom het. Verse is geselekteer op grond van gewig met paring en vervangings is gedikteer deur die die sub-lyn wat die kleinste getal geskikte diere gehad het (> 265 kg). Data wat oor ‘n 40-jaar periode verteenwoordigend van 6 geslagte se seleksie versamel is, is ontleed ten einde te bepaal a) watter genetiese en omgewingsfaktore kalfgroei en –oorlewing en koeivrugbaarheid beïnvloed, b) wat die direkte en gekorreleerde responsie op seleksie is en c) die teenwoordigheid en belangrikheid van genotipe- x omgewings-interaksies.

Wat betref kalfgroei en koeivrugbaarheid was produktiwiteit in die S-omgewing meerderwaardig teenoor dié in die NS-omgewing. Terwyl daar geen verskille in geboortegewigte was nie, is beraam dat kalwers wat vroeg in die S-omgewing gebore is, 90 kg (33%) swaarder op 18 maande was as dié wat laat in die NS-omgewing gebore is. Die prestasie van kalfgroei vanaf geboorte tot 18 maande in hierdie studie het beklemtoon hoe belangrik dit is om ‘n dier se fisiologiese status by seisoenale veranderinge in die sub-trope aan te pas. Gegewe die betekenisvolle en konsekwente

nadelige effekte van vorige laktasie-status van die koei, is dit aan te beveel dat hierdie effek in aanmerking geneem moet word in roetine-evaluasies.

Die hoë generasie-intervalle (6.7 en 5.5 jaar onderskeidelik voor- en na-uitruiling) weerspieël die koei-ouderdom met eerste kalwing (4 en 3 jaar vir die twee periodes). Direkte kumulatiewe seleksie-differensiale vir speengewig was baie laag (0.08 en 0.05 standaardafwyking eenhede/generasie vir die S- en NS-lyne onderskeidelik). Die gekorelleerde kumulatiewe differensiale vir voor-speense gewigtoename was negatief vir die voor-oorgangsperiode en positief vir die na-oorgangsperiode, en tesame met die lae direkte kumulatiewe seleksie-differensiale gee dit die indruk dat betekenisvolle aandag aan sekondêre eienskappe gegee is. Seleksie-response was gevolglik laag (2.35±0.045 en 2.22±0.047kg/generasie vir speengewig vir die S- en NS-lyne onderskeidelik). Alle gekorreleerde direkte genetiese tendense was positief en lineêr, terwyl maternale genetiese tendense baie laag en negatief vir die S-lyn was.

Direkte en maternale (tussen hakies) oorerflikheidsberamings vir geboortegewig, speengewig en 18-maande gewig was 0.39±0.03 (0.14±0.02), 0.19±0.03 (0.21±0.04), en 0.36±0.06 (0.15±0.04) onderskeidelik. Afgesien van die nie-betekenisvolle direk-maternale genetiese korrelasie vir geboortegewig, was alle ander korrelasies redelik negatief (-0.35 tot -0.57). Met die uitsondering van korrelasies met geboortegewig wat gevarieer het en dikwels na aan zero was, direkte en maternale genetiese korrelasies tussen eienskappe was hoog, veral vir eienskappe wat gemeet is op ouderdomme na aan mekaar.

Die gemiddelde voorkoms van kalwingsukses (CS: sluit in voltermyn-aborsies en doodgeboortes) was 68%. Oorerflikheids- en herhaalbaarheids- (in hakies) beramings vir kalwingsukses en kalwingsdatum (CD: met 'n 21 dae boete vir gesensoreerde rekords) was 0.08±0.02 (0.10±0.02) en 0.09±0.02 (0.17±0.02) onderskeidelik. Diensvaar was belangrik vir beide eienskappe, maar was aanspreeklik vir slegs <2% van die totale fenotipiese variasie. Gunstige genetiese tendense is vir beide eienskappe aangedui (1.2±0.14% en 0.8±0.13%/generasie vir CS vir die S- en NS-lyne onderskeidelik, en –0.8±0.09 dae/generasie vir beide lyne vir CD). Die genetiese

korrelasie tussen CS en CD was hoog (-0.95) en die korrelasie van vaars se beraamde teelwaardes (EBVs) het aangedui dat ‘n eendaagse verbetering in CD EBV geassosieer word met ‘n 1% toename in CS EBV. Korrelasieberamings van vaar-EBVs tussen metings van vrugbaarheid en groei was egter almal ongunstig, maar nie betekenisvol verskillend van zero nie.

Daar was geen aanduiding van lyn x omgewing-interaksie vir al die groei-eienskappe nie. ‘n Betekenisvolle interaksie is egter vir CS waargeneem en was te wyte aan die merkbaar swakker prestasie van die S-lyn koeie in die NS-omgewing. Terwyl geen vaar x omgewings-interaksies aangedui is nie, is betekenisvolle vaar x jaar-interaksies vir al die groei-eienskappe sowel as CS gevind, wat die geweldige seisoenale verskille wat in die sub-trope ondervind word, sterk na vore bring.

Hierdie studie het getoon dat gelyktydige genetiese verbeterings in beide groei en vrugbaarheid haalbaar is. Dit word aanbeveel dat vrugbaarheid en kalf-oorlewing by roetine ras-evaluasies ingesluit word. Daar is egter ‘n dringende behoefte aan die implementering van dataversamelingstrategieë wat sal verseker dat alle kalwingsaktiwiteite volledig aangeteken word en veral ook dat kontemporêre groepe voldoende gedefinieer word.

Sleutelwoorde: Afrikaner vleisbeeste, sub-trope, groei, vrugbaarheid, oorlewing, genetiese beramings, seleksie responsie, genotiepe x omgewing interaksie

ACKNOWLEDGEMENTS

Project implementers must be applauded for the courage to embark on a large-scale experiment with cattle only three years after Falconer & Latyszewski raised the notion of a genotype x environment interaction in mice in 1952. I feel honoured to have been involved in such an experiment, particularly as am I aware of only one other long-term selection experiment with cattle in the sub-region, the Bartlow-Combine Nguni herd in Natal. There are however many deficiencies in the experimental design which are beyond my control (choice of breed, creation of adapted lines, selection criteria, confounding of time of mating and supplementation regime). I am acutely aware of the fact that I was privileged to 'take over' the herd from a competent management team but was not afforded the opportunity to hand the project on. I therefore feel obligated to extract what I can from this meticulously recorded 40-year data set and as a result I have retained additional information in the appendices.

With an experiment spanning 40 years, it is obvious that a great number of people have played a significant role in ensuring that it was executed successfully. Not least, the management and ground staff where cattle husbandry is a 365-day a year duty carried out with commitment. Profound gratitude to the late Harry Ward, not only for prodding me into a meaningful direction, but for ensuring that against all odds the experiment continued largely unhindered, particularly during the late 1970's and early 1980's.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 THE AFRIKANER BREED OF CATTLE

Cattle breeds indigenous to parts of central and all of southern Africa, termed sanga cattle (Mason & Maule, 1960), are characterized by a cervico-thoracic hump. These breeds are thought to have originated from interbreeding between the ancestral cattle breeds of Africa: the Hamitic Longhorn (*Bos taurus longifrons*), the humpless shorthorn (*B. taurus brachyceros*) and the humped Zebu cattle (*B. indicus*) in the north of Africa and as people migrated southwards along the east coast of Africa, they brought these cattle breeds with them (Oliver, 1983). Recent DNA studies show that all the southern African sanga breeds of cattle, including the Afrikaner, are largely *B. taurus* and are now classified as *Bos taurus africanus* (Mostert *et al.*, 1998).

The Afrikaner breed was developed from the cattle of the Khoikhoi people in the west coast of southern African (Scholtz, 1988) by the Dutch Settlers in the 17th century. Migrations of these early settlers encouraged the development of a breed of cattle that were excellent travelers and tolerant to disease and drought. However, little attention was given to fertility (Oliver, 1983). Until the mid 1970's the Afrikaner was the dominant breed in southern Africa and has been fairly extensively used in the formation of composite breeds (Faulkner & Epstein, 1957; Mason & Maule, 1960; Oliver, 1983).

Referring to the Afrikaner in South Africa, Hirzel (1972) notes that despite the predominance of the breed in the commercial sector, the Afrikaner has failed to progress in some ways for many years and laments 'There is no intensive search for lines without genetic faults, and rigid culling for commercial characteristics is not common practice. Calving percentages are low on average and a fine show cow will not automatically be penalized in the show ring or culled by all breeders for low fertility.' However, the Afrikaner remains an important breed in South Africa, being promoted as a dam line for crossbreeding purposes. The introduction of the Brahman into Zimbabwe in the mid 1970's led to the rapid marginalization of the Afrikaner in the country and currently there are no stud breeders breeding Afrikaner cattle.

An important objective in beef cattle production is to maximize the number of calves weaned per year. A major controlling factor is the ability of the cow to produce a calf each year. In order to do so, a beef cow with a gestation interval of approximately 283 days must conceive and maintain a pregnancy by 82 days *postpartum*. However, the gestation interval of the Afrikaner is approximately 15 days longer (Rakha *et al.*, 1971) thereby shortening the period in which the cow must reconceive in order to produce a calf each year. The Afrikaner cow is noted for its low annual calving rate in the region of 55 to 65% compared with 70 to 85% of other more fertile breeds in southern Africa (Table 1.1). However it must be noted that the Afrikaner is a hardy breed being used almost exclusively for extensive farming (Rust *et al.*, 2004)

The low reproductive performance of the Afrikaner cows has been attributed to the protracted *postpartum* anoestrus period extending beyond the normal breeding season (Holness & Hale, 1980; Wells, 1986). It appears that low levels of progesterone in the peripheral blood of the Afrikaner accounts for the delayed resumption of normal ovarian activity (Holness *et al.*, 1977), where it has been postulated that increasing levels of progesterone are necessary to remove a refractoriness of the endocrine system caused by high level of estradiol prior to parturition (Holness *et al.*, 1977). The length of the *postpartum* period seems to be associated with a suppression of estrus (silent ovulations) rather than a lack of luteal activity, since the estimated time of ovulation of the Afrikaner compares favorably with other beef breeds (Holness *et al.*, 1978; 1980).

Table 1.1 Reproductive performance of the Afrikaner dam across the sub-region

Calving rate (%)[1]				
Afrikaner	Other	Breed	Country	Reference
64	78	Sussex	South Africa	Harwin *et al.* (1967)
61	85	Mashona	Zimbabwe	Holness *et al.* (1980)
65	71	Tswana	Botswana	Trail *et al.* (1977)
	85	Tuli		
65	83	Mashona	Zambia	Rakha *et al.* (1971)
	83	Angoni		
56	74	Mashona	Zimbabwe	Moyo (1990)
	67	Nguni		
	69	Tuli		
	67	Brahman		
	56	Sussex		
	66	Charolais		

1 Cows calving as a proportion to the number of cows mated on an annual basis

Although temporary weaning has been used to stimulate the onset of ovarian activity, implying that nursing exerts a large effect on the brain-pituitary-ovarian axis, the Afrikaner did not respond to such treatment (Holness *et al.*, 1980). Wells (1986) found that Afrikaner cows were particularly sensitive to the physical act of suckling with a high proportion of cows being anovulatory 100 days *postpartum*. Removal of the suckling stimulus significantly reduced the *postpartum* interval. Furthermore, when Afrikaner and Mashona cows were subjected to under-nutrition, Afrikaner cows stopped cycling after losing 19% of their body weight, whereas Mashona cows, with a similar body fat reserve to that of the Afrikaner, continued cycling and only ceased sexual activity when they had lost 33% of their initial body weight (Hale & Holness, 1977) suggesting inherently different endocrine functions (Holness, 1992).

Similarly, performance of the Afrikaner, as measured by calf weights, was remarkably similar across the region (Table 1.2), despite wide variation in environment and management systems. Sanga types of cattle show lower calf mortality rates than exotic cattle types (*B. indicus* & *B. taurus)* (Schoeman, 1989; Moyo, 1990), and this has been found to have an important impact on herd productivity (du Toit *et al.*, 1995).

Table 1.2 Growth performance (kg) of Afrikaner calves across the region

	Botswana			South Africa		Zimbabwe
	Trial *et al.* (1977)	APRU (1979)	APRU (1990)	Mostert *et al.* (1998)	Collins-Lusweti (2000)	Moyo (1990)[1]
Birth weight	29.9	30.6	31.0	31.6	30.2	31.6
Weaning weight	174	174	175	179	174	189
18-month weight	-	277	276	295	-	273

1. Afrikaner dams mated to a range of terminal sires

A major objective of animal breeders is to select superior animals to be parents of the next generation. The sub-tropical production environment, such as experienced in Zimbabwe, pose atypical challenges to breeders striving to select the 'best' animal, where conditions vary greatly within and between seasons. Another major environmental challenge is the dramatic decline in quality and quantity of available grazing in the dry season. Additional environmental stresses include the large diurnal temperature fluctuations, the high summer temperatures, and the internal and external parasite load. However, information of genetic parameters of sanga cattle in sub-tropical environments remains scant and the general assumption is that the individual's genetic merit does not interact with these seasonal environmental changes.

1.2 GENOTYPE X ENVIRONMENT INTERACTION

A genotype x environment interaction is manifested when genotypes (individuals, lines, varieties, breeds, etc) show a differential phenotypic response across one or more environments. Stated differently, an interaction occurs when selection gains made in a particular environment are not transferable to another environment. The presence of a genotype x environment interaction with widely divergent genotypes and environments is well known and documented in both plants and animals. Studies of genotype x environment interactions are becoming more important as cattle genotypes are now being managed in a diverse range of environments (Bryant *et al.*, 2004). Furthermore, Dominik *et al.* (2001) postulate that different genetic relationships exist between different traits across environments. This is supported by different genetic correlations for milk, fat and protein in the high and low yield environments in dairy cattle reported by Castillo-Juarez *et al.* (2002). The latter authors suggest that differences in management between the two environments modify the genetic expression of the traits studied. The problem that remains is to understand and be able to predict to what extent a seemingly small genetic and/or environmental change can elicit an interaction of biological and economic importance.

Intrinsic to the study of interactions is the subject of adaptation, which is the ability of genotypes to cope with environmental challenges and changes. As an example, Frisch (1981) suggests that selection response for growth in a stressful environment is not due to an improvement in inherent genetic potential, but due to increased resistance to environmental stress, while Ordonez (1990) notes that ‘breeding for increased production [under tropical conditions] will be just an indirect selection for adaptability.’

Hammond (1947) proposed that selection of parents should be carried out within the ‘best’ nutritionally non-limiting environment that facilitated the expression of an individual’s true genetic potential thereby improving the efficacy of selection and selection response. However, in a classic experiment with mice, Falconer & Latyszewski (1952) found that selection gains made in one environment were not necessarily transferable to another environment. Similar results were found and conclusions drawn from an experiment with pigs (Fowler & Ensminger, 1960). It was suggested that gene expression differed across environments, so much so that a measurement such as pup-weight could be considered as two different traits in two different environments under the control of different sets of genes, but with some genes in common (Falconer, 1989). Referring to the experiment with mice, Falconer (1977a, 1990) postulated that response to selection for pup-weight on the 'low' (restricted) plane involved genes for improved efficiency of gain compared with selection on the high (*ad libitum*) plane where genes for increased appetite were important. Genetic gains for improved efficiency were transferable across environments, whereas genetic gains for increased appetite did not improve weight gains of mice on restricted feed.

Genotype x environment interactions are caused by many factors. The differential production potentials and adaptation of genotypes to specific environmental stresses may give rise to genotype x environment interactions (Frisch & Vercoe, 1978, 1983 and 1984; Frisch, 1981; Vercoe & Frisch, 1983, 1988 and 1992). In their studies of growth rate of taurine (Hereford-Shorthorn cross) and indicus (Brahman) cattle breeds and their crosses in the tropics of Australia, these authors presented examples elucidating the mechanisms giving rise to interactions. Taurine cattle, which had a higher growth potential, also had higher metabolic rates, but under restricted nutrition, they were less efficient with lower weight gains than indicus cattle. The differential response of growth rates between taurine and indicus cattle reared under pen-fed conditions (limited environmental stress) and under normal grazing conditions (high environmental stress) was a reflection of the differences in adaptive capacities and not related to their true growth potential. Vercoe & Frisch (1983) stated that stress acts primarily, but not solely, by depressing potential food intake. Furthermore, the response to selection for growth rate under stressful environmental conditions was due to an improvement in environment adaptation and not due to an improvement in growth rate, which along with appetite, actually declined under pen-fed conditions.

In a review of the importance of genotype x environment interactions in poultry, Hartmann (1990) reported that egg and body weight were barely affected by interactions while, in spite of the fairly uniform production environments across test stations, there were considerable interactions for egg production and mortality, which could not be attributed to any specific factor(s). While the possible advantage of selection for general adaptability has been recognized, the exclusive use of crossbred poultry for commercial egg and meat production may have had an important influence on general adaptability (Hartmann, 1990). With respect to the pig industry, Webb & Curran (1986) summarize several important interactions for daily gain, weight for age, feed conversion ratio and feed efficiency between station and on-farm tests carried out across Europe and Britain. They surmise the most likely causes of interactions to be the selection objective, the feeding level and number per pen (behavioural implications) and propose strategies to avoid interactions and suggest that the best long-term strategy is to understand the causes.

Large differences in genotypes and (or) environments are likely to give rise to genotype x environment 'directional' interactions (Hohenboken, 1985; Notter & Hohenboken, 1990). However, Neser *et al.* (1996) reviewed numerous reports of more subtle interactions in the form of 'random' sire x environment interactions and beef cattle genetic evaluation schemes such as BREEDPLAN routinely fit sire x herd interactions as random effects in the model of analysis (Graser *et al.*, 1999). These interactions are possibly due to the failure of genotypes to show specific environmental adaptation to considerable environmental variation, where environment can be herd, year, season, etc. (Turner & Young, 1969; Frisch & Vercoe, 1978; Frisch, 1981) and may be caused by heterogeneity of variances, use of small numbers of sires, non-random mating and preferential treatment of certain paternal half-sib groups (Notter *et al.*, 1992). These interactions reduce the direct heritability and therefore selection progress and can give rise to a change in ranking of sires across regions. An understanding of this type of interaction is important in across regions breed evaluations, but are difficult to account because of complicated modeling requirements and more importantly, due to the need for adequate across region reference sires (normally taken care of by the extensive use of AI sires).

1.3 STUDY OBJECTIVES

The experiment at Matopos Research Station was initiated in 1956, from lines of grade Afrikaner cattle emanating from the breed evaluation study initiated in 1938, to determine the efficacy of selection within the local environment (Anon., 1955).

In the analysis of measures of calf growth from birth to 18 months of age, calf survival to weaning and measures of cow fertility, the objectives of this study were to:

a) Characterize non-genetic factors;
b) Estimate genetic parameters;
c) Quantify the magnitude of direct and correlated selection response; and
d) Determine the presence and importance of a genotype x environment interaction.

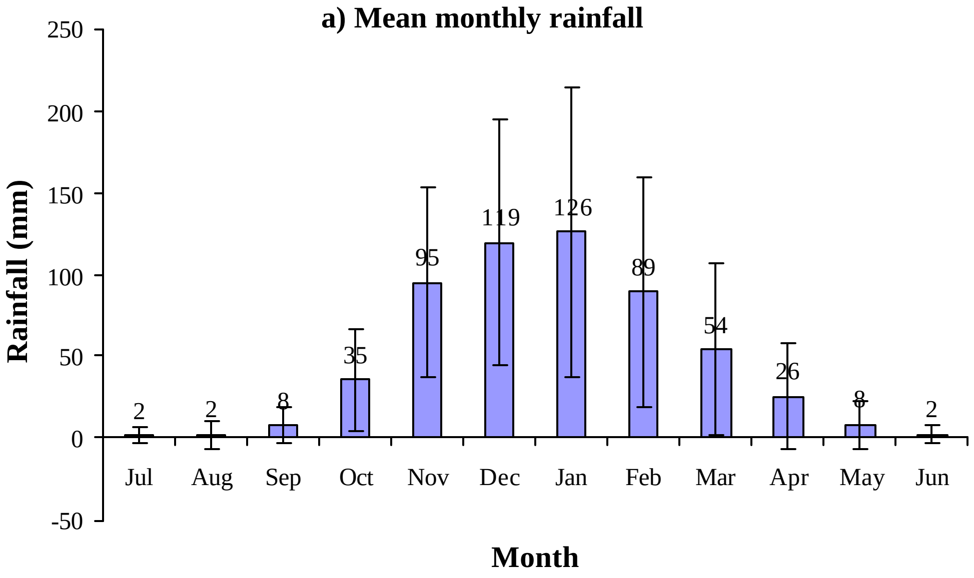
CHAPTER 2

MATERIALS AND METHODS

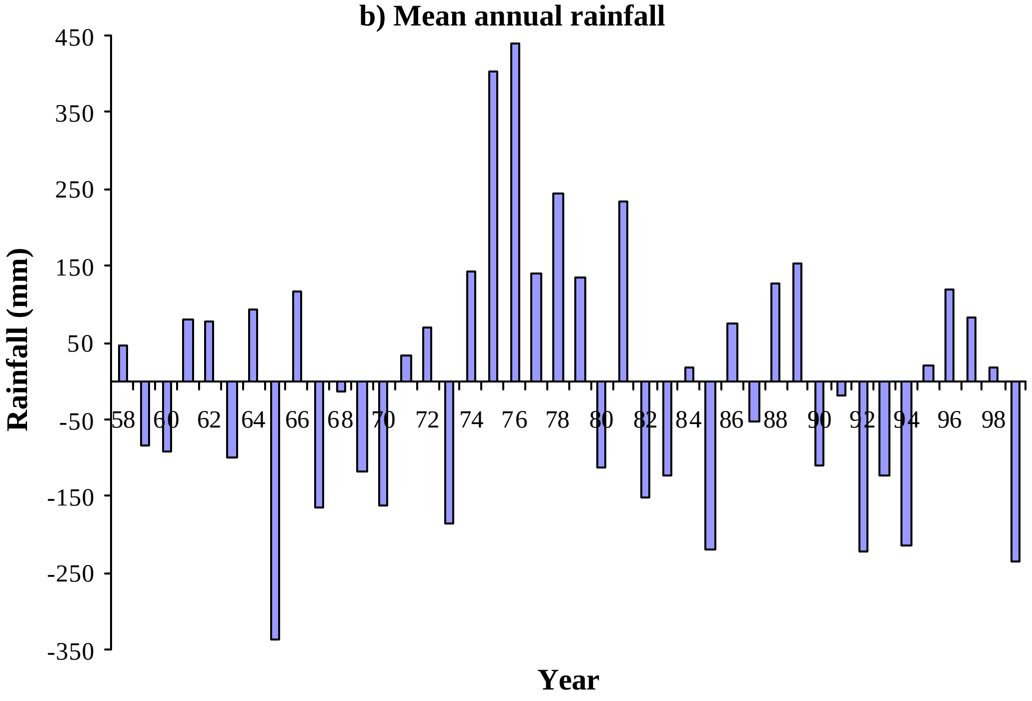
2.1 EXPERIMENTAL SITE

Beef production in Zimbabwe is primarily based on the natural range, where nutrition in the dry season, particularly of the breeding female, is limited in both quantity and quality (Elliott & Croft, 1958; Richardson, 1983; de Waal, 1990; Leng, 1990) and is probably the major cause of the low fertility (60% annual calving rate) experienced in the beef industry.

Matopos Research Station is situated in southwest Zimbabwe (Ward *et al.*, 1979), an area primarily suited to semi-extensive forms of land utilization (Vincent & Thomas, 1961). The climate is characterised by wide fluctuations in the quantity and distribution of rainfall within and across season. Rainfall normally occurs between November and March and is followed by a long dry season (Figure 2.1a). For the period of the study in this report (1957 to 1999) the mean annual rainfall was 566 mm and the yearly pattern of rainfall can be crudely described as wet 70's and dry 60's, 80's and 90's (Figure 2.1b). Of significant importance were droughts recorded in 1965, 1985 and 1992 to 1994. The vegetation on the predominantly red soils is dominated by Acacia species and the dominant grass species are *Heteropogon contortus*, *Themeda triandra* and *Cymbopogon plurinodes* (Rattray, 1957).



a) Mean monthly rainfall



b) Mean annual rainfall

Figure 2.1 Matopos Research Station a) mean monthly (± one standard deviation) and b) annual rainfall (deviated from a mean of 566 mm), 1957/8 to 1998/9

2.2 HISTORY OF THE AFRIKANER HERD AT MATOPOS RESEARCH STATION

In Zimbabwe, and in particular under the more extensive ranching conditions, it was recorded that calving rates were ‘shockingly low, namely, about 50%’, and were ascribed to the low plane of nutrition during certain times of the year, including the time of the year when cattle were bred (towards the end of the rains, February to May) (Murray, 1940). Romyn (1935) noted ‘as things are at present more improvement could be affected by better management and the provision of supplementary feed, than by the use of better bulls or by the usual change of bulls advocated when the cattle are “not growing out as they should”’. In reference to the Afrikaner, Romyn (1935) noted ‘The breed is hardy and fattens more readily under ranching conditions than improved beef breeds’ and ‘The first cross of a European beef breed on [indigenous] or Afrikaner cattle is usually very successful; subsequent crosses are progressively less satisfactory and the amount of deterioration is often proportionate to the concentration of European blood’.

A trial was initiated at Matopos Research Station in 1938 to evaluate the effects of different breeding systems on the improvement of ranching cattle, where commercial (mainly Hereford-Afrikaner) and communal type cows were subjected to one of four mating systems: Afrikaner; Hereford; Afrikaner-Hereford crossbred and an Afrikaner-Hereford crisscross. It was reported that ‘the failure of the imported breeds to thrive on free range may largely be ascribed to the poor quality of winter grazing’ (Vorster, 1954) and ‘the greatest single problem facing the station is that of preventing winter loss of weight of livestock’ coupled with a low calving rate of around 60% and high mortality (Kennan, 1956). In a separate experiment Vorster (1964) reported that calving rate could be improved by 24% with the provision of supplementary feed in the dry season.

As a result the genotype x environment interaction study was initiated in 1956 ‘to determine to what extent the beef producing abilities of the grade Afrikaner cattle can be increased by selecting stock on their response to the local environment’ (Anon., 1955).

2.3 EXPERIMENTAL DESIGN

Two lines of 100 grade Afrikaner cows each were established, from a common gene pool, and subjected to different nutritional and management regimes, hereafter termed environments. In the supplemented (S) line cows were offered supplements during the dry season (9kg maize silage and 1kg cottonseed meal per head per day) and were mated to calve early (October to December) relative to the expected onset of the rains. In the non-supplemented (NS) line cows were mated to calve two months later than those in the supplemented line. In addition, two open herds of 25 pedigree cows each were maintained in both environments. While it is readily understood that supplementation afforded a relatively ‘early’ mating and calving season compared with non-supplementation, it is however important to note that both the effect of supplementation and the effect of time of calving are individually large ‘environmental effects’ and are totally confounded in this experiment and are therefore not possible to separate. In addition, routine practices such as castration, weaning, dosing and vaccinations were performed at fixed times in the year where calf age differed by approximately two months.

For the first eight years (1957 to 1964) six foundation sires were rotated among the lines (Table 2.1), thereafter the lines have been closed. However, the rotation was not uniform: bulls numbered 4, 5 and 9 were used for 3 to 6 years in the S environment, and only one year each in the NS environment. Similarly bulls numbered 6 and 11 were used for 3 to 4 years in the NS environment but only one year each in the S environment. Only bull numbered 2 was used for more than one year in both environments. A fixed mating season of 90 days and four single-sired herds of 25 cows each were used within each line. After 1964, three bulls were replaced each year and one was retained as a repeat sire. Selection for weight within line was to establish lines adapted to their respective environments and was based on weight at weaning for bulls and weight prior to mating (three years) for replacement heifers. In the pre-crossover phase, a total of five male calves were retained at weaning as potential replacement bulls, with at least one bull being selected from each mating herd in an attempt to maintain four sire families and reduce the effects of inbreeding.

Table 2.1 Rotation across the supplemented and non-supplemented lines of six foundation bulls (in bold italics) during the establishment of the line-environment interaction study with grade Afrikaner cattle (identity numbers less than six digits represent foundation animals)

	Cow herds							
	Supplemented lines				Non-supplemented lines			
Year	1	2	3	4	5	6	7	8
57	1	***2***	***4***	***5***	***6***	7	8	3
58	***9***	***5***	***2***	***4***	10	***6***	7	8
59	***5***	***6***	83	***2***	***9***	10	***4***	***11***
60	***11***	83	***5***	***9***	444	***2***	10	***6***
61	572040	***9***	83	***5***	***2***	444	***11***	10
62	83	572040	***5***	***9***	***11***	10	444	***2***
63	572040	572036	***9***	83	572003	***5***	***2***	444
64	602338	602362	572036	572040	602323	572003	602325	***6***

In the analysis of the first phase of the genotype x environment study (1957 to 1976) marked differences were observed between environments for all traits considered (Kinghorn *et al.*, 1978) (Table 2.2). Differences among the growth parameters for calves were largely due to their age – a function of the calving seasons. The performance of the grade and pedigree herds in the non-supplemented environment had much lower fertility rates than their grade counterparts. Productivity (weight of calf per cow exposed) largely reflected these fertility differences and the pedigree cows in the non-supplemented environment were the least productive (Table 2.2). Kinghorn *et al.* (1978) concluded that the non-supplemented 'pedigree cows were the least adapted of the four [groups]. Feeding ameliorated problems of adaptability in pedigree cows, whilst selection of animals within their respective environments was effective in increasing lifetime performance'.

Table 2.2 Performance of grade and pedigree Afrikaner cattle in supplemented and non-supplemented environments (1957-1976)

	Supplemented		Non-supplemented	
Trait	Grade	Pedigree	Grade	Pedigree
Weaning percent	78	73	67	60
Birth weight (kg)	33.6	32.6	30.9	30.7
Weaning weight (kg)	201	200	157	163
Heifer weight at 30 months (kg)	369	360	312	310
Weight of calf weaned/cow exposed/year (kg)	158	145	106	98

Source: Kinghorn *et al.* (1978)

From 1976 to 1978 the number of breeding females in each line was increased to 150 and two equal sub-lines were created (Figure 2.2). One sub-line remained within each environment as a control (S/S and NS/NS, leading symbol denotes selection line, trailing symbol environment post-crossover). The remaining sub-lines were interchanged between environments (S/NS and NS/S). Significantly, the supplementation regime in the supplemented environment was altered so that animals were offered 0.5kg of protein-rich concentrates per head per day during the dry season. In addition, the mating season was decreased to 65 days for the 1977 to 1982 matings, but subsequently reverted to 90 days.

Bulls were selected within the control sub-lines and were used within line across environments. Bull selection took place two weeks before weaning and in the post-crossover phase, six animals were selected with a proviso that not more than two animals would be selected from a particular cowherd. Candidates had to have reasonably well developed testes and sound animals were selected on weight linearly adjusted for age. From 1988 onwards selection criteria was based on weight adjusted for other known environmental factors, derived from a fixed effects model, which were line, environment, year of birth and age and previous lactation status of the dam (heifer, suckling or not suckling). Cows were mated in five single-sire herds of 15 cows each. Four bulls were replaced each year and one was retained as a repeat sire.

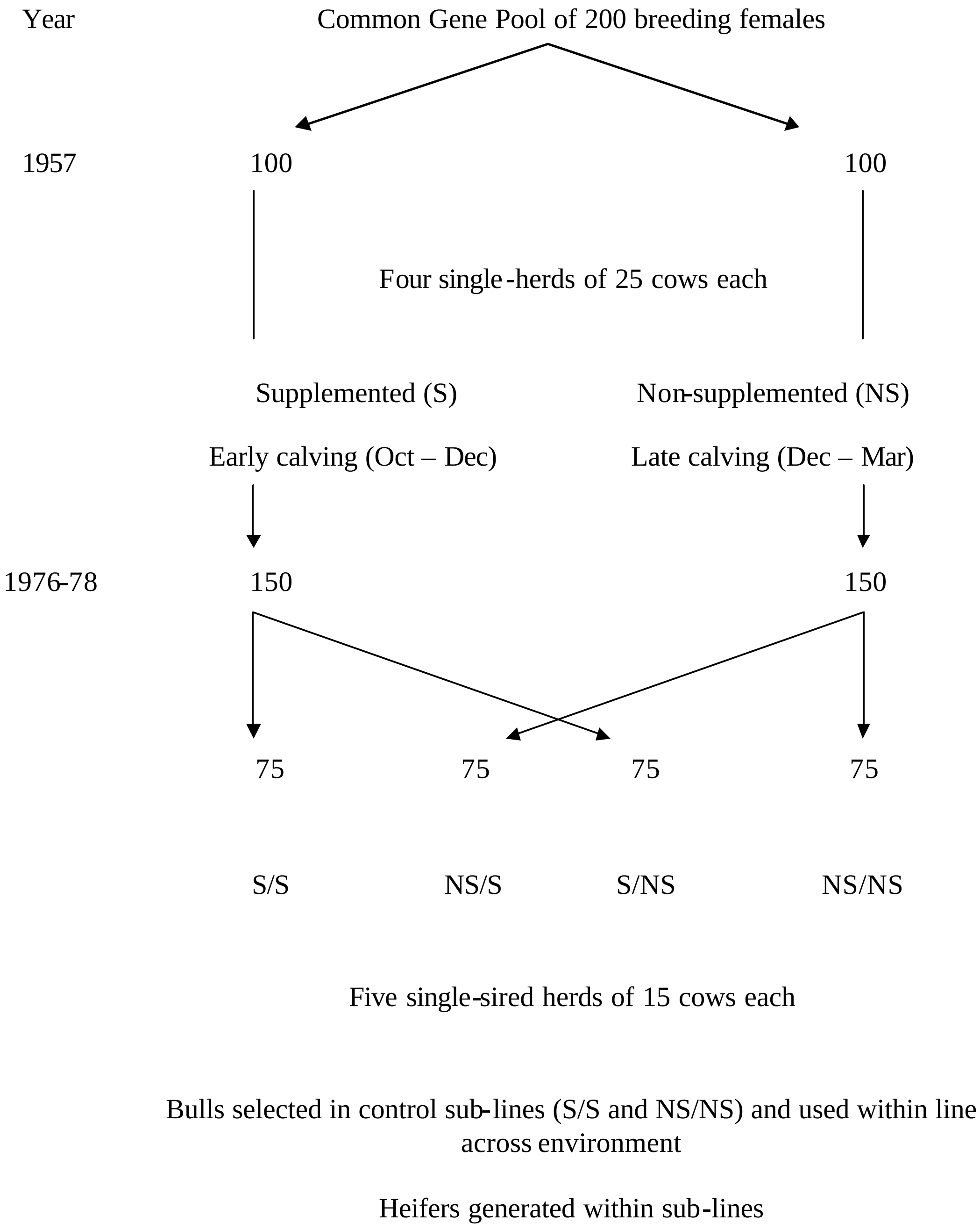


Figure 2.2 Schematic representation of the experimental design of the genotype-environment interaction study with grade Afrikaner cattle

Replacement heifers were generated within sub-lines and entered their respective mating groups at 27 months of age. Replacement rates were kept constant across sub-lines and were dictated by the sub-line with the least number of suitable replacement heifers. Only sound heifers weighing in excess of 265kg were deemed suitable and selection was based on weight linearly adjusted for age. Thus selection and culling intensities differed for the sub-lines. Cows were culled for poor production (infertility and low calf weaning weight). In the post crossover phase cows in excess of 12 years of age were generally not retained for breeding purposes. The allocation of sires and heifers to the mating herds was based on minimizing relationships as far as possible. It is important to note that after the crossover was implemented, only half the genetic material, i.e. sires, continued to be crossed over environments, while selection of heifer replacements within sub-line catered for any within sub-line adaptation.

2.4 ROUTINE MANAGEMENT PRACTICES

2.4.1 Grazing

The experimental site was subdivided into 35 paddocks and as far as possible lines were offered similar grazing. This was not always possible during the mating season (December to May) that necessitated 10 non-adjacent paddocks and was subject to water reticulation limitations particularly during droughts and borehole and water pump failures.

2.4.2 Calving

As cows displayed signs of approaching parturition they were moved from the large ‘dry season’ management herds and placed in a ‘calving’ paddock close to the homestead. All cows in this camp were checked daily and cow-calf pairs were rounded-up and taken to the handling facilities within 24 hours of birth. Calves were identified by means of ear notching and particulars, including weights, of the cow and calf were recorded.

2.4.3 Prophylaxis and tick control

All cattle were rounded-up and dipped in an acaricide plunge-dip once a week in the wet season and once every fortnight at the height of the dry-season, normally June through to August. All animals were annually vaccinated against rabies, anthrax, botulism and young animals were vaccinated against quarter-evil and contagious abortion (heifers). It was also recommended that young animals be treated for round worms and fluke at the beginning and end of the wet season (in October and in May).

2.4.4 Weighing, castration, and weaning

As a standard procedure cattle were individually weighed on a monthly basis. Up and until 1974 all weights were measured on a pounds scale. All male calves not retained for breeding purposes were castrated approximately two weeks before physical weaning in mid-August where calf ages ranged from four to seven months for the NS environment and from seven to ten months for the S environment.

2.5 DATA COLLATION AND EDITING

The data in the pre-crossover phase were manually recorded in large books, where the weights of an individual were captured on a single page from birth until the animal either rejoined the main breeding herd, in the case of breeding heifers and bulls, or was culled in the case of cull heifers and steers. This data had been captured on the railways computer, but the magnetic tape could not be located. However, a printout where weights had been converted to kilograms was available, which was then used to recapture the data.

The data in the post-crossover phase were recorded on large preprinted sheets that were bound for each year. This manual data was captured on computer into spreadsheets, where column totals were employed to check data entries.

Dates of calving were transformed to a standard calving date within year where the first of September was taken as one. As complete sets of dates for the bulling period in the pre-crossover phase were not available, the calving distribution within the early and late mating groups were scrutinized for obvious ‘out of season’ calves using Proc Univariate (SAS, 1985). Fourteen out of a total of 3775 calvings were deemed ‘out of season’ and deleted. This was based on the assumption that the bulling seasons were approximately 90 days and ranged from mid-December to mid-March and mid-February to mid-May for the S and NS environments respectively, together with a gestation interval ranging from 280 to 300 days. The calving pattern in the S environment indicated that the mating season extended beyond mid-March; there were however no obvious breaks in the distribution to assist in distinguishing ‘in’ and ‘out’ of season calvings. In the S environment, two records were deemed early and eight late, while in the NS environment one record was deemed early and three late, relative to the expected calving season.

Complete records detailing the start and end of the mating seasons were available for the post-crossover phase, and assuming a gestation interval of 280 to 300 days, 53 records out of a total of 4552 were deemed ‘out of season’ and deleted, where 44 records were ‘early’ in the late mated groups. In all instances, a cow was credited with calving in the season in question for early calves and was credited for calving in the next season for late born calves.

CHAPTER 3

NON-GENETIC FACTORS AFFECTING CALF GROWTH FROM BIRTH TO 18 MONTHS

3.1 INTRODUCTION

The influence of non-genetic factors on the growth of range beef calves has been very well documented for *Bos taurus* and *B. indicus* cattle in temperate and tropical environments and is reasonably well documented for Sanga cattle in the sub-tropics (see Moyo, 1990, for a comprehensive breed evaluation). While the need to accurately quantify these influences is obvious for their understanding, particularly in terms of management, it is of importance that these influences are appropriately accounted for in genetic analyses to remove any systematic biases.

Modern programmes and computing technologies now facilitate the application of complex mathematical models to data analyses on portable computers. Mixed model methodologies (Henderson, 1984), incorporating the numerator relationship matrix (NRM), facilitate the use of genetic linkages across contemporary groups to yield more accurate measures of both non-genetic factors as well as improved estimates of genetic parameters. Furthermore, the inclusion of the NRM allows for the accounting of genetic trends (Blair & Pollak, 1984). It is however, important to appreciate that these complex mathematical models are at best a crude attempt to model very complicated biological events that is subject to numerous non-systematic interacting factors and Henderson (1984) states ‘It seems to me that modeling is the most important and most difficult aspect of linear models applications’.

In addition to the standard factors typically influencing calf growth (such as herd-year-season, age of dam, sex and age of calf) the long calving season in the trial carried out at Matopos (September to February) poses additional challenges. The grazing season, reflecting rainfall, is the most important influence on cow fertility and calf growth. The inconsistent rainfall experienced within and across season at Matopos (Figure 2.1) as well as the variation in soil types on the experimental unit, renders it difficult to even define the 'start' of the grazing season, and as such was deemed outside the scope of this study.

In contrast to reports in the temperate regions, a number of reports in the sub-tropics and tropics have noted the significant influence of the previous lactation of the cow on calf growth (Hetzel *et al.*; 1989; Moyo, 1990). Authors have concluded that it is important to account for this factor in order to remove a systematic negative bias in the evaluation of the more productive cows.

The objective of the study was to quantify the nature of non-genetic factors influencing calf growth from birth to 18 months of age.

3.2 MATERIALS AND METHODS

The animals, experimental procedure, and general management thereof have been described in detail in Chapter 2.

3.2.1 Growth traits

The growth traits from birth to 18 months of age are summarized in Table 3.1. Typical measures of calf growth reported in the literature (weights at birth, weaning, yearling and 18 months) were analyzed. The effect of the prolonged calving season (September to February) on calf growth was studied by considering weights at 90, 150 and 205 days of age. The choice of 90 and 205-day weights correspond to standard measures in the industry, the former taken to be a measure of the dam's maternal ability, while the latter is typically referred to as weight at weaning. The measurement at 150 days was simply an intermediate point. Weight gains between birth and 205 days of age were also analyzed, as they were considered to be more sensitive indicators of environmental stress (grazing season relative to the birth date), bearing in mind that calves in the S and NS environments would obtain these ages at very different stages of the grazing season.

Table 3.1 Description of calf weight and weight gain traits

Abbreviation	Trait description
<u>Body weights, (kg):</u>	
BW	Weight within 24 hours of birth
W90, W150 and W205	Weights closest to 90, 150 and 205 days extracted from monthly weighings
WW	Weight recorded in July of each year approximately two weeks prior to castration and physical weaning
W12	Weight recorded in October at the end of the first dry season approximating one year of age
W18	Weight recorded May at the end of the second wet season when calf age was approximately 18 months
<u>Weight gains, (g/day)</u>	
G1, G2 and G3	Average daily gains between birth and W90, W90 and W150, and W150 and W205
ADG	Pre-weaning (birth to W205) average daily gain
EPWG	Early post-weaning gains to October (WW to W12)
PWG	Post-weaning (W12 to W18) average daily gain

Weights at 90, 150 and 205 days of age were extracted from the monthly weights where weighings occurred within 20 days of the target date. The actual age and month at weighing was also noted. Post-weaning, the weights in October and in May were extracted to define the start and end of the second grazing season. These weights approximated yearling and 18 month weights.

Pre-weaning gain was measured between birth and 205 days of age, rather than that between birth and physical weaning (July) due to the large difference in ages between the S and NS environments. Two measures of post-weaning gain were analyzed: weaning to October and October to May. The former was complicated by the fact that male calves were castrated in addition to the physical effect of weaning, where presumably the reliance on milk by the calves in the S and NS environments differed. Furthermore, cattle generally maintain or lose weight in the period from ‘late’ winter (July to August) to ‘early’ summer (September to October).

Growth traits were also scrutinized within year and mating season for obvious outliers. In the pre-crossover phase, the 90 day weights and weight gains from birth to 90 days of eight calves in the early-mated group and six calves in the late-mated group were discarded where only weights at birth and in the month of January were available. Pre-weaning weights and weight gains for a further five calves in the late-mated group were discarded where gains were less than 3kg per month and in most instances the calf died before weaning. A total of 31 pre-weaning weights and weight gains for calves in the post-crossover phase were discarded, 25 of which died before weaning. The post-weaning growth patterns of six calves in the post-crossover phase were exceptionally poor resulting in the discarding of three yearling and three 18-month weights.

3.2.2 Fixed effects

In preliminary analyses, year of birth was the most important factor accounting for the greatest proportion of total variation in the growth traits. However, significant two- and three-way interactions were expressed with most other fixed effects considered. Furthermore, in terms of the accounting for variation in the observed values, the interaction between environment and year of birth was the most important; bearing in mind that ‘environment’ refers to supplemented and early calving versus non-supplemented and late calving. Procedures below describe methods used to account for fixed effects while taking into account the interactions.

3.2.2.1 Line-year of birth -environment

It was neither practical nor feasible to account for all interactions with year of birth. The interaction of year with environment was typically the most important, and in an attempt to accommodate line x year interactions, a concatenation of line-year-environment (LYE) classification was employed in the analyses of the growth traits from birth to 18 months of age.

3.2.2.2 Sex

For all the traits, only two classes of sex were considered. Pre-weaning, these were entire male versus female and post-weaning, just after castration, these were steer versus heifer. Data of bull calves post-weaning were excluded from analyses.

3.2.2.3 Age of dam and previous lactation status

In the pre-crossover phase, age of dam ranged from 4 to 17 years in the S line and from 4 to 16 years in the NS line, apart for 1975 and 1976 matings in the S line where heifers were mated to calve as three-year-olds. In both lines, the number of observations for cows older than 12 years was less than 8% for number of matings, less than 4% for number of births and more than 80% of year-age of dam classes had less than five observations. In the post-crossover phase, age of dam ranged from 3 to 14 years and less than 2% of the observations were of cows older than 12 years of age.

While preliminary analyses revealed that age of dam (in years) included both as linear and quadratic covariates or as a class model accounted for a similar proportion of the total variance in the observed values, the covariate did not cater for the confounding with cow lactation status of heifers in the previous season. Furthermore, previous lactation status (PLS) tended to interact with age of dam, the effect of PLS being greatest for young (<5 years) and old (>10 years) cows. In order to account for the interaction as well as confounding of heifer with PLS status, a class model concatenating three classes for PLS (0 for three year old heifers; 1 for cows not suckling in the previous season; and 2 for cows that had suckled a calf at least up to and until the calf had attained 90 days of age) with five age of dam classes (3, 4, 5 to 7, 8 to 10 and >10 years of age) was employed (see Table 3.2).

Table 3.2 Class model used combining age of dam and previous lactation status

		Age of dam (years)				
Previous lactation status		3	4	5 to 7	8 to 10	>10
0	Heifer	v				
1	Not suckling		v	v	v	v
2	Suckling		v	v	v	v

Heifers calving for the first time as four-year-olds (in the pre-crossover phase) were classified as not having suckled in the previous season (i.e. PLS=1). Age of dam classes were derived after perusal of the least squares means for the various traits, where it was found that the performance of cows between 5 and 7 and between 8 and 10 years of age were similar. While the performance of cows older than 10 years generally declined with increasing age, only one class, that of older than 10 years, was accommodated after taking into account that only 4% of the observations were due to cows being older than 12 years of age.

3.2.2.4 Birth date

With a long calving season extending 150 days across the two environments (October to February), it was not surprising to find important effects due to birth date (BD, relative to a base date of 1st September) in preliminary analyses. Given the vagaries of the rainfall season and therefore grazing season it was deemed inappropriate to account for month of birth as a cross-classified effect. A model where month of birth was nested within year would be partially confounded with environment. It was also not possible to treat BD as a simple covariate due to the partial confounding with the environment as well as significant interactions with year of birth. As the environment effect was accounted for by fitting a line-year-environment class model, the effects of BD were accounted for by its inclusion as a cross-classified covariate regressed from the year-environment subclass means. Therefore, it was assumed that BD did not interact with other fixed effects, in particular with environment.

3.2.2.5 Age of calf

Calf age for weights taken at a fixed time in the year (e.g., WW, W12 and W18) and birth date was totally confounded. However, for weights at 90, 150 and 205 days derived from monthly weighings, age deviated from the target date was included in the analyses.

3.2.3 Fixed effects models

The following model was employed for the analyses of fixed effects of growth traits (SAS, 1985):

$$Y_{ijkl} = \mu + LYE_i + S_j + A_k + ß_1(BD_{ijkl} - \overline{X}_{YE}) + ß_2(BD_{ijkl} - \overline{X}_{YE})^2 + ß_3(Age_{ijkl} - \overline{X}_t) + e_{ijkl}$$

where: Y_{ijkl} is the vector of observations;

μ is the overall mean;

LYE_i is the effect of i^{th} line-year-environment class (i=1 to 122) for all traits except W18 and PWG where i=1 to 116;

S_j is the effect of j^{th} sex class (j=1 to 2);

A_k is the effect of k^{th} age-of-dam – previous lactation status class (k=1 to 9);

$ß_1$, $ß_2$ and $ß_3$ are the regression coefficients of the covariable on the observation;

$(BD_{ijkl} - \overline{X}_{YE})$ and $(BD_{ijkl} - \overline{X}_{YE})^2$ are the linear and quadratic effect of the birth date deviated from the year-environment subclass mean;

$(Age_{ijkl} - \overline{X}_t)$ is the linear effect of calf age deviated from target date for W90, W150 and W205 only; and

e_{ijkl} is the error term.

Mixed model procedures (MTDFREML; Boldman *et al.*, 1995) allowing for the inclusion of random components were used to derive best linear unbiased estimates (BLUE) of the various fixed effects, regression coefficients, and specific contrasts together with their respective standard errors. The model, incorporating the fixed effects as described above, allowed for the inclusion of direct and maternal genetic random effects as well as their correlation and permanent environmental random effects due to repeated measures on the dam (discussed in greater detail in Chapter 4). Boldman *et al.* (1995) describe procedures for the calculation of contrasts, sampling variances and solutions for the fixed effects.

3.3 RESULTS AND DISCUSSION

The number of observations, means and standard deviations of the weights and weight gains after editing are presented in Table 3.3. The coefficients of variation (CV) for weights at birth, 90, 150, and 205 days were within the range of 15-17%. However, the CV for weights at weaning and 12 months were 20%, presumably reflecting the differences between environments, in particular differences in age. Despite these differences, the CV for W18 had reverted back to 15%. Of importance were the large CV for weight gains, which increased with age from 19% for gain between 0 and 90 days to 52% for gain between 150 and 205 days. The similar performance of the Afrikaner across a range of environments is remarkable (Table 1.2) and could be referred to as a stable genotype as opposed to a plastic genotype where the degree of phenotypic expression of a genotype varies under different environmental conditions (Bryant *et al.*, 2004).

Perusal of the line means (Figures 3.1 & 3.2; Appendix 1 & 2) reveal markedly different response of calves to environment post 90 days. Calves in the S environment gained weight at 530 g/day between 150 and 205 days compared with 320g/day for calves in the NS environment (Figure 3.2b). Post-weaning, calves barely gained weight (<2kg) between July and October (EPWG: 28g/day; Table 3.3). Calves showed similar post-weaning weight gains across lines and environments in the post-crossover period. However, in the pre-crossover phase, gains tended to be lower and there were large line differences in certain years (Figure 3.2c), presumably reflecting different management practices.

Table 3.3 Number of observations, means, standard deviations (SD) and coefficients of variation (CV) for calf growth

Variable	Number	Mean	SD	CV, %
Birth weight (kg)	6818	32.1	4.89	15.2
90-day weight (kg)	6393	103	16.5	16.0
150-day weight (kg)	6406	144	22.4	15.6
205-day weight (kg)	6384	168	28.5	17.0
Weaning weight (kg)	6386	173	34.9	20.2
Age at weaning (days)		225	35.4	
12-month weight (kg)	5897	175	34.4	19.7
Age at 12-month weighing (days)		318	35.7	
18-month weight (kg)	5401	269	40.8	15.2
Age at 18-month weighing (days)		529	35.6	
Gain 0 to 90 days (g/day)	6341	783	151.6	19.4
Gain 90 to 150 days (g/day)	6338	691	205.3	29.7
Gain 150 to 205 days (g/day)	6382	437	228.6	52.3
Pre-weaning gain (g/day)	6330	663	135.2	20.4
Early post-weaning gain (g/day)	5895	28	129.7	-
Post-weaning gain (g/day)	5393	451	102.1	22.6

- not estimated due to presence of negative growth rates.

The total variation in the observed values accounted for by the fixed effect models for the growth traits tended to increase with age and varied from 25 to 64% (Appendix 3). The effect of LYE was the most important effect accounting for 14 to 44% of the total variation and between 38 and 86% of variation accounted for by the models. The magnitude of the effect is clearly illustrated in a sample of the yearly trends for the various traits (Figures 3.1 & 3.2) that shows the tremendous year-to-year variations as well as the large environmental effect and the interaction of year x environment.

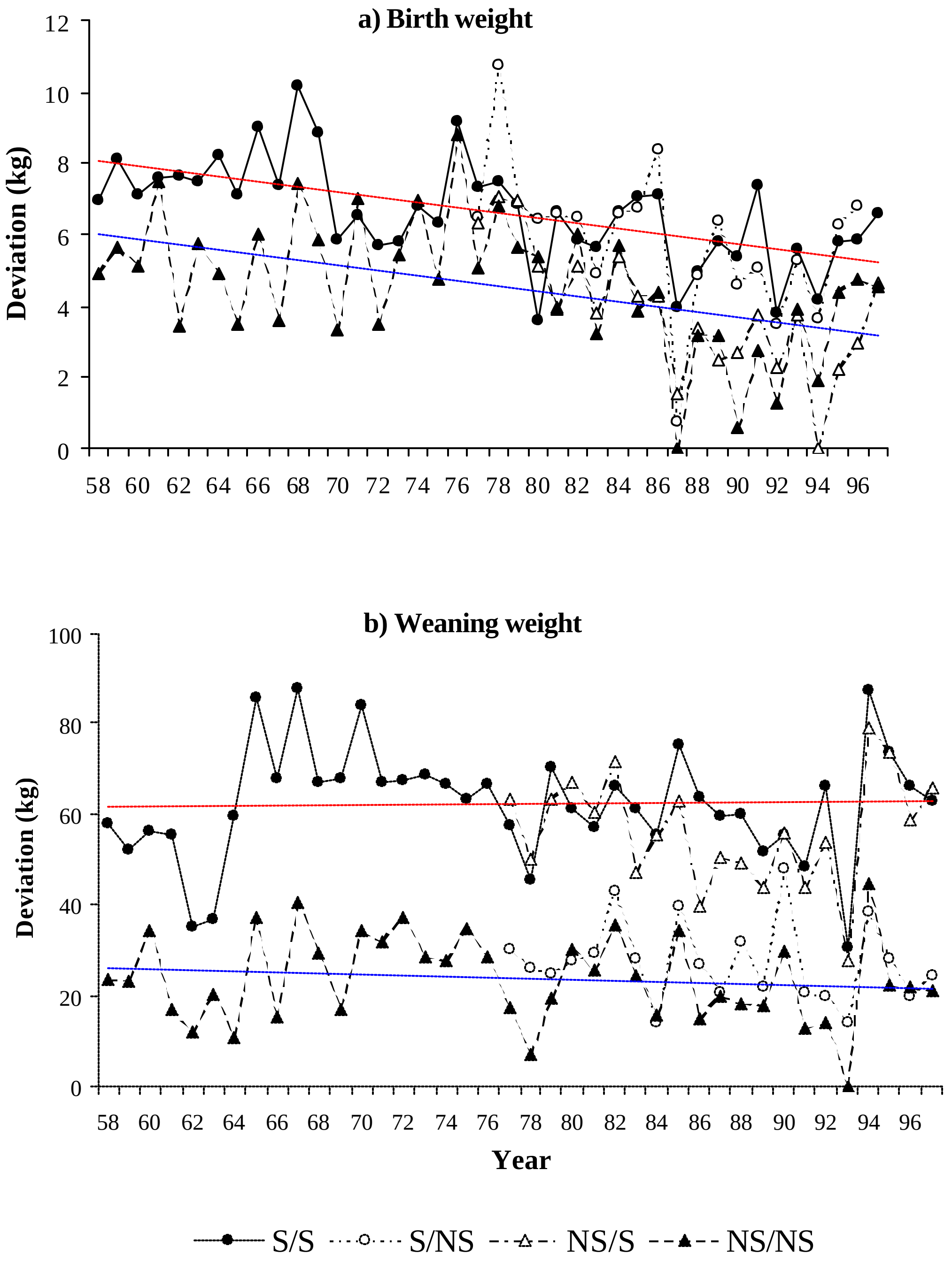


Figure 3.1 Yearly trends for weights at a) birth and b) at weaning (deviated from lowest class mean)

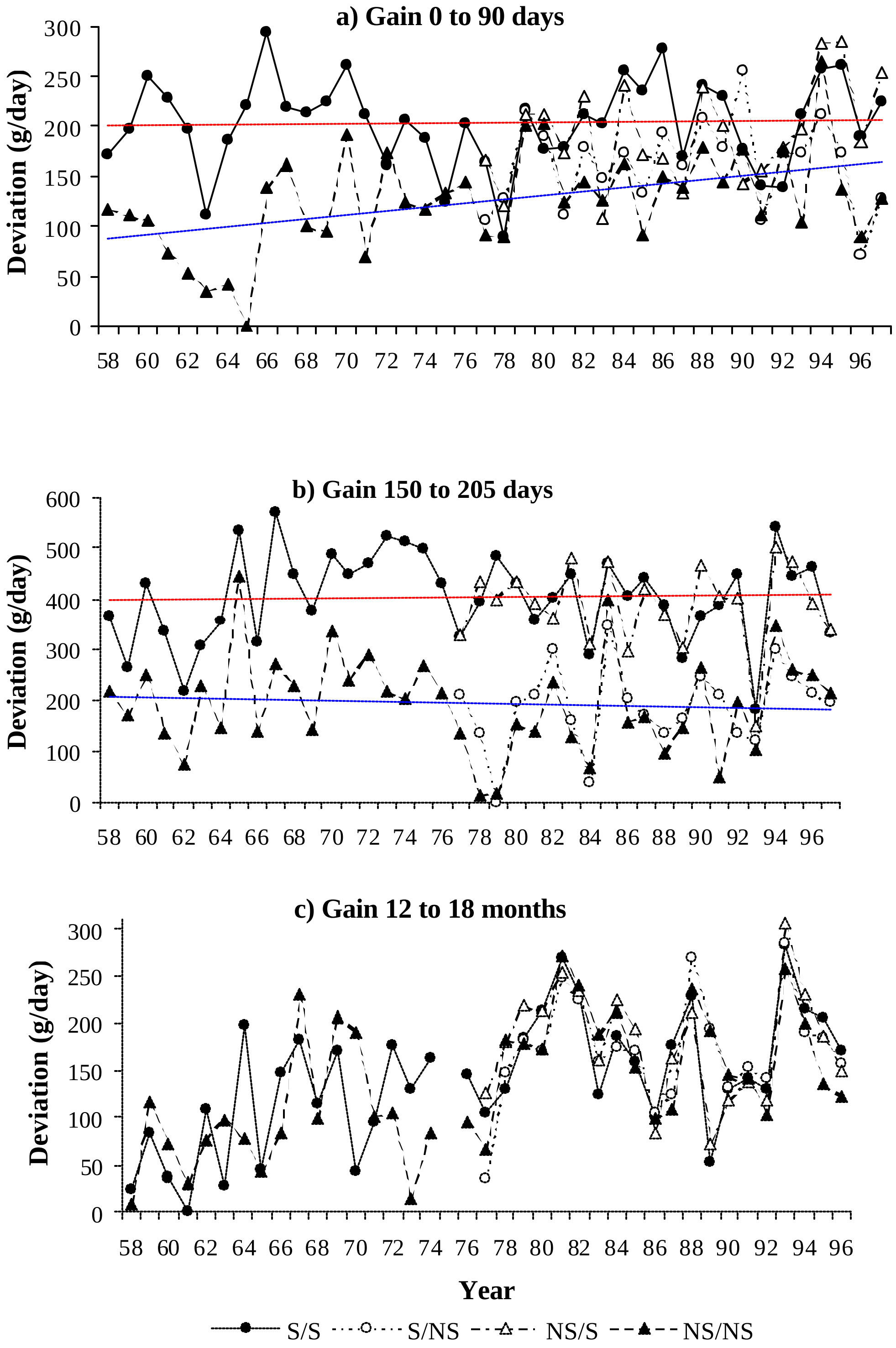


Figure 3.2 Yearly trends for pre-weaning gains between a) birth and 90 days, b) 150 and 205 days and c) 12 and 18 months of age (deviated from lowest class mean)

The large year-to-year variations are consistent with findings from other studies in the region (Baker *et al*., 1991; MacNeil *et al*., 1992; Rege & Moyo, 1993; van der Westhuizen, 1997). Point estimates of the effects of line and environment, derived from contrasts of BLUE solutions of the LYE effect, are shown in Figure 3.3. Calves from the S line had small but consistently greater weights and weight gains than their NS counterparts.

While there was no apparent environmental effect for BW, calves born in the S environment had a distinct advantage to calves born in the NS environment that increased with age. The effect was marked for weight gains between 150 and 205 days where weight gains of calves in the S environment were 212g/day greater than those of their NS contemporaries. On average, calves in the NS environment would attain 150 days of age in June, which is well into the dry season. At this time, grazing quality and quantity would be limiting and would presumably have a marked impact on the dam's ability to nurse its young calf. At weaning, calves from the S environment were 34kg heavier (Figures 3.1 and 3.3), a difference that persisted to 18 months. Part of this difference is also due to the difference in age between environments of 53 days. The sub-line means post-crossover did not indicate the presence of genotype x environment interactions (Figures 3.1 & 3.2; Appendix 1 & 2).

While the effects of BD (linear and quadratic covariates) accounted for 4.6% of the total variation for BW, BD only accounted for 0.7% of variation for W90, which increased to 10.3% for WW (Appendix 3). The effect of BD persisted, as calves grew older and accounted for 6.5% of the total variation for W18. Similarly, BD accounted for only 0.7% of the total variation for G1, but this increased to 7 to 9% for G2, G3 and ADG, before declining to 0.7% for PWG.

With a calving season extending over 100 days within environment it was not surprising to note the dramatic influence of birth date on growth traits (Figure 3.3 & 3.4; Appendix 4). The estimated effect of BD for a calf born early in the season versus one born late is graphically illustrated in Figure 3.3. Late born calves were on average 4kg heavier than early born calves. The increase in birth weight as the season progresses has been attributed to the improved grazing conditions with the onset of the rains (Carvalheira *et al*, 1995).

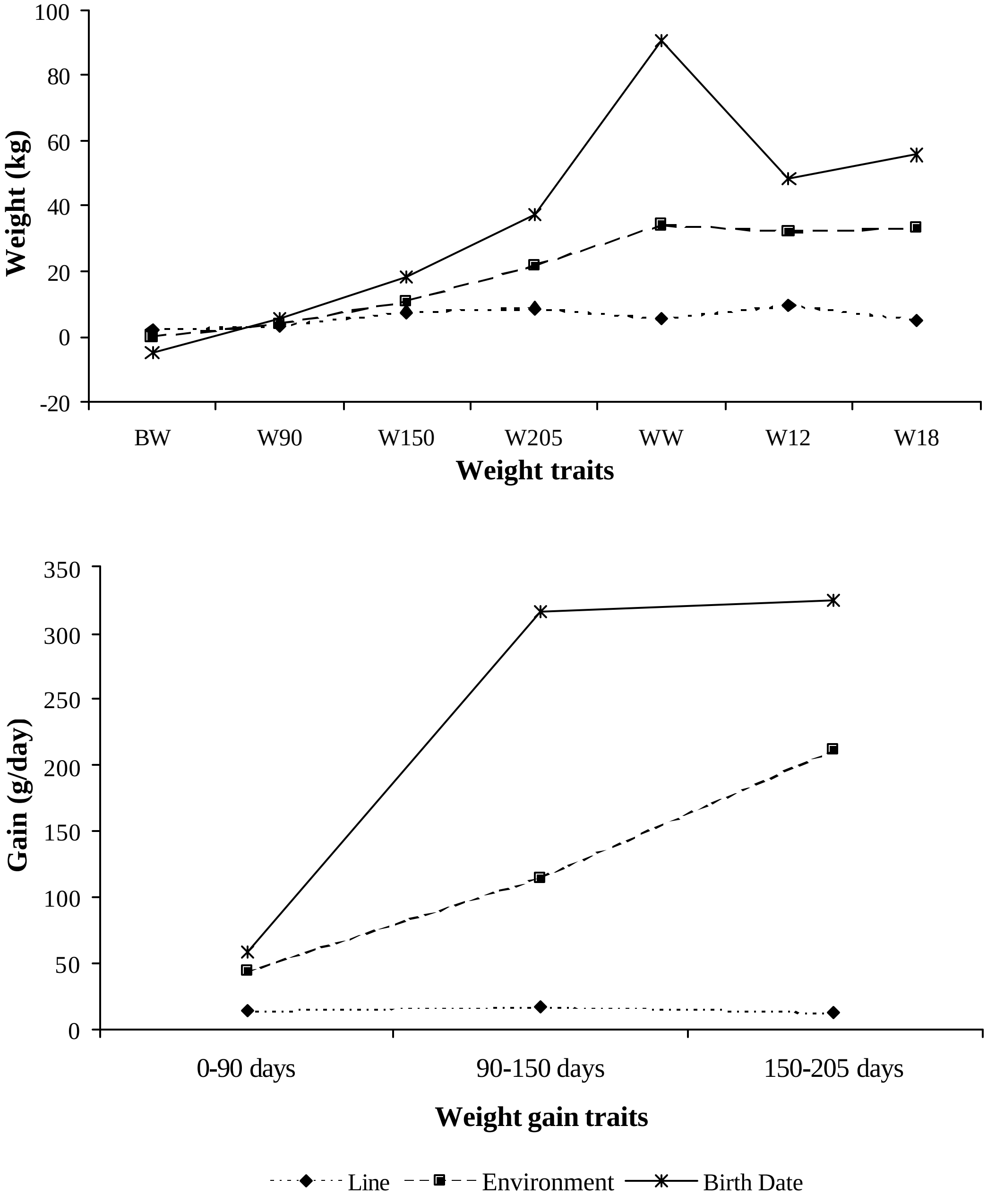


Figure 3.3 Effect of line and environment (performance of NS deviated from S) and effect of birth date (born at start of season compared with born 100 days later) on weights and weight gains

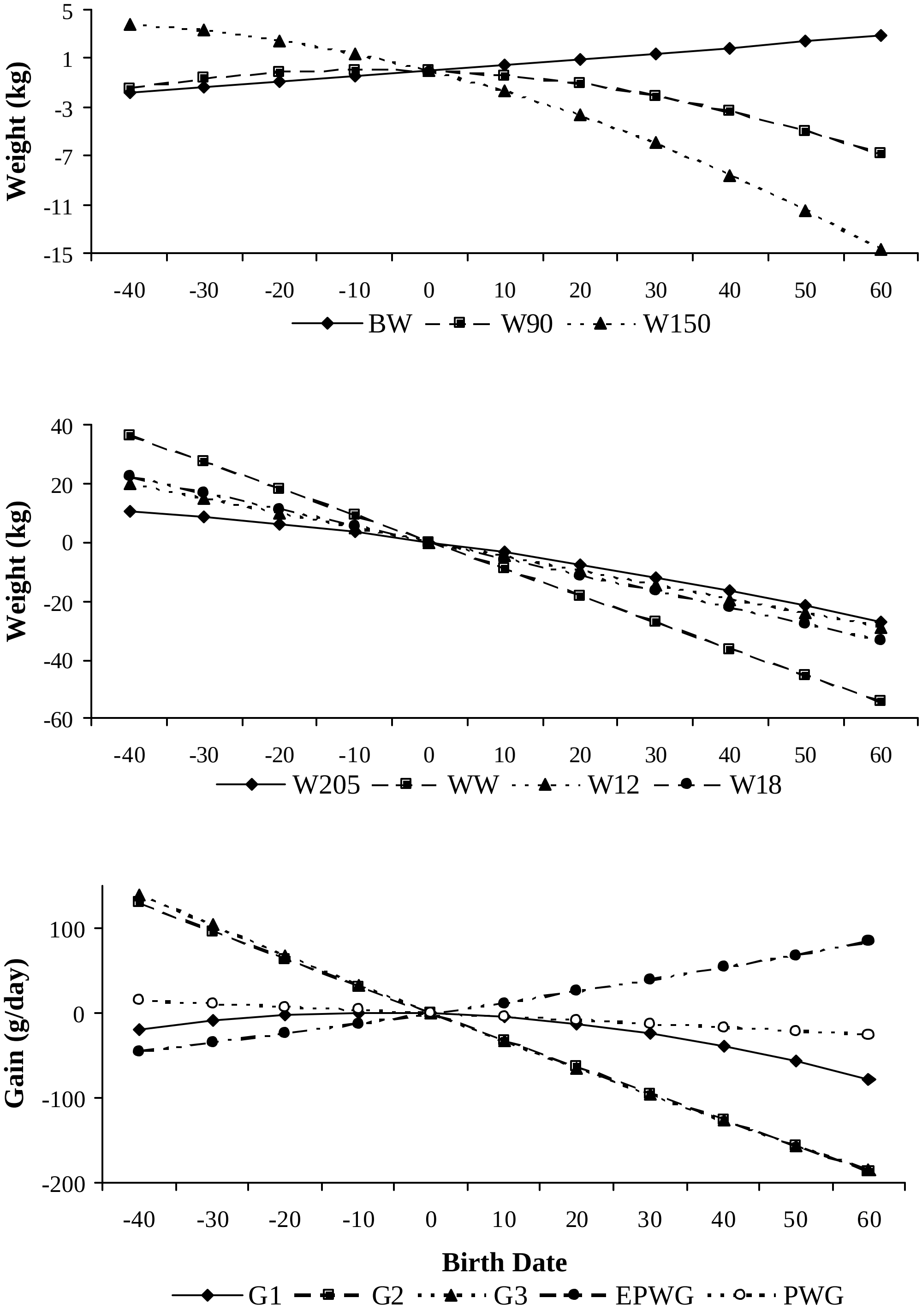


Figure 3.4 Linear and quadratic effects of date of birth on calf weights and weight gains (see Table 3.1 for trait definitions)

Birth date appeared to have a minor effect on weights at 90 days and weight gains from birth to 90 days of up to 5kg or 60g/day. The effect on weights at 150 and 205 days and the weight gains between 90 and 205 days (G2 and G3) were, however, pronounced, affecting weights and weight gains by up to 40kg or 325g/day. The effect of birth date on weaning weight was dramatic with early born calves being up to 90kg heavier than their late born contemporaries. In a study of Mashona cattle, Buvanendran (1990) also found that later born calves were significantly lighter (1 to 9%) than early born calves. Similarly, Niemann & Heydenrych (1965: cited de Waal, 1990) found that weight at weaning decreased by 2.86kg/week for calves born after 1st October.

While late born calves showed compensatory gains immediately post-weaning (EPWG), birth date did not appear to influence PWG, but the effect of birth date persisted up to 18 months and was of the order of 56kg (Figure 3.4). Rege & Moyo (1993) also noted that the effect of delayed BD of calf was more apparent at older ages and was attributed to a declining maternal influence.

The analysis within line indicated that the covariate of birth date did interact with environment for BW, W90, G1 and PWG (Figure 3.5), but the effect of the covariate was remarkably constant across environment for all the other growth traits. While BW increased as the season progressed from late September to December, BW did not increase for calves born in January and February. Calves born early in the season in the S environment were as equally disadvantaged as late born calves and possibly reflect the increased stress of lactation placed on cows calving when the grazing conditions are poorest (September and October). While birth date did not appear to affect PWG of calves in the S environment, birth date continued to exert a detrimental effect on PWG of calves in the NS environment.

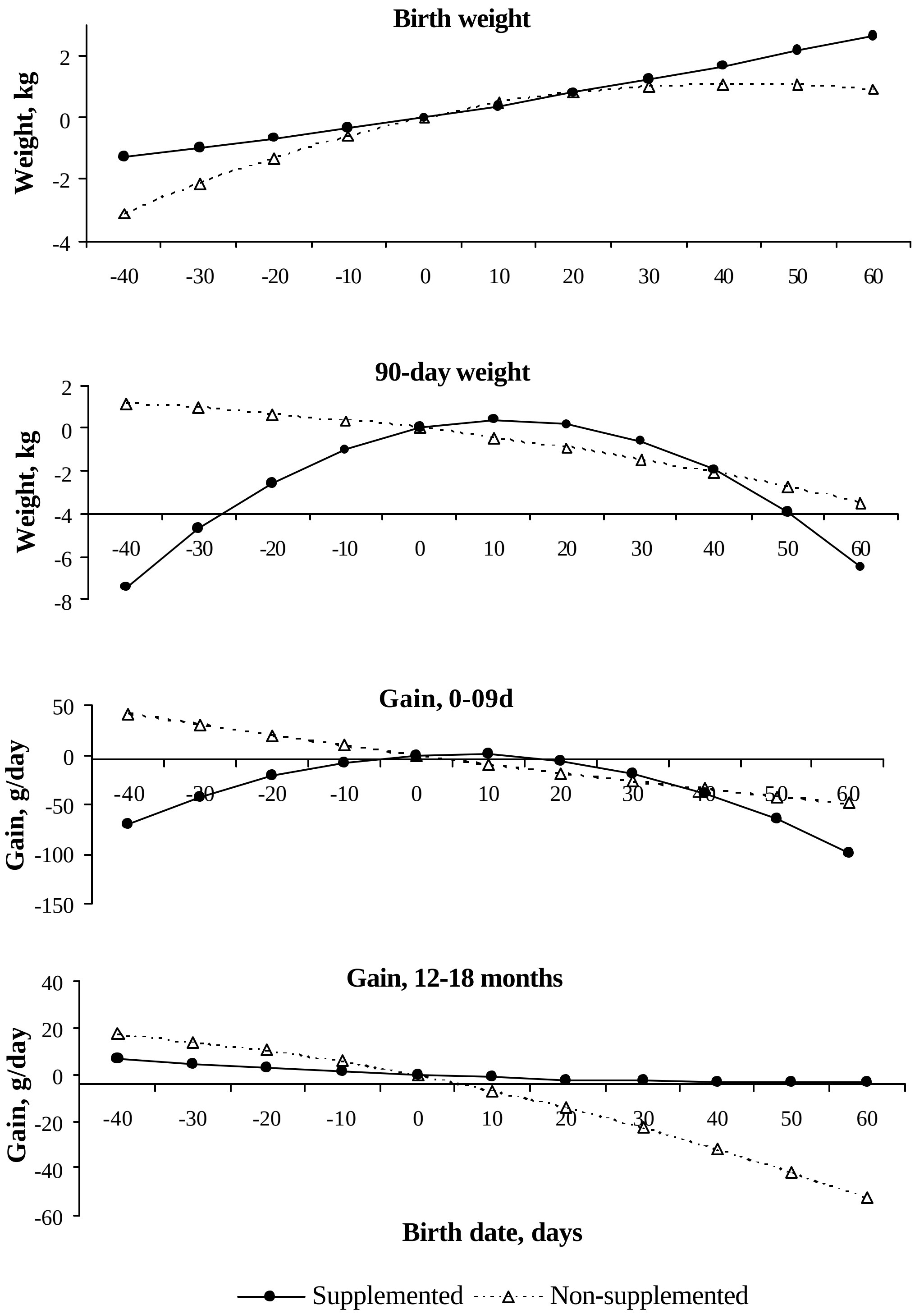


Figure 3.5 Effect of birth date on growth traits determined from analysis within supplemented and non-supplemented environments

The combined effects of environment and birth date imply that performance of calves born late in the NS environment are at a great disadvantage compared with calves born early in the S environment; a disadvantage that persists at least until the end of the second grazing season and is estimated to be in the order of 90kg for 18-month weight (Figure 3.3). The persistent effect of late calving on growth post-weaning has been found in numerous other studies. However, among Nguni calves in the lowveld, Tawonezvi *et al.* (1986) reported that late born calves grew faster and maintained that advantage to 18 months of age. This differential response was ascribed to the different production environments.

The effect of sex was fairly consistent and accounted for 3 to 6% of the total variation, except for G3 and ADG where sex only accounted for 0.5% and 0.3% respectively (Appendix 4). Male (entire pre-weaning and steers post-weaning) were consistently 7% heavier from birth through to 18 months. Similar effects due to sex of calf have been reported with sanga cattle (Tawonezvi, 1989; Buvanendren, 1990; Carvalheira *et al.*, 1995; van der Westhuizen, 1997), in contrast to larger effects (10 to 13%) shown for *Bos taurus* cattle breeds in temperate regions.

The effect of age of dam and PLS tended to decrease as calves grew older and accounted for 5% of total variation in pre-weaning traits, but only 0.2% for PWG (Appendix 3). The effect of PLS increased from 1kg at birth to 6kg at 150 days of age, a difference that persisted to 18 months (Appendix 4). The effect of PLS was important for pre-weaning gains, but was small and reversed for post-weaning gains. The consistent effect of age of dam and previous lactation status on weights from birth to 18 months and on pre-weaning weight gains is well illustrated in Figures 3.6 and 3.7. Weights and weight gains increased with age of dam and peaked for 5 to 7 year-old dams before decreasing for older dams, while the effect of PLS tended to be least for calves from 5 to 7 year-old dams. However, compensatory gains were shown for the two post-weaning weight gain traits (Figure 3.7).

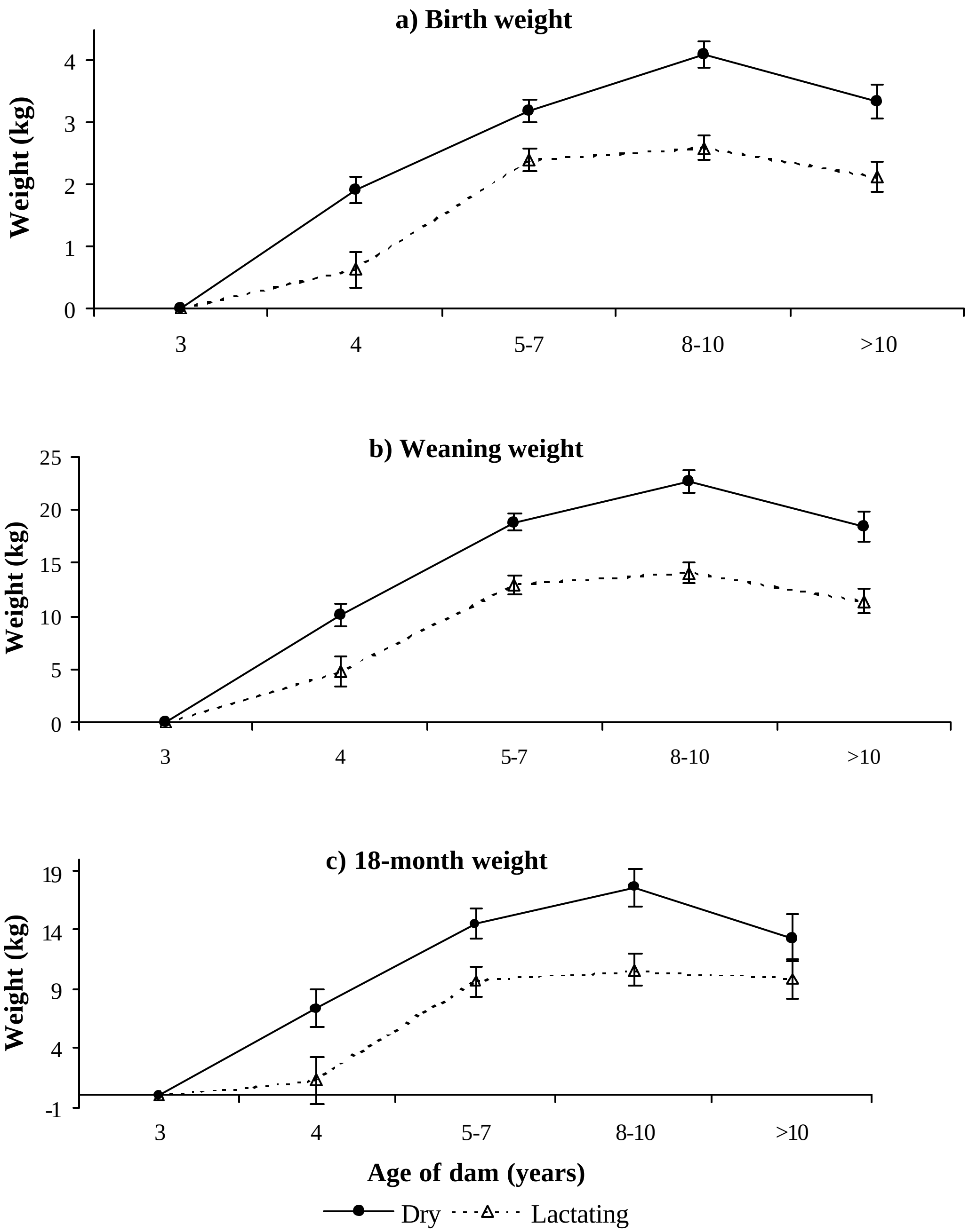


Figure 3.6 Effect of dam age and previous lactation status on a) weights at birth, b) weaning, and c) 18 months (vertical lines about the means denote standard errors)

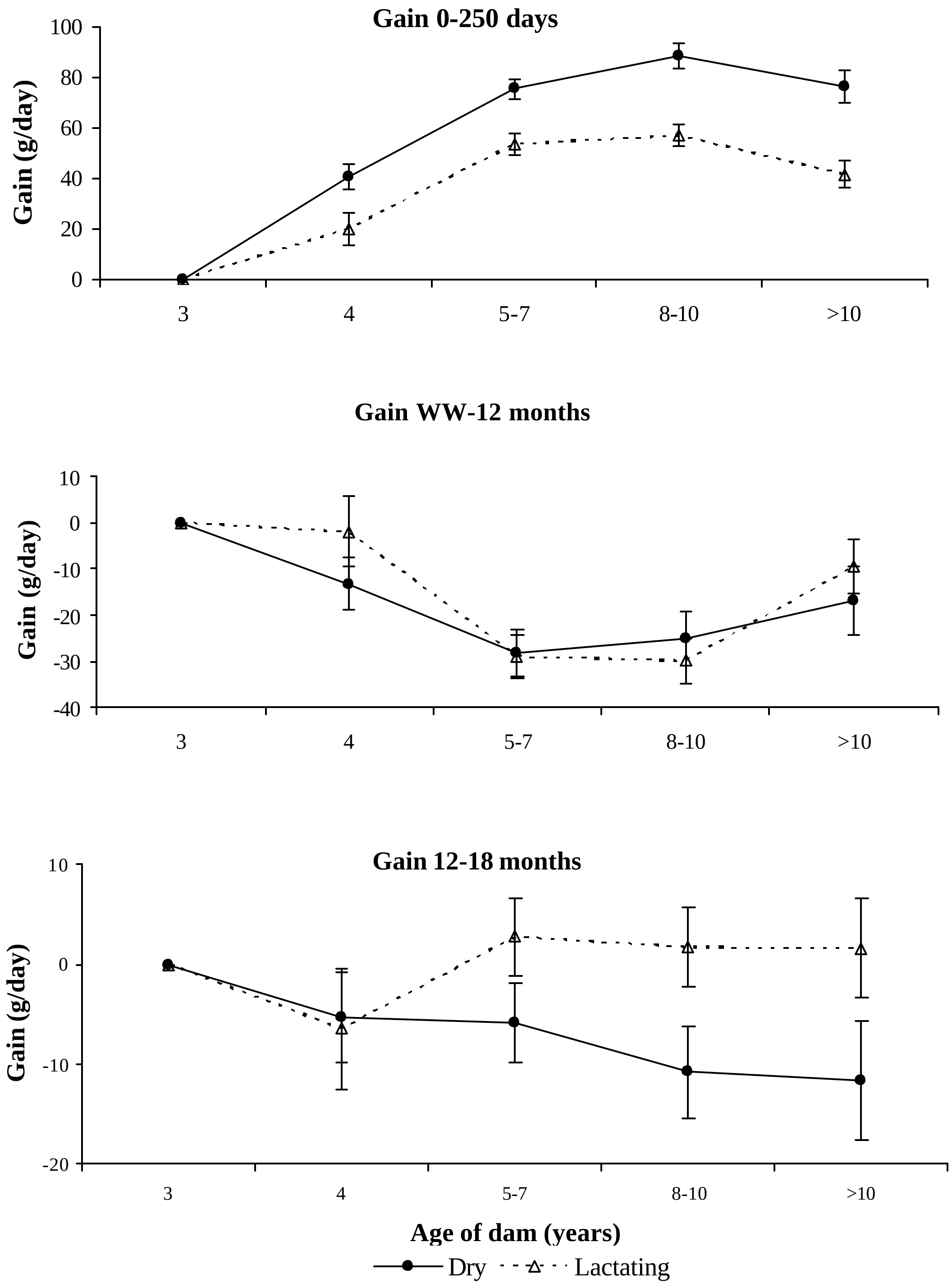


Figure 3.7 Effect of dam age and previous lactation status on pre- and post-weaning weight gains (vertical lines about the means denote standard errors)

The analysis within environment did not reveal evidence to support the assumption that cows in the NS environment were under greater stress to provide milk for their calves, particularly between 150 and 205 days of age (Figure 3.8) as portrayed by the dramatic difference between environments for weights and weight gains (Figures 3.1, 3.2 and 3.3).

Similar effects due to previous lactation have been reported where the larger effect found in young cows was attributed to the extra nutrient requirements for growth (Vorster, 1964; Thorpe, *et al.* 1980; Tawonezvi *et al.*, 1986; Hetzel *et al.*, 1989; Tawonezvi, 1989). Hetzel *et al.* (1990) found that the effects of PLS were highest in Hereford-Shorthorn, intermediate in Afrikaner cross and lowest in Brahman cross, with the authors concluding that the magnitude of maternal dam age and PLS effects were inversely proportional to the level of tropical adaptation of the genotypes. The persistent effects of both age and previous lactation status of dam post-weaning concurs with some studies (Tawonezvi *et al.*, 1986; MacKinnon *et al.*, 1990; Moyo 1990; Rege & Moyo, 1993), others show compensatory gains (Vorster, 1964; Tawonezvi, 1989) and Hetzel *et al.* (1990) found no carry-over effects. In contrast, in an experiment with Afrikaner calves in Mozambique, Carvalheira *et al.* (1995) only found an effect of PLS at birth.

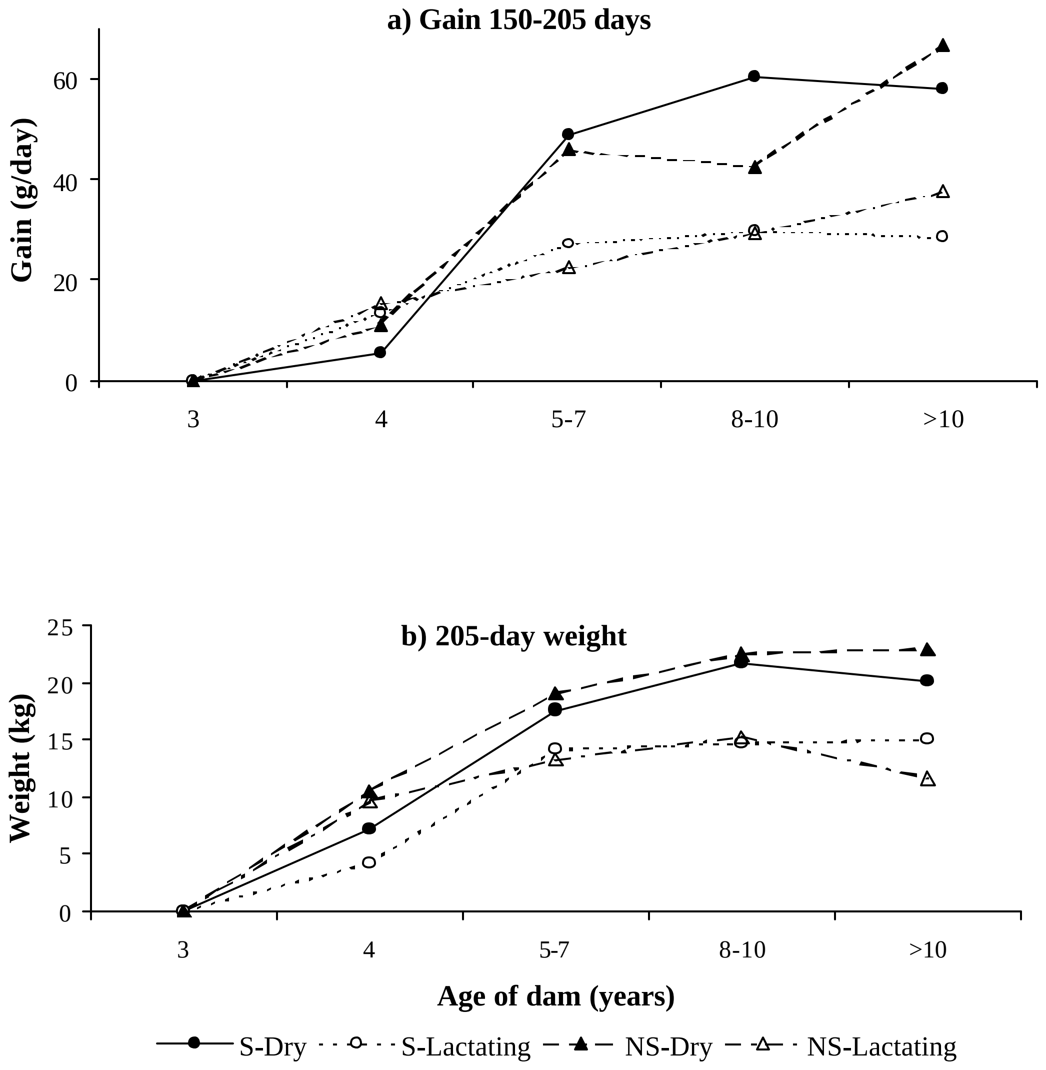


Figure 3.8 Effect of dam age and previous lactation status on a) pre-weaning weight gain and b) weight at 205 days within line supplemented (S) and non-supplemented (NS) lines

3.4 CONCLUSIONS

The remarkable stability of the performance of the Afrikaner across production environments is probably related to many generations of selection under harsh environmental conditions. While the Afrikaner is not suited to intensive production systems, the popularity of recent (less stable genotypes) has regrettably led to the demise of the Afrikaner in Zimbabwe, even in the extensive production areas.

It is important to appreciate the dramatic differences in production environment both within and across seasons in the sub-tropics. This is determined by the quantity and distribution of rainfall and the effect is well illustrated by the extremely large seasonal (early vs. late calving) and yearly variation in calf growth (Figures 3.1 & 3.2). The analysis of performance data in such environments is complicated by the variations within season and the prolonged calving seasons.

The performance of calf growth from birth to 18 months in this study has emphasized the importance of matching animal physiological status with seasonal changes in the sub-tropics (de Waal, 1990). Late born (February) calves had markedly poorer growth compared with their early (October) born contemporaries and were 33% lighter at the end of their second growing season (at 18 months). The effect of late calving has been reported to be detrimental to subsequent reproductive performance (Lesmeister *et al.*, 1973; Steenkamp & Pretorius, 1976; Buck & Light, 1982)

The effects of previous lactation status of the cow on calf growth concur with findings from sub-tropical and tropical production environments. Routine evaluations need to consider this factor to avoid penalizing calves from more productive cows, particularly where the proportion of previously dry cows is high due to poor reproduction performance.

CHAPTER 4

GENETIC PARAMETERS, SELECTION RESPONSE AND GENOTYPE X ENVIRONMENT INTERACTION OF CALF GROWTH TRAITS FROM BIRTH TO 18 MONTHS

4.1 INTRODUCTION

Accurate estimates of genetic parameters are essential for the design and implementation of efficient genetic improvement programmes. There are numerous genetic parameter estimates for *Bos taurus* and *B. indicus* breeds in temperate and tropical environments (review Koots *et al.*, 1994). However, estimates for Sanga cattle in sub-tropical environments are scarce, particularly from reasonably large data sets using the current commonly adopted mixed model and REML (restricted maximum likelihood) procedures described by Henderson (1984).

Estimates of variances and covariances of cattle in the tropics and sub-tropics have, in general, been similar to those in temperate environments (van der Westhuizen, 1997; Groeneveld *et al*., 1998; Mostert *et al*., 1998). Some studies have, however, reported differences between these regions (Hetzel *et al*., 1990) and Meyer (1994) reported that the genetic determinants of growth at various ages were more diverse in the tropics. The large year-to-year and within season environmental variation experienced in the sub-tropics (mainly as a result of variable quantity and distribution of rainfall) may give rise to 'random' sire x year interactions (Notter & Hohenboken, 1990), posing additional difficulties in the identification and selection of superior individuals to be parents for future production (Frisch, 1981; Vercoe & Frisch, 1988; 1992).

Falconer (1952; 1960) proposed that the calculation of the genetic correlation between two traits can be extended to the genetic correlation of a trait measured in two environments, where it is treated as two different traits. A genetic correlation of unity would imply the absence of an interaction, while a genetic correlation less than 0.8 is indicative of the presence of an interaction of biological and agricultural importance (Robertson, 1959). In a review of methodologies for the estimation of genotype x environment interactions, Cameron (1993) reported that 'genetic variances and covariances estimated using bivariate REML methodology result in unbiased estimates of the genetic correlation, which is a measure of the genotype with environment interaction', while Mathur (2002) states 'It seems more appropriate to use the multivariate approach to estimate the genetic correlation for each pair of environments to evaluate the significance of the interactions on breeding programmes'.

Veerkamp *et al.* (1994) did not find evidence of interactions between feeding system and genetic line for a number of traits in dairy cattle and concluded that interactions of this nature were unlikely to be important given the range of feeding levels in the UK. Cromie *et al.* (1998) concluded that there appears to be little evidence of serious re-ranking of bulls with regard to milk, fat and protein yield. There was however evidence of a considerable scaling effect between high and low concentrates input herds in Ireland. In the comparison between grazing *vs*. confined dairy herds in the United States, Kearney *et al.* (2004a & b) reported that while genetic correlations were significantly less than one, suggesting some re-ranking among sires in both environments, these differences were not so large as to justify separate genetic evaluations for each system.

Across country evaluations for growth traits in beef cattle have also not revealed important interactions (Meyer, 1995; de Mattos *et al*, 2000; Lee & Bertrand, 2002). However, in their comparison between daughters of Canadian and New Zealand sires in Canadian and New Zealand dairy herds, Charagu & Peterson (1998) reported that while interactions at the macro level (strain x environment) were not important, there were significant interactions for all economic efficiency traits at the micro level (sires within strain x environment). Similarly, in their analyses of across country genetic dairy evaluations, Cienfuegos-Rivas *et al*. (1999) and Costa *et al.* (2000) found evidence of genotype x environment interactions, indicated by genetic correlations significantly less than unity and by change in sire ranking. Interestingly, both analyses found that information from low environments in the United States were better predictors of performance in Mexico and in Brazil, respectively.

Selection experiments in beef cattle have been mainly concerned with improvements in growth traits, with published reports of 1.8 to 6.3 generations of selection (Mrode, 1988b; Baker *et al.*, 1991; Koch *et al.*, 1994; Parnell *et al.*, 1997; Razook *et al.*, 1998; Mercadante *et al.*, 2003). However, Mrode (1988a) noted that many earlier experiments suffered from inadequate designs with respect to population size and levels of inbreeding. In their review, Baker & Morris (1984) reported that selection responses for weights have been closer to half of the expected response of 1%/generation. Two primary reasons for this have been a lower realized heritability and that the applied selection differential has been less than expected due to natural selection and attention paid to secondary traits. Realized heritability estimates have been widely used to determine the effect of selection. It is, however, important to be cognizant of the wide variations and large errors associated with these estimates being mostly attributed to chance effects of random drift, so much so that Falconer (1977b), referring to a 'large' experiment with an effective population size of 192, laments 'It is discouraging to find how imprecise an experiment on this scale is for estimating the realized heritability'. Even in dairy cattle where focus is on a single trait – milk yield – actual response has been much lower that predicted due to lower applied selection intensities and attention being given to non-production traits (Van Vleck, 1977). The variation in experimental results is summed up by Hill's (1979) statement that 'Each line is just one realization of the selection process.'

Numerous studies have reported positive correlated responses of weights at different stages of growth, as expected, given the positive genetic correlation between these traits. In one exception, selection for weight for age under conditions of moderate to high stress, birth weight decreased while weight at all other ages increased (Frisch, 1981). As discussed in Chapter 1, selection for growth in a stressful environment did not improve inherent growth potential, but resulted in increased resistance to environmental stress.

The Matopos Research Station long-term selection and genotype x environment interaction study offers several opportunities to explore the genetic properties of Afrikaner cattle in the sub-tropics. The focus of this study was three fold:

a) to estimate genetic parameters of calf growth traits between birth and 18 months of age;
b) to determine direct and correlated selection response for calf weights and weight gains over a 40-year period and
c) to investigate the presence of a genotype x environment interaction where environmental differences are due to management (that is early calving and supplemented in the dry season *vs.* late calving and no supplements).

4.2 MATERIALS AND METHODS

The animals, environment, and experimental protocol have been described in Chapter 2, while the derivation of the calf growth traits and development of fixed effect models have been described in Chapter 3.

4.2.1 Generation number, inbreeding coefficients and cumulative selection differentials

The generation number of an individual (G_i) was calculated using the formula of Brinks *et al.* (1961): $G_i=1+(G_s+G_d)/2$ where G_s and G_d are the generation number of the sire and dam respectively. The generation numbers of the base population sires and dams were set to zero. The base population was defined as foundation animals and their progeny (i.e. includes progeny born in the experiment which did not result from selection). Individual inbreeding coefficients were calculated according to the algorithm of Quaas (1976).

Direct and correlated cumulative selection differentials (CSD's) were calculated within the control lines (S/S and NS/NS) using the methods of Pattie (1965) and Newman *et al.* (1973). James (1986) reports that the method of Pattie for calculating CSD's is biased upwards as better parents will tend to leave more above average progeny in any generation, whereas the method of Newman *et al.* is correct. The approach of Newman *et al.* adds an individual's selection differential, calculated as a deviation from the mean performance of its contemporary group, to the mean accumulated selection differential of all parents contributing progeny to the group, whereas Pattie's method adds an individual's selection differential to the average individual accumulated selection differential of the individual's parents.

Only pre-weaning weight and weight gain traits were considered as males selected to be parents were managed separately post-weaning. Pre-weaning observations were either 'unadjusted' (except for age of calf for W90, W150, W205 and WW) or were 'adjusted' for fixed effects described in Chapter 3 and the 'phenotypes' were taken as the residuals from the fixed effects analyses within control lines (S/S and NS/NS).

4.2.2 Univariate models

All growth traits were analyzed with six different models. The models differed in their inclusion or exclusion of maternal genetic effects, permanent maternal effects and the correlation between direct and maternal genetic effects as adopted by Meyer (1989; 1992). Both MTDFREML (Boldman *et al.*, 1995) and AIREML (Johnson & Thompson, 1995) software packages were utilized to analyze the data. The different models in matrix notation are shown below:

Model A $Y = \mathbf{X}\beta + \mathbf{Z}_1 a + e$
AC $Y = \mathbf{X}\beta + \mathbf{Z}_1 a + \mathbf{Z}_3 c + e$
AM $Y = \mathbf{X}\beta + \mathbf{Z}_1 a + \mathbf{Z}_2 m + e$
AMR $Y = \mathbf{X}\beta + \mathbf{Z}_1 a + \mathbf{Z}_2 m + e$, $\mathrm{Cov}(a,m) = \mathbf{A}\sigma_{am}$
AMC $Y = \mathbf{X}\beta + \mathbf{Z}_1 a + \mathbf{Z}_2 m + \mathbf{Z}_3 c + e$
AMCR $Y = \mathbf{X}\beta + \mathbf{Z}_1 a + \mathbf{Z}_2 m + \mathbf{Z}_3 c + e$, $\mathrm{Cov}(a,m) = \mathbf{A}\sigma_{am}$

where: Y is the vector of observations;
β is the vector of fixed effects (see Section 3.2.3);
X is the incidence matrix that associates β with Y;
a is the vector of breeding values for direct genetic effects;
m is the vector of breeding values for maternal genetic effects;

c is the vector of permanent environmental effects due to dam;
$\mathbf{Z}_1$, $\mathbf{Z}_2$ and $\mathbf{Z}_3$ are the incidence matrices that associate a, m and c with Y; and
e is the vector of residual effects.

Furthermore, with **A**, the numerator relationship matrix between animals, $\mathbf{I}_n$, an identity matrix with order n, the number of dams, and **I**, an identity matrix with order of the number of records. The (co)variance structure of random effects can be described as: V(a) = $\sigma_a^2\mathbf{A}$, V(m) = $\sigma_m^2\mathbf{A}$, V(c) = $\sigma_c^2\mathbf{I}_n$, V(e) = $\sigma_e^2\mathbf{I}$, where σ_a^2 is the direct genetic variance; σ_m^2 is the maternal genetic variance; σ_c^2 is the maternal permanent environment variance; σ_e^2 is the residual variance and σ_{am} is the genetic covariance between direct and maternal effects. There were a total of 7175 animals in the pedigree file that included 254 base animals. In order to reduce the large (co)variances from the analyses of daily gains (g/day), all gain traits were divided by a factor of 10 (g/dayx10^{-1}). All output results were converted back to g/day.

After convergence with a convergence criterion of $1\text{x}10^{-9}$, three cold restarts for the MTDFREML runs were adopted to ensure that the global maximum had been found. Standard errors of the parameter estimates were derived from AIREML outputs. The ‘best’ model was determined by comparison of the difference of minus twice the log likelihoods with $\chi^2_{.05}$ test with one degree of freedom to determine if the addition of a random factor significantly improved the model fit (Meyer & Hill, 1992).

The formula given by Willham (1972) was used to calculate total heritability as follows: $h_T^2 = (\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am}) / \sigma_p^2$, where σ_p^2 is the phenotypic variance.

For simplicity the animal solutions from the full (AMCR) model were used to derive direct and maternal estimated breeding values (EBV’s). Environmental trends were calculated by regressing line-year-environment solutions against year of birth for the control lines (S/S and NS/NS).

Realized heritability estimates for pre-weaning weight and weight gain traits were calculated within control lines (S/S and NS/NS) by either the regression of an individual's breeding value estimate on its' CSD (Falconer, 1989), where regressions were forced through the origin as suggested by Hill (1972) and confirmed by Baker *et al.* (1991), or by the ratio of total response to total cumulative selection differential after six generations. Responses were derived from the BLUP estimates, bearing in mind that these are subject to the REML estimate of heritability. The regression standard error seriously underestimates the standard error of the realized heritability estimate and the procedures described by Falconer (1989) were adopted to derive standard errors that accounted for random drift and measurement error (Appendix 5).

4.2.3 Bivariate analyses

The programme MTDFREML was used to carry out all possible bivariate analyses of growth traits. The full (AMCR) model was adopted allowing for all possible covariances within and between traits. Procedures recommended by Boldman *et al.* (1995) were adopted to build the model, commencing with univariate estimates as priors, setting covariances to zero and running each analysis to a 'moderate' ($1x10^{-6}$) level of convergence. Cold starts were then adopted with single-trait variances held constant and guessed covariances used as starting values and run to a 'low' ($1x10^{-3}$) level of convergence. Convergence criterion was set at $1x10^{-9}$ for each analysis. Restarts were continued until the criterion was attained, after which a further three cold starts were run.

4.2.4 Determination of genotype x environment interactions

The presence of genotype x environment interactions was estimated by determining the genetic correlation of the trait treated as different traits in each of the two environments, where only the post-crossover (1977 to 1997) data were considered. In all instances the 'full' AMCR model was utilized for the analyses of calf growth traits. Procedures described in the above section were utilized to build models that allowed for estimation of correlations between the traits. An approximate formula for the standard error of the genetic correlation is given by Falconer (1989):

$s_{rA} = \frac{1-r_A^2}{\sqrt{2}}\sqrt{\frac{s\,(h_x^2).s\,(h_y^2)}{h_x^2.h_y^2}}$, where r_A is the genetic correlation; h_x^2 and h_y^2 are the trait heritabilities within environment and s denotes standard error.

Genotype x environment interactions were also estimated using the MTDFREML algorithm by the inclusion of an additional random component involving the interaction of sires with environment, year and environment x year to the ‘full’ AMCR model fitted to the post-crossover data set (1977 to 1997). The importance of the interactions was estimated by the improvement of model fit by the reduction in log likelihoods as well as by the calculation of the intraclass correlation (Dickerson, 1962): $r_G^{'} = s_G^2 /(s_G^2 + s_{GE}^2)$, where $r_G^{'}$ is the genetic correlation; s_G^2 is the genetic variance; and s_{GE}^2 is the variance due to interaction of genotype with environment. The intraclass genetic correlation for sires’ performance in different environments is given by: $t = s_a^2 /(s_a^2 + 4s_i^2)$, where s_a^2 is the direct genetic variance and s_i^2 is the variance due to interaction of sires with environment as adopted by Neser *et al*., 1996.

4.3 RESULTS AND DISCUSSION

A total of 214 sires and 1578 dams had records for progeny birth weight across the data set. A detailed breakdown of the number of sires and dams and the number of observations per sire and dam line, environment and crossover phase is shown in Table 4.1.

Table 4.1 Number of sires, dams and progeny with birth records within and across supplemented (S) and non-supplemented (NS) lines and environments and pre- and post-crossover phases

					Number of progeny birth records		
Phase	Line	Environment		Number	Minimum	Maximum	Average
Overall			Sires	214	5	118	32
			Dams	1578	1	11	4
Pre-crossover	S	S	Sires	32	14	111	47
			Dams	339	1	11	4
	NS	NS	Sires	36	12	82	37
			Dams	337	1	10	4
Post-crossover	S	S	Sires	75	4	33	14
			Dams	261	1	10	4
		NS	Sires	76	3	30	12
			Dams	251	1	10	4
	NS	S	Sires	76	4	32	14
			Dams	277	1	11	4
		NS	Sires	77	4	32	13
			Dams	262	1	10	4

4.3.1 Generation number and inbreeding coefficient

The crossover was initiated after an average of two generations of selection had taken place in both lines and the average generation number of calves born in 1997 was 6 (Figure 4.1) compared with a range of 1.8 to 6.3 generations of selection reported in the literature. In the pre-crossover phase, the average age of sires and dams at the time of birth of their progeny was 5.9 and 7.5 years respectively. This was reduced to 4.4 and 6.5 years respectively in the post-crossover phase. These are similar to generation interval of 5.1 reported by Razook *et al.* (1998) and Mercadante *et al.* (2003) for selection experiment with Nelore cattle in Brazil, but are in general higher than generation intervals reported in the literature of 2 to 4.3 years for sires and 4 to 6.6 years for dams (Mrode, 1988b; Baker *et al.*, 1991; Koch *et al.*, 1994; Parnell *et al.*, 1997) and is primarily due to the late age at first mating of both sexes and shorter retention of cows in the herd (Mercadante *et al.*, 2003).

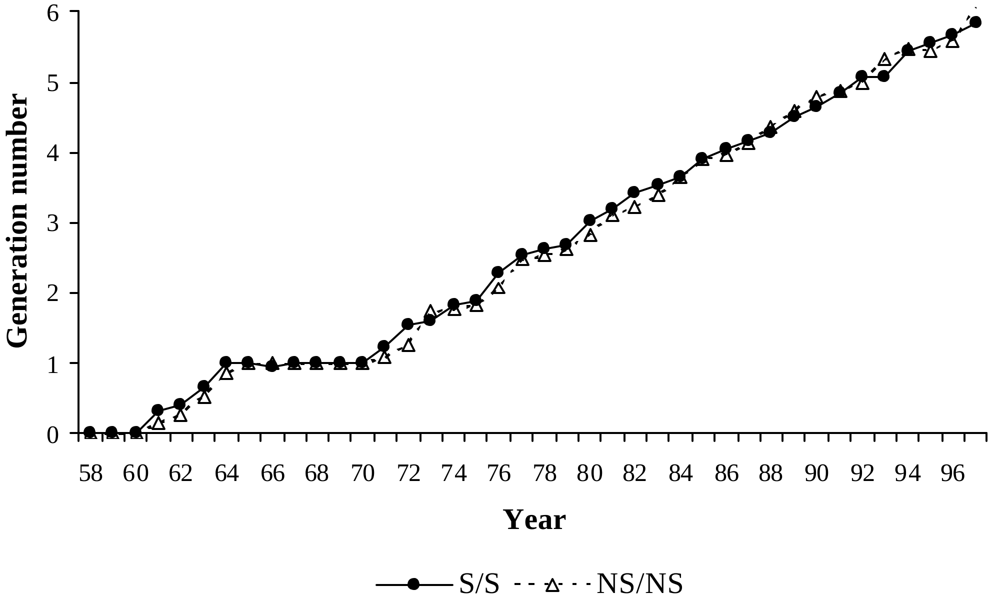


Figure 4.1 Progression of generation number by year of birth

The average inbreeding coefficient gradually increased with generation number and was slightly higher for the S lines reaching a level of 7.4% compared with 5.7% for the NS lines for calves born in 1997 (Figure 4.2). However, the maximum levels of inbreeding generally remained below 20% for the S lines and below 15% for the NS lines. The rate of inbreeding across lines and environments was 0.2%/year or 1.2%/generation and is similar to estimates in the literature (0.07 to 0.30%/year or 0.3 to 1.3%/generation) (Baker *et al.*, 1991; Koch *et al.*, 1994; Parnell *et al.*, 1997).

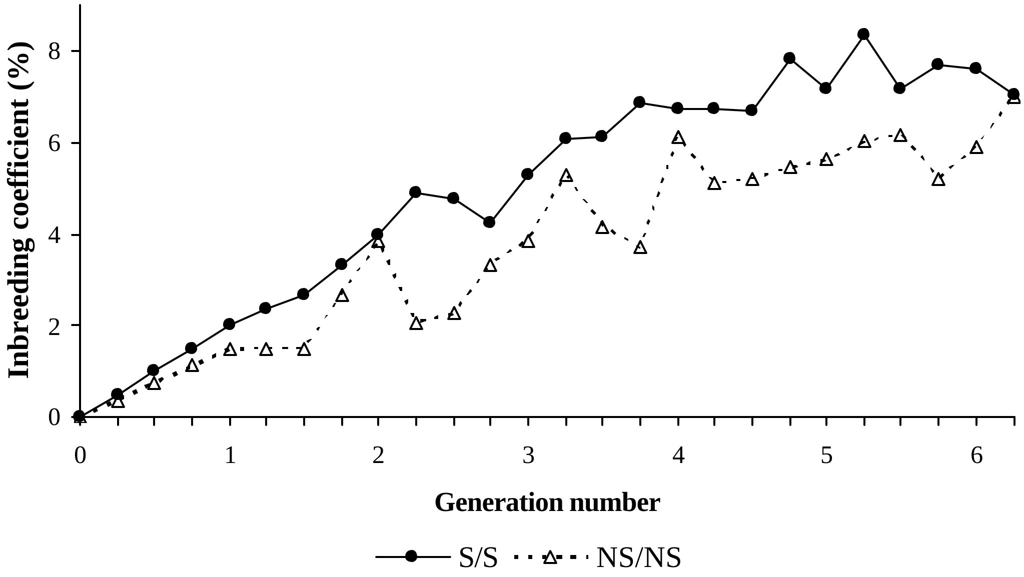


Figure 4.2 Progression of average inbreeding coefficient by generation number

4.3.2 Univariate analyses

According to the LogL ratio tests the 'full' (AMCR) model was indicated for the analysis of most of the growth traits (Appendix 6). However, the AM model appeared best suited for BW and PWG where the inclusion of both the direct-maternal genetic correlation and permanent effects due to the dam were not indicated; the AMC model appeared best suited for W90, G1 and G3 where the inclusion of the direct-maternal genetic correlation did not improve model fit, while the AC model was best suited for EPWG where only the inclusion of direct genetic and permanent effects due to the dam were indicated.

The direct heritabilities (h_a^2) were low (0.03 to 0.10) for W90, G1 and G3, moderate (0.24 to 0.39) for BW, W18 and PWG and intermediate (0.13 to 0.19) for the remaining traits (Table 4.2). The maternal heritabilities (h_m^2) were low for BW (0.14) and W90 (0.11) and gradually increased with calf age peaking at 0.26 for W12 and before dropping to 0.15 for W18. The h_m^2 of calf weight gains was moderate (0.21) for ADG and were low (0.05 to 0.011) for all the other gain traits.

Table 4.2 Genetic parameter estimates (±se) for growth traits derived from the 'best' model[1]

				Estimates[2]			
Trait[3]	h_T^2	h_a^2	r_{am}	h_m^2	c^2	e^2	σ_p
BW	0.46	0.39 ± 0.033		0.14 ± 0.017		0.47	4.30
W90	0.16	0.10 + 0.022		0.11 + 0.026	0.17 + 0.022	0.59	13.2
W150	0.16	0.17 ± 0.033	-0.35 ± 0.129	0.15 ± 0.035	0.23 ± 0.025	0.51	18.1
W205	0.16	0.18 ± 0.032	-0.43 ± 0.112	0.19 ± 0.039	0.28 ± 0.028	0.43	21.0
WW	0.15	0.19 ± 0.033	-0.49 ± 0.099	0.21 ± 0.042	0.32 ± 0.030	0.38	21.8
W12	0.14	0.19 ± 0.036	-0.53 ± 0.095	0.26 ± 0.046	0.27 ± 0.031	0.40	23.0
W18	0.31	0.36 ± 0.057	-0.37 ± 0.113	0.15 ± 0.037	0.14 ± 0.023	0.44	27.1
G1	0.10	0.04 ± 0.016		0.11 ± 0.024	0.16 ± 0.022	0.69	134
G2	0.08	0.13 ± 0.031	-0.57 ± 0.142	0.08 ± 0.027	0.13 ± 0.019	0.72	159
G3	0.06	0.03 ± 0.015		0.05 ± 0.016	0.06 ± 0.016	0.87	166
ADG	0.10	0.15 + 0.030	-0.57 + 0.041	0.21 + 0.041	0.28 + 0.028	0.46	98
EPWG	0.13	0.13 ± 0.026			0.06 ± 0.013	0.81	94
PWG	0.27	0.24 ± 0.035		0.06 ± 0.015		0.70	74

1. See Appendix 6;
2. h_T^2, h_a^2 and h_m^2 are the total, direct and maternal, heritabilities; c^2 and e^2 are the permanent maternal environment effect and residual variance expressed as a ratio of the phenotypic variance; r_{am} is the correlation between direct and maternal genetic effects; σ_p is the phenotypic standard deviation;
3. See Table 3.1 for trait definitions.

In the analyses of Afrikaner data from the National Beef Performance Testing Scheme in South Africa, direct heritabilities were higher for BW (0.51), similar for WW and W12 and lower for W18 (0.17), while all maternal heritabilities were much lower and ranged from 0.03 to 0.10 (Groeneveld *et al.*, 1998; Mostert *et al.*, 1998). With the exception of BW and W18, the total heritability (h_T^2) estimates for the intermediate weight traits were remarkably similar (0.14 to 0.16).

The low heritability estimates for W90, G1 and G3 are difficult to explain and could be due to the fact that the traits were measured at different times of the year for the two environments. Direct heritability estimates of Pedi cattle weights at 100 and 205d were also low and the authors suggested that this could be due to the local environment that disturbs the normal growth of animals (Lubout & Swanepoel, 1992).

The presence of maternal effects for post-weaning traits has been ascribed to a part-whole relationship between pre- and post-weaning traits (Meyer, 1992; 1994). The complex interaction known as 'maternal effects' may arise from interplay between progeny and uterine and post-natal nursing environment. Through these effects, the mother has the potential to modify the expression of genes in her progeny. Referring to embryo transfer experiments with inbred strains of mice, Cowley *et al.* (1989) show that the genotype of the mother providing the uterine development environment significantly influenced the post-natal growth and adult body size of progeny.

Meyer (1997) notes that the estimation of maternal effects and corresponding genetic parameters are problematic. The direct and maternal effects are generally confounded; expression of maternal effects is sex limited, occurs late in the life of a female and lags by one generation. Numerous studies have reported large antagonistic (as great as -0.5 or larger) direct-maternal correlation and while weak adverse relationship has been considered plausible, strong negative ones have been viewed with skepticism (Meyer, 1997). In the current study the r_{am} estimates (where significant) were all negative and increased as calf age increased from –0.35 for W150 to –0.53 for W12, before dropping to –0.37 for W18 and were –0.57 for both G2 and ADG. Mostert *et al.* (1998) reported remarkably similar r_{am} estimates for WW, W12 and W18, but also found a negative correlation for BW (-0.60), in contrast to the non-significant and positive correlation (0.15) in the current study (Appendix 6). Similarly, in their analysis of Bonsmara field data, Maiwashe *et al.*, (2002) reported moderate negative direct-maternal genetic correlations for BW and WW (-0.44 and -0.54, respectively). The large negative correlations could be due to other sources of variation, e.g. sire x year interactions (Robinson, 1996; Meyer, 1997; Eler *et al.*, 1998) and failure to account for sources of variation such as paddocks or management groups which inflate the variance between paternal sibs in a contemporary group (Meyer, 1997).

The estimates of permanent maternal effects (where significant) similarly increased with calf age from 0.17 for W90 and peaked at 0.32 for WW before dropping to 0.14 for W18. In contrast, estimates of permanent maternal effects were greatest (0.28) for ADG and decreased from 0.16 for G1 to 0.06 for G3. Hetzel *et al.* (1990) similarly found negligible permanent environment effects for BW and sizeable effects for pre-weaning traits for cattle breeds in the Australian tropics. In the analysis of large Australian beef field data sets Meyer (2002) reported that maternal effects (h_m^2 and c^2) gradually decreased with increasing calf age, but were still important at 700d, whereas in the current study maternal effects were higher and remained relatively constant to one year of age. The proportion of the residual variance to the phenotypic variance ranged from 0.38 to 0.59 for the weight traits and ADG in contrast to weight gains where the proportion ranged from 0.69 to 0.87.

4.3.3 Cumulative selection differentials, genetic and environmental trends

Generally, the effect of adjusting the pre-weaning weights and weight gains for known factors influencing these traits did not materially affect the cumulative selection differentials (CSD's). Similarly, no consistent patterns were found for method of calculating the CSD's as exemplified for calf weight at weaning where the method of Pattie (1965) underestimated the CSD for the supplemented line, but tended to overestimate the CSD for the non-supplemented line relative to the method of Newman *et al.* (1973). Mrode *et al.* (1990) also noted little difference in method adopted to calculate CSD's. According to James (1986), the method of Pattie tends to overestimate the CSD while the method of Newman *et al.* is correct and Blair (1986) reported that the method of Pattie overestimated CSD by between 1 and 35%.

The effect of selection on calf pre-weaning weight and weight gain traits calculated by the method of Newman *et al.* (1973), after adjusting observations for known fixed factors, are illustrated in Figures 4.3a & b. The CSD's trends for both the S and NS lines for weaning weight plotted against generation number were relatively linear and greater for the S line (0.08 standard deviations/year) compared to the NS line (0.05 standard deviations/year). Much higher correlated selection differentials for weaning weight in beef cattle have been reported (0.14 to 0.22 standard deviations/year) (Mrode, 1988b; Baker *et al.*, 1991).

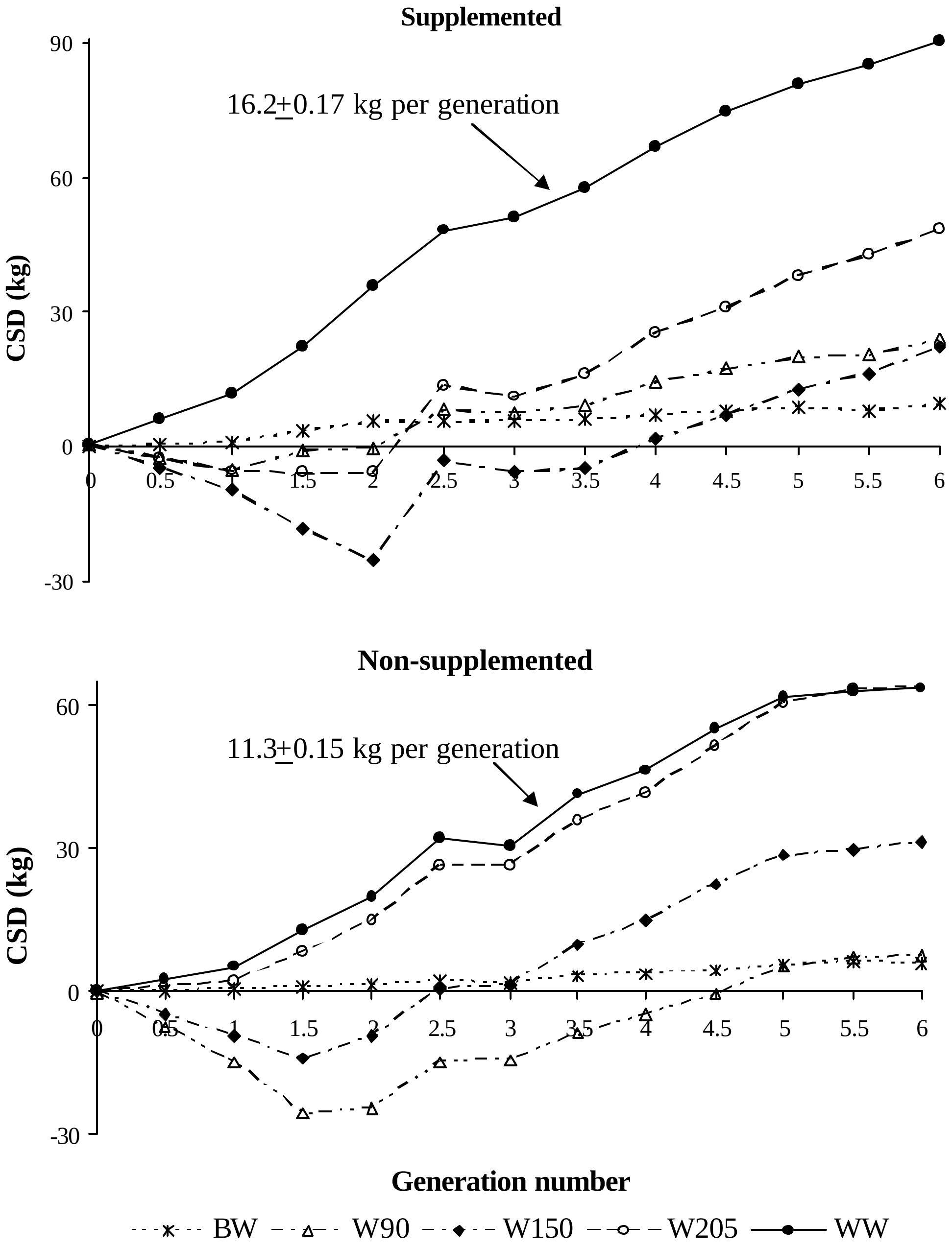


Figure 4.3a Cumulative selection differential (CSD) calculated by the method of Newman *et al.* (1973) after adjusting calf weights

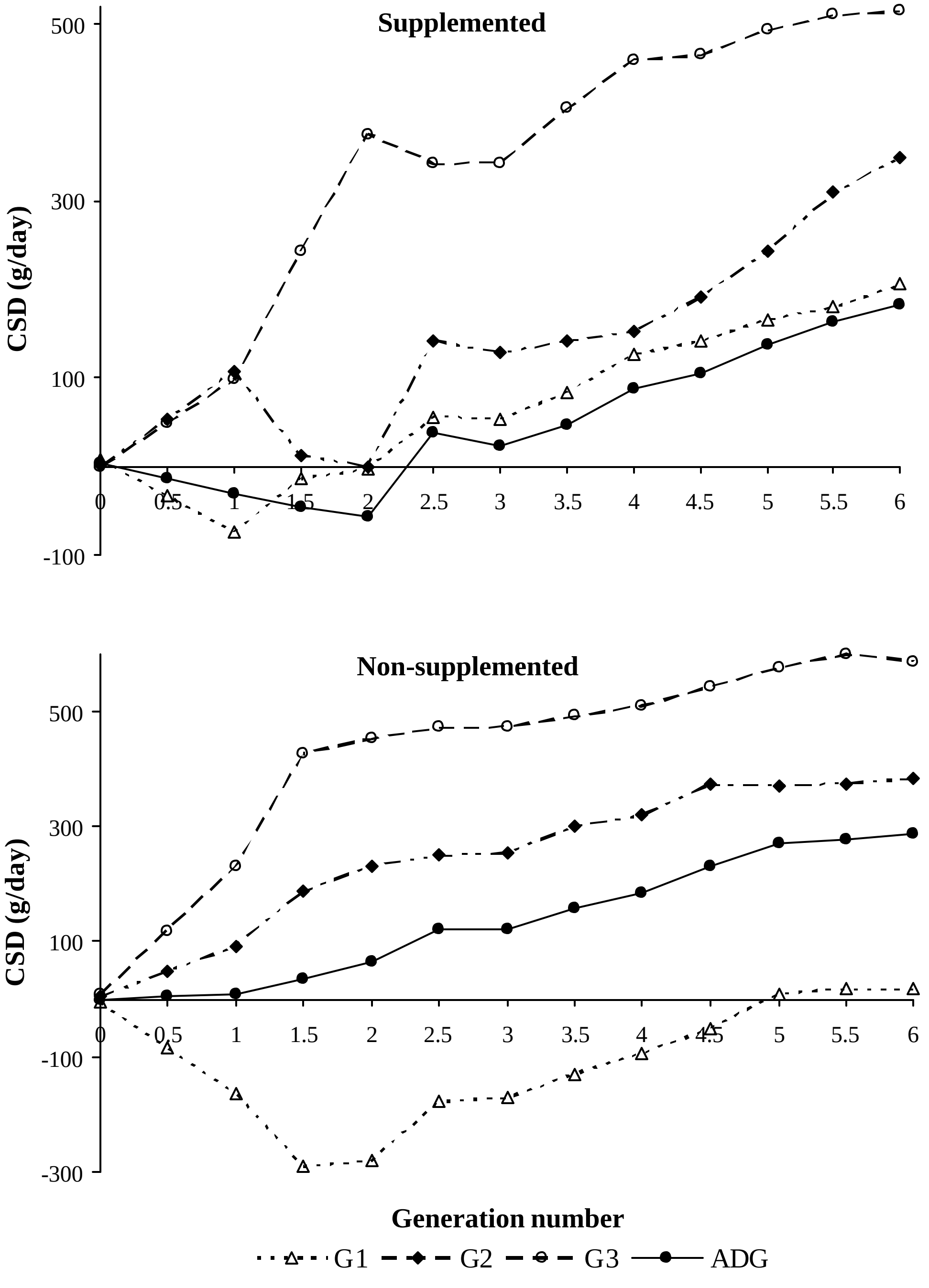


Figure 4.3b Cumulative selection differential (CSD) calculated by the method of Newman *et al.* (1973) after adjusting calf weight gains

Mrode (1988b) attributed the inability to achieve maximum possible selection differentials to unsoundness, selection on colour, death before production of any offspring and failure to conceive as heifers. The W205 trends for the NS line were very similar to WW (Figure 4.3a), which is to be expected given that the average calf age at weaning for calves in the NS environment was approximately 200d. While the BW trends were also linear across pre- and post-crossover phases, trends for the other correlated weight and weight gain traits show distinctly different patterns according to the crossover phase. In particular W90, W150 and G1 show negative trends in the pre-crossover phase followed by positive trends post-crossover (Figures 4.3a & b), while G3 shows a large positive response pre-crossover for both lines that plateaus post-crossover (Figure 4.3b). The varied differentials suggest changes in selection criteria over the period of the experiment.

Direct and correlated responses to selection were calculated by regressing EBV's against generation number or year of birth (Appendices 7 & 8) and the direct and maternal genetic trends for calf weights and weight gains plotted against generation number are illustrated in Figures 4.4a, b & c. In contrast to the CSD trends, the direct genetic trends for all the weight and weight gain traits displayed a positive correlated response. Relative to the trait means, selection for weaning weight (in males) resulted in the greatest response in direct genetic breeding values of 1.2% and 1.4%/generation for the S and NS lines respectively. The 'total' direct genetic selection response across six generations of selection, expressed as a fraction of the phenotypic standard deviation, were generally greater than 50% for the weight traits and were highest for WW and W18 (61-72%), but tended to be low (<20%) for W90 and ADG.

However, the yearly trends for weaning weight, the primary selection trait, were lower than correlated trends reported in the literature (0.37kg/year *vs.* 0.48 to 1.01kg/year) (Baker *et al.*, 1991; Arthur *et al.*, 1997), while the correlated yearly trends for yearling weight in the current study are 6 to 14 times lower than both direct and correlated literature estimates for *Bos taurus* and *B. indicus* cattle in the temperate and tropical regions (0.2kg/year *vs*. 1.2 to 2.8kg/year) (Baker *et al.*, 1991; Koch *et al.*, 1994; Parnell *et al.*, 1997; Razook *et al.*, 1998; Mercadante *et al.*, 2003). Interestingly, the correlated selection response of BW in the NS line (0.07kg/year) was twice that of calves in the S line, and not surprisingly these were generally lower than literature estimates (-0.06 to 0.25kg/year) (Baker *et al.*, 1991; MacNeil *et al.*, 1992; Arthur, *et al.*, 1997).

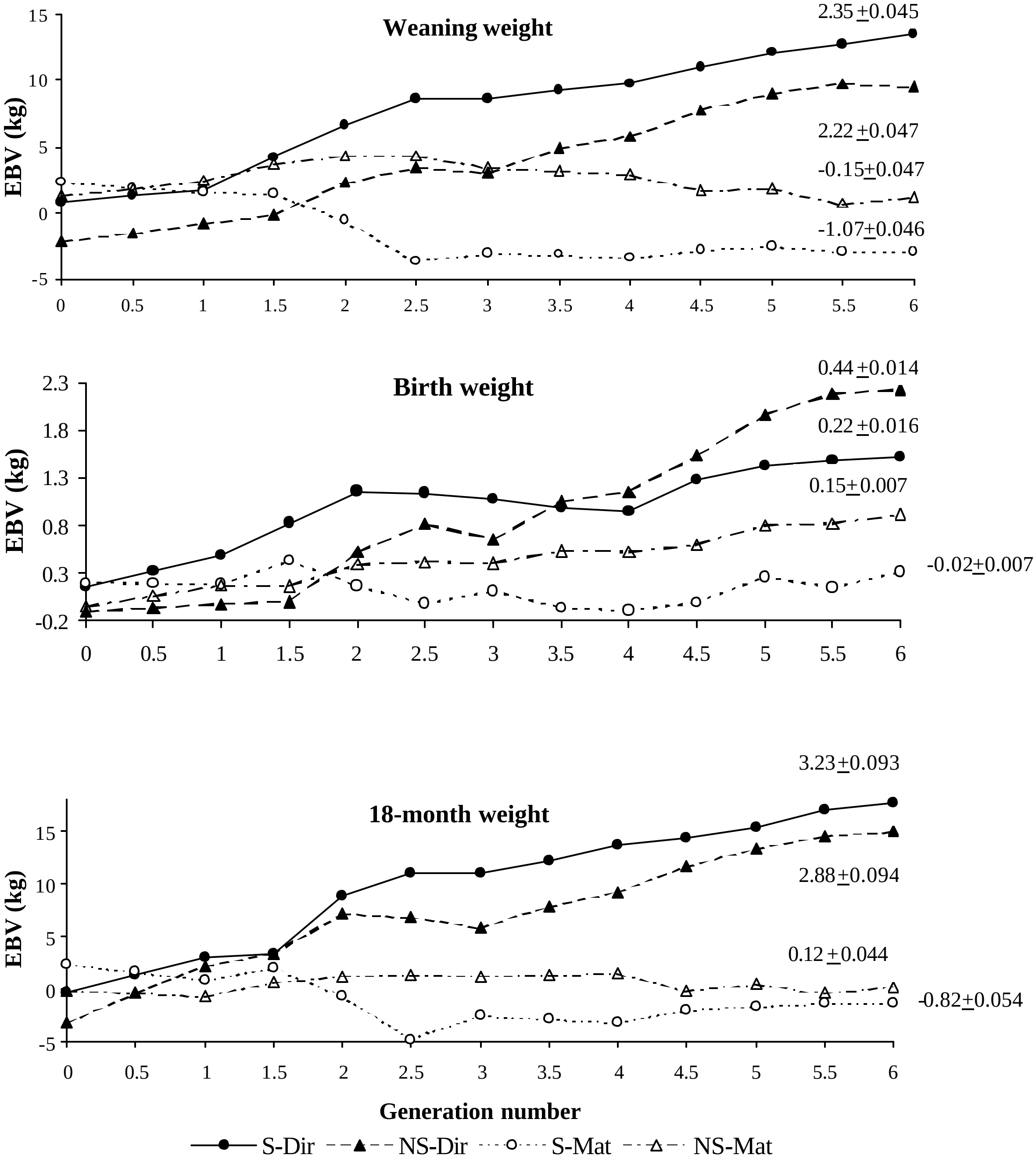


Figure 4.4a Direct (Dir) and maternal (Mat) estimated breeding value (EBV) trends and regression coefficients (± standard errors) for weights at weaning, birth and 18 months for the supplemented (S) and non-supplemented (NS) lines

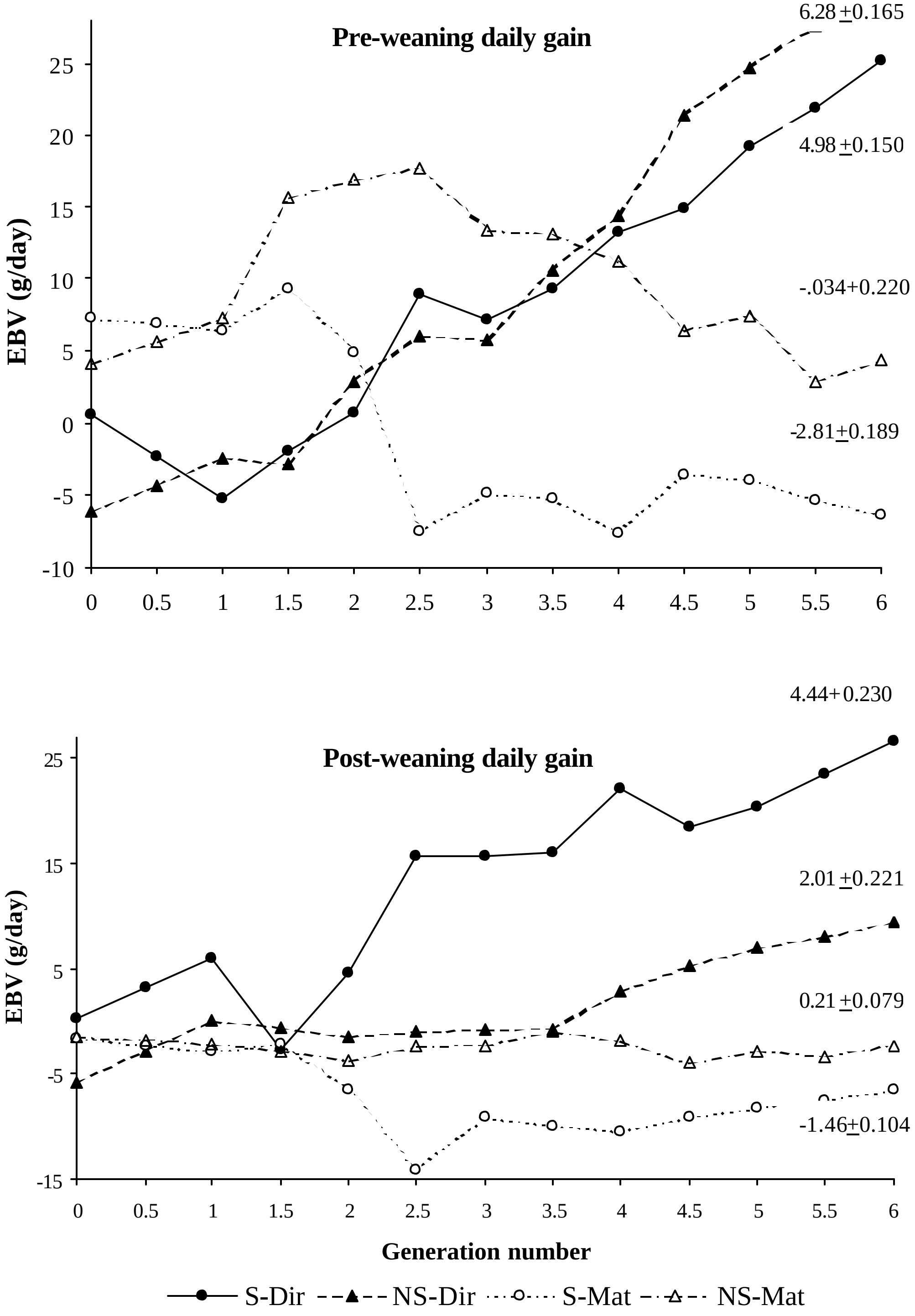


Figure 4.4b Direct (Dir) and maternal (Mat) estimated breeding value (EBV) trends and regression coefficients (± standard errors) for pre- and post-weaning gains for the supplemented (S) and non-supplemented (NS) lines

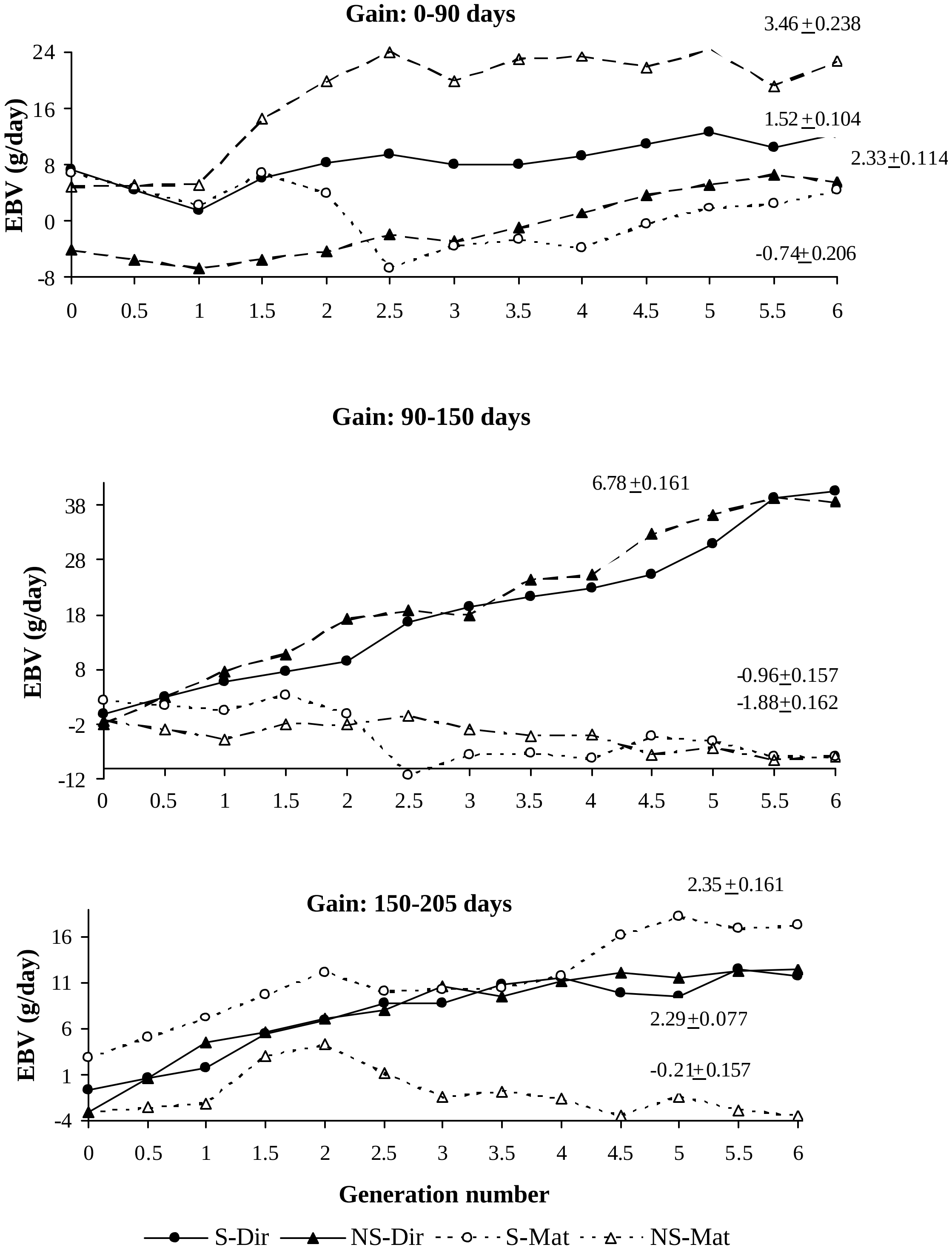


Figure 4.4c Direct (Dir) and maternal (Mat) estimated breeding value (EBV) trends and regression coefficients (± standard errors) for pre-weaning gains for the supplemented (S) and non-supplemented (NS) lines

The small direct and correlated selection responses are obviously a reflection of the very low selection pressure applied. A possible reason for the low selection differential could be due to selection being carried out on observed values pre-1988. However, no consistent differences were found between CSD's calculated with or without adjustments for fixed effects and indicate that emphasis was placed on secondary criteria.

Generally, the correlated responses for maternal genetic effects were low and tended to be negative for the S line and positive for the NS line. Despite the very low maternal heritabilities for G1, G2 and G3 (ranging from 0.05 to 0.11: Table 4.2), there was however a dramatic difference between lines and growth phase for the maternal genetic trends (Figure 4.4c). A large positive trend was displayed for the non-supplemented line for calf gain between 0 and 90 days compared with a small negative trend for the supplemented line. In contrast, for gain between 150 and 205 days, a large positive trend was shown for the supplemented line compared with a trend, not significantly different to zero, for the non-supplemented line (Figure 4.4c). Some studies have shown that maternal effects positively and significantly contributed to correlated responses in weaning and yearling weights (Herd, 1990; MacNeil *et al.*, 1992; Koch *et al.*, 1994), while other reports have shown marginal contribution (Carter *et al.*, 1990; Morris *et al.*, 1992). Arthur *et al.* (1997) note that the differences may partly be due to the absolute importance of maternal ability on expression of growth and partly due to the magnitude and sign of genetic correlations between direct and maternal effects.

Direct and correlated realized heritabilities are presented in Table 4.3. With the exception of W150 for the S line and W90 and G1 for the NS line, the estimates of realized heritability by regression and by the ratio of total response to the cumulative selection differential after six generations were remarkably similar. However, the standard errors accounting for random drift and measurement error were several times greater than that of the standard error of the regression coefficient, but were, in many instances, remarkably similar to the REML standard errors. Despite differences in CSD and breeding value trends, the realized heritabilities were remarkably similar for the two control lines and ranged between 60 and 110 percent of the REML heritability estimate. However, as depicted by the coefficient of determination, the model fit for several of the regression estimates indicate a poor fit. It is also important to appreciate that the realized heritabilities estimates are influenced by the REML heritability estimate used to derive breeding value estimates. Taking into consideration the standard errors (either those accounting for random drift and measurement error or the REML ones) it is unlikely that the realized heritability estimates were different to the REML estimates.

Table 4.3 Within line direct and correlated realized heritabilities[1] compared to within line REML heritability estimates

	Supplemented			
	Regression	R^2	Response/ CSD	REML
Birth weight	0.24 (0.003)	68	0.18 (0.13)	0.39 (0.07)
90 day weight	0.10 (0.002)	45	0.11 (0.09)	0.09 (0.04)
150 day weight	0.11 (0.002)	45	0.19 (0.14)	0.08 (0.04)
205 day weight	0.14 (0.002)	61	0.16 (0.08)	0.14 (0.05)
Weaning weight	0.15 (0.002)	77	0.15 (0.05)	0.18 (0.05)
Gain 0-90 days	0.04 (0.001)	28	0.06 (0.09)	0.05 (0.03)
Gain 90-150 days	0.10 (0.002)	51	0.13 (0.08)	0.12 (0.05)
Gain 150-205 days	0.02 (0.001)	39	0.02 (0.05)	0.05 (0.04)
Pre-weaning average daily gain	0.10 (0.002)	45	0.14 (0.10)	0.13 (0.05)
	Non-supplemented			
	Regression	R^2	Response/ CSD	REML
Birth weight	0.34 (0.003)	81	0.38 (0.15)	0.29 (0.07)
90 day weight	0.06 (0.002)	27	0.32 (0.25)	0.08 (0.04)
150 day weight	0.14 (0.003)	51	0.18 (0.11)	0.22 (0.06)
205 day weight	0.13 (0.002)	62	0.14 (0.06)	0.20 (0.05)
Weaning weight	0.13 (0.002)	59	0.16 (0.06)	0.21 (0.06)
Gain 0-90 days	0.03 (0.001)	21	0.34 (1.01)	0.05 (0.03)
Gain 90-150 days	0.09 (0.001)	63	0.10 (0.06)	0.14 (0.06)
Gain 150-205 days	0.02 (0.001)	36	0.02 (0.03)	0.05 (0.03)
Pre-weaning average daily gain	0.09 (0.002)	44	0.10 (0.05)	0.20 (0.05)

[1] Realized heritabilities calculated by either regressing response on cumulative selection differentials or by ratio of total response to total cumulative selection (CSD) after six generations of selection. Standard error of regression estimate is given together with coefficient of determination (R^2), while standard error for the ratio accounts for random drift and measurement error (see Appendix 5)

The lower realized heritabilities for the weight gain traits are consistent with findings in other selection studies (Baker & Morris, 1984). Thompson & Juga (1989) show that both the methods of Pattie and Newman *et al.* are biased downwards as a result of a reduction in variance due to linkage disequilibrium (Bulmer, 1971) and propose a recursive method to estimate realized heritabilities.

Reporting on a selection experiment with sheep, Johnson *et al.* (1995) found lowest realized heritabilities estimated by the methods of Pattie and Newman *et al.*, followed by those estimated using the method of Thompson & Juga which were similar to, but still lower than, the REML estimates. In theory, REML techniques using an animal model and complete relationship matrix yield unbiased estimated of base population parameters (Johnson *et al.*, 1995). However, Meyer & Hill (1991) found that REML analyses did not account for a decrease in genetic variance in the analyses of 23 generations of selection in mice.

4.3.4 Bivariate analyses

With the exception of the correlation between direct effects of ‘trait 1’ with maternal effects of ‘trait 2’, model parameters in all the bivariate analyses stabilized fairly quickly. The parameter estimates did not vary greatly from the univariate analyses (Appendix 9).

The direct and maternal genetic correlations for selected weight and weight gain traits are shown in Table 4.4 (the complete set of correlations is given in Appendix 10). In comparison with the parameters obtained from a four-trait model used to analyze field data of Afrikaner weights (Groeneveld *et al.*, 1998, Mostert *et al.*, 1998), direct heritability estimate in the current study for BW was lower and that for W18 was higher, while all maternal heritabilities were higher. The direct genetic correlations were similar across reports, however the direct maternal correlations showed great variability, particularly with BW, in contrast to remarkably consistent estimates (-0.20 to –0.60) reported by Groeneveld *et al.* (1998) and Mostert *et al.* (1998).

Table 4.4 Estimated variance ratios (x100) from the bivariate analyses[1]

		Direct					Maternal				
		BW	WW	W18	ADG	PWG	BW	WW	W18	ADG	PWG
Direct	BW	**36**	58	46	33	20	15	0	-10	-2	-11
	WW	*33*	**19**	79	94	43	13	-45	0	-51	1
	W18	*33*	*78*	**32**	78	81	15	8	-26	-14	-15
	ADG	*14*	*91*	*74*	**15**	47	23	-57	-39	-56	9
	PWG	*15*	*4*	*54*	*3*	**33**	24	5	-11	-1	-40
Maternal	BW	-	-	-	-	-	**12**	21	28	2	5
	WW	-	-	-	-	-	-	**22**	93	98	-46
	W18	-	-	-	-	-	-	-	**13**	90	0
	ADG	-	-	-	-	-	-	-	-	**20**	-31
	PWG	-	-	-	-	-	-	-	-	-	**9**

[1] Heritabilities on the diagonal (in bold), genetic correlations above and phenotypic correlations below (in italics)

4.3.5 Expression of genotype x environment interaction

The estimates of the direct genetic correlations of the weight traits treated as different traits across the environments were high and ranged from 0.79 to 0.99, but were lower for the gain traits (0.57 to 0.88) and was very low (0.13) for G3 (Table 4.5). Similarly, the maternal genetic correlations were generally high (0.72 to 0.96) for most of the weight traits, except for W150 and W205 (0.44 and 0.42). However, the maternal genetic correlation estimates for the weight gain traits were highly variable ranging from –0.51 for PWG to 0.68 for G1. The phenotypic correlations for the weight traits were moderate and ranged from 0.27 for W205 to 0.50 for BW. In contrast the estimates for the weight gain traits were highly variable ranging from 0.03 for G3 to 0.90 for EPWG.

The direct genetic and maternal genetic correlation estimates for the traits typically reported in the literature (BW, WW and W18) were high, and in many instances close to unity, indicative that genotype x environment interactions were not important. In addition, the very large sampling errors associated with low genetic correlation estimates suggest that even these estimates are not significantly different from a correlation of 1.0, also implying the absence of important genotype x environment interactions.

Table 4.5 Direct and maternal genetic and phenotypic correlations for growth traits treated as different traits across environments (1977 to 1997)

Trait[1]	Direct genetic (r_A)[2]	Maternal genetic (r_M)	Phenotypic (r_P)
BW	0.99 ± 0.003	0.96	0.50
W90	0.96 ± 0.017	0.86	0.35
W150	0.84 ± 0.055	0.44	0.30
W205	0.79 ± 0.072	0.42	0.27
WW	0.93 ± 0.026	0.72	0.35
W12	0.96 ± 0.017	0.89	0.39
W18	0.93 ± 0.023	0.94	0.43
G1	0.78 ± 0.136	0.68	0.21
G2	0.57 ± 0.206	0.01	0.08
G3	0.13 ± 0.516	0.21	0.03
ADG	0.62 ± 0.136	0.32	0.19
EPWG	0.70 ± 0.109	0.54	0.90
PWG	0.88 ± 0.044	-0.51	0.27

1. See Table 3.1 for trait definitions; and
2. Plus or minus an approximate standard error (see text for details).

In pair-wise across country (Argentina, Canada, Uruguay and United States) genetic evaluations of growth in Hereford cattle, Lee & Bertrand (2002) reported direct and maternal correlations generally greater than 0.8. The lower correlations with data from Uruguay were ascribed to the smaller size of the data set. These authors concluded that while sires generally rank the same for both direct and maternal genetic performance for pre- and post-weaning growth traits, adjusting for heterogeneous variances was recommended. However, in their analysis of 205-day weights of Nellore calves across four widely different regions in Brazil, Souza *et al.* (1998) reported low genetic correlations. Spearman correlation coefficients of breeding values confirmed the presence of significant sire x environment interactions.

The inclusion of an additional random effect of sire x environment interaction in the analyses did not improve model fit for all traits, except for G2. In all instances the variance due to interaction accounted for less than 2% of the phenotypic variance. Of concern, however, was the significant improvement in model fit with the inclusion of sire x year interaction for most traits and while the variance due to interaction accounted for less than 5% of the phenotypic variance, the intraclass correlation for traits post-90 days ranged from 0.4 to 0.6, indicative of a significant interaction, and highlights the tremendous year to year variations experienced in the sub-tropics. In general, the inclusion of the interaction term reduced both the direct heritability and the direct-maternal correlation estimates. Similar findings have been reported by Robinson (1994 & 1996), Neser *et al.* (1996), Meyer (1997), van der Westhuizen (1997), Berweger Baschnagel *et al*. (1999), Maniatis & Pollott, (2002) and Meyer (2003). A genotype x environment interaction was more evident for traits with low heritability estimates (<0.20: eg G1 and G3) in agreement with Cahaner (1990). The inclusion of sire x year x environment was, in most instances, a poorer fit compared with models with only the sire x year interaction term.

4.4 CONCLUSIONS

The most significant finding in these analyses is the remarkably low selection pressure applied and as a consequence, direct and correlated rates of genetic progress for all the weight traits were low. In accordance with the objective to test the presence of an interaction, selection for calf weight at weaning (in males) was carried out within two lines to create lines adapted to their respective environments. Line differences were small (Chapter 3) and while direct and correlated genetic trends for the S line were in general greater than the NS line (a reflection of the greater selection pressure), actual differences were small. The correlated cumulative selection differentials suggest that applied selection criteria differed in the course of the experiment. This is particularly evident for measures of pre-weaning growth measures (W90, W150 & G1) which were negative in the pre-crossover phase and positive in the post-crossover phase.

The generation interval and increase in inbreeding were consistent with other long-term selection experiments with cattle. Similarly, genetic parameters were in general consistent with literature estimates, apart from no apparent direct-maternal correlation for BW and varied and often close to zero direct and maternal genetic correlations with other growth traits. While direct genetic response of WW was low, all other growth traits showed significant linear correlated responses, in contrast, however, to the low (and negative for the S line) maternal correlated responses.

In spite of the rather large imposed environment treatment effect (as evidenced by the dramatic differences in growth rates in Chapter 3), no evidence of line x environment interactions was manifested. However, in concurrence with literature reports, significant sire x year interactions were found for all the growth traits, which serves to highlight the tremendous seasonal differences experienced in the sub-tropics. Therefore there is a need to consider selection for genotypic stability, particularly for the more extensive farming environments.

Genetic parameters of the pre-weaning weight traits (W90, W150 & W205) were remarkably similar to those of WW and showed high direct and maternal correlations with WW, suggesting that any one of these traits can be used in the genetic evaluation of calf growth to weaning. However, the genetic parameters for the pre-weaning gains (G1, G2 and G3) were variable with low direct and maternal heritability estimates and a significant proportion (67-85%) of the total phenotypic variation was not accounted for. This suggests that the genetic expressions of these traits is masked and are therefore not useful in the genetic evaluation of calf pre-weaning growth.

CHAPTER 5

COW FERTILITY AND CALF SURVIVAL TO WEANING

5.1 INTRODUCTION

Fertility and survival are of paramount importance to all livestock enterprises and to this end these traits should be included in beef cattle breeding objectives (Newman *et al.*, 1992; Ponzoni, 1992; Goyache *et al.*, 2003; Kadarmideen & Wegmann, 2003; Prayaga, 2004). However, the genetic analysis of such traits, particularly in range beef cattle, have received little attention as they are difficult to measure and interpret (Donoghue *et al.*, 2004a; Prayaga, 2004). This is partly due to the low additive genetic variation and (or) an excess of non-heritable variation; the difficulty and time span required to measure them; information not directly recorded; expression of the trait constrained by the management system, and to the categorical expression of the phenotype of many traits. As a result, it is generally considered that there is limited potential to genetically improve fertility and calf survival in beef cattle (Patterson *et al.*, 1987; Cubas *et al.*, 1991; Davis *et al.*, 1993; Morris *et al.*, 2000, Gutiérrez *et al.*, 2002; Rust & Groeneveld, 2002; Prayaga, 2004).

It has been assumed that categorical traits, such as calving success and survival rates, where the observed value falls into two mutually exclusive classes, have an underlying normal distribution, with the observed values being determined by thresholds (Dempster & Lerner, 1950). However, until the early 1990's, the distributions of the binomially distributed traits, in many instances had not been taken into consideration, and were analyzed with linear models, violating the assumption of normal distribution of the observed values. Heritability estimates of binomially distributed traits on the observed scale derived from linear models have been underestimated and estimates were dependent on the mean of the trait, in contrast to estimates derived from the use of threshold models (Koots *et al.*, 1994).

The genetic analysis of categorically distributed traits has by in large been overcome with the availability of distribution free techniques (e.g., Bayesian analyses) (Gianola, 1990) and appropriate transformations with mixed models (e.g., logit transformation for binomially distributed data in ASREML) (Gilmour *et al.*, 2002). While nonlinear models have theoretical advantages over linear models for discrete traits (Gianola, 1980), Matos *et al.* (1997) reported that there were no advantages between these models with respect to goodness of fit or predictive ability for discretely distributed reproductive traits in sheep.

No completely satisfactory measure of reproduction has been found (Gutiérrez *et al.*, 2002; Rust *et al.*, 2004). Ponzoni (1992) advocates the use of calving day (defined as the day number in which the cow calved within the season) over calving success (defined as the presence or absence of a calf at calving). The prediction and estimation of a quasi-continuous trait with linear models are straightforward and the analysis of calving day includes genetic variance within cows calving, distinguishing between early and late calvers. Furthermore, days to calving are easy to record and economically important as heavier calf weaning weights are associated with early calving (Buddenberg *et al.*, 1990).

While the inclusion of a predicted date for non-calvers for calving day increases the additive genetic variation and heritability of the trait (Buddenberg *et al.*, 1990), some researchers have had to assign arbitrary values for non-calvers (Ponzoni & Gifford, 1994; Johnston & Bunter, 1996). Since 1993, the days to calving has been routinely analyzed and reported for beef cattle in Australia and New Zealand (BREEDPLAN: Schneeberger *et al.*, 1991; Johnston *et al.*, 2001). However, in the analyses of tropical data with large yearly fluctuations in fertility, O’Neill *et al.* (1997) note that the assignment of a predicted value to calving day ensures that a large proportion of non-calvers in a year of particularly low fertility (especially in lactating cows) would be allocated this value. This procedure would be expected to reduce the normality of the trait, which is not readily overcome by transformations (Ponzoni & Gifford, 1994).

Heritability estimates for fertility traits have been found to be considerably higher in heifers than in cows (Koots *et al.*, 1994; Rust & Groeneveld, 2001), which have been attributed to the culling of infertile cows thereby reducing the genetic variance (Johnson & Notter, 1987). Age at first mating has also been found to influence heritability of pregnancy success and Dias *et al.* (2002) reported estimates of 0.37±0.03 at 18 months vs. 0.08±0.03 at 27 months in Nelore heifers. In general higher heritabilities for days to calving rather than calving success have been reported (Johnston *et al.*, 2001; Rust & Groeneveld, 2001; Donoghue *et al.*, 2004b). Recent studies have however reported relatively high estimates for pregnancy rate in heifers (0.14 to 0.37) (Evans *et al.*, 1999; Doyle *et al.*, 2000; Dias *et al.*, 2002), which have been attributed to the adoption of adequate procedures to handle categorical traits.

Recording of survival traits in extensively managed range beef cattle is problematic and survival data are often derived from presence or absence of live-weights at certain ages/weighings in the course of the animals' life, with survival from birth to weaning being commonly reported. Perinatal survival (within 24-48h of birth) is of major concern in both the beef and dairy industry. Patterson *et al.* (1987) reported that of the total losses up to weaning in beef cattle, 67% were recorded within the first 48 hours, while Prayaga (2004) found that 80% of pre-weaning mortalities had occurred within the first week of birth, 50% of which were due to abortions. In both the beef and dairy industry, losses have been reported to be twice as high in heifers than in cows (Harbers *et al.*, 2000; Meyer *et al.*, 2001; Goyache *et al.*, 2003).

Perinatal heritability estimates for survival traits are typically low, but are reported to be twice as high in beef (0.15 in heifers and 0.10 in cows) (Koots *et al.*, 1994) compared with dairy cattle (Luo *et al.*, 1999; Harbers *et al.*, 2000). Studies indicate that stillbirths in heifers and in cows are different traits (Philipsson, 1996; Harbers *et al.*, 2000). Philipsson (1996) suggests the biological reason for the difference may be due to calf size relative to cow size.

Late mortality, occurring from the perinatal period to weaning is generally considered to be caused by environmental factors such as sporadic disease or accidental losses (Bellows *et al.*, 1987; Patterson *et al.*, 1987). Consequently genetic studies on late calf mortality are scarce (Goyache *et al.*, 2003; Tarrés *et al.*, 2005).

Adequate nutrition, particularly at critical stages of the cows' production cycle, is requisite to maximize fertility. While it is widely accepted that a rising plane of nutrition, and corresponding weight gain, will stimulate resumption of normal ovarian activity *postpartum*, studies have shown a strong relation between the body weight *per se* and conception (Ward, 1968; Lammond, 1970; Richardson *et al.*, 1975). The recording of body weight of the reproductive cow is relatively easy, although it is a crude attempt to express body condition, which is one of the most important factors likely to affect the cow's ability to reconceive (van Niekerk, 1982). Fertility in the tropics is relatively poor compared with temperate regions and is largely attributed to poor nutrition of the breeding female, compounded by other environmental stresses such as heat, humidity and parasites.

The objectives of the chapter are to quantify the genetic and environmental factors affecting cow fertility and calf survival to weaning and to determine the presence and importance of a genotype x environment interaction for measures of fertility and survival.

5.2 MATERIALS AND METHODS

A detailed description of the experimental design and units is given in Chapter 2.

5.2.1 Fertility and survival traits

Two measures of fertility, calving success (CS) and calving date (CD), were analyzed. CS was defined as the presence (1) or absence (0) of a calf, where the presence of a calf included abortions at term (>8 months) and stillbirths. As the mating season start date was not known with certainty (particularly for the pre-crossover period), CD as opposed to 'days to calving' was analyzed. Calving date was taken as the number of days from a base date of 1st September (approximately three weeks before the start of the calving season). Non-calvers were assigned a penalty date equal to the last day of calving within year-environment cohort plus 21 days (Johnston & Bunter, 1996). The constant is equal to one estrous cycle and suggests that open cows would have calved given an extra cycle with the bull. Donoghue *et al.* (2004a) reported that while a simulated date for non-calvers provided a better fit to the data than the assignment of a 21day penalty, differences between methods were small and either method can be successfully used for genetic analyses of days to calving. Days to calving and CD yield the same information when the joining date of the cohort is the same (Rust & Groeneveld, 2001). However, in this study, no adjustments were made to account for 5.4% cows calving after the start of the mating season. Hence the measures of fertility analyzed in this study were recorded on the same animal and only differed in definition.

Typically perinatal survival, particularly in the dairy industry, is defined as calf survival to 48h, and includes stillbirths. In this study however, with daily inspection of cows, only observations up to 24h from birth were available. Thus for all cows calving, abortions at term (>8 months) and stillbirths (STIL), analyzed as a trait of the cow, was defined as the presence of a live (1: birth weight present) or dead (0: calving date but no birth weight) calf. Calf survival between birth and 205d (SURV) was analyzed as a trait of either the cow or the calf and was defined as alive (1) or dead (0) at 205 days.

In the analyses of all the traits, data for heifers and cows were combined for two primary reasons. The age at first mating of heifers in the pre-crossover phase was at three years compared with two years in the post-crossover phase, and secondly, the small number of observations in the line-year-environment cohorts (ranging from 4 to 16 for number of matings in the post-crossover phase), resulted in very few observations per sire (one third of the total of 193 sires with less than five observations on heifer matings).

5.2.2 Fixed and random effects

Fixed effects considered for all traits analyzed were year of mating, line, environment, age of dam and previous lactation status (PLS: heifer, suckling or not suckling a calf in the previous season). After perusal of means for the various dam age groups, it was found that age of dam effect on CS and calf growth traits were similar and hence the following categories were assigned: 3, 4, 5 to 7, 8 to 10, and >10 years. The effects of dam age and PLS were concatenated to account for confounding of heifer age and PLS, yielding nine classes. For the fertility traits, the effects of year, line and environment were concatenated to account for interaction with years.

For the survival traits, year-environment contemporary groups were defined and line was fitted as a separate effect. Data were discarded where contemporary groups showed no variation (i.e. no losses). Furthermore, for STIL, it was obvious that no attempt had been made pre-1983 to capture all calving activities (i.e. abortions and stillbirths) and hence only post-1982 data was considered. Age of dam categories for >10 years were recoded to 8-10 years to account for lack of variation in the >10 years and previously not suckling group. The sex of calf was not known with the indirect method of determination of calf loss at birth for STIL, and hence could not be used as a fixed effect in the analyses.

Calving date (relative to a base date of 1st September), calf sex (male or female) and calf birth weight were taken into account for SURV. Calving date and birth weight were treated as linear and quadratic covariates, deviated from their means, and divided by their standard deviations.

Random effects of the animal (cow or calf), maternal genetic, service sire, and repeated measurements on either the cow or dam were considered for all the traits. Records on foundation cows were discarded in the analyses of traits of the cow, as well as records for the first progeny crop of heifers mated in 1961 due to confounding of age of dam, PLS and year of mating. Records were also discarded where there were less than five observations per sire.

5.2.3 Model building

The binomially distributed traits (CS, STIL and SURV) were analyzed with the ASREML programme by fitting a univariate animal model with a logit link function to link the binomially distributed data to the normal distribution (Gilmour *et al.*, 2002). The F ratio was used to determine the significance of the fixed effects, after which significance of the addition of random effects were tested individually. The LogL ratio is not a good indicator of whether to include or exclude a random effect with a logit model. Hence the REML estimate of variance component divided by the square root of the diagonal element of the inverse of the average information matrix (Component/SE) (Gilmour *et al.*, 2002) and standard error of the variance ratio were adopted to give an indication of the significance of a random component, where a Component/SE ratio of less than 1 or standard error of more than twice the variance ratio indicated non-significant contribution to the model fit.

The ASREML algorithm was also utilized to analyze both CS and CD, assuming these traits were normally distributed traits (linear approach). The analysis of the CS was undertaken to determine the effect of ignoring the binomial distribution the trait. The general model used in matrix notation was:

$$Y = \mathbf{X}ß + \mathbf{Z}_1 a + \mathbf{Z}_2 m + \mathbf{Z}_3 c + \mathbf{Z}_4 c + e$$

where: Y is the vector of observations;

ß is the vector of fixed effects (line-year-environment with 114 levels and age of dam-previous lactation status with 9 levels);

X is the incidence matrix that associates ß with Y;

a is the vector of breeding values for direct genetic effects;

m is the vector of breeding values for maternal genetic effects;

c is the vector of permanent environmental effects due to cow;

s is the vector of effects due to service sire;

$\mathbf{Z}_1$, $\mathbf{Z}_2$, $\mathbf{Z}_3$ and $\mathbf{Z}_4$ are the incidence matrices that associate a, m, c and s with Y and

e is the vector of residual effects.

The (co)variance structure of random effects have been described in Chapter 4.2.2.

CS breeding values (tbv) were derived from the back transformation of the animal solutions on the underlying scale, bv, to the probability scale, tbv, by the formula: $tbv = 1 / (1+e^{-bv})$ (Neter *et al.*, 1983). Correlations of breeding values for sires with more than 10 daughters with mating records were used to determine the relation between CS analyzed with nonlinear procedures and CD analyzed with linear procedures. In addition, the genetic correlation between CD and CS was estimated in a bivariate analysis using the MTDFREML programme and following procedures outlined in Chapter 4.2.3.

5.2.4 Measurement of genotype x environment interaction

The ASREML programme with a logit link was used for all binomially distributed traits to test for the presence of a line x environment interaction. For CS, the post-crossover data set after the mating season had reverted to 90d (1983 to 1997) was used, similarly for STIL (as discussed above), whereas the complete crossover data set (1977 to 1997) was analyzed for the calf survival traits. The random effects found to be of importance in the analyses of the full data sets were included as well as all possible fixed effects: however effects of year, line and environment were separated and the two way interaction of line x environment was included. The F ratio was employed to test for a significant interaction.

Considering the full dataset, additional random components of sire x environment, sire x year and sire x year-environment were individually included in the univariate analyses of CD. The difference of minus twice the log likelihoods with $\chi^2_{.05}$ test with one degree of freedom was used to determine if the addition of a random factor significantly improved the model fit (Meyer & Hill, 1992).

5.2.5 Analyses of heifer and cow body weights

A comment often passed by personnel managing the experiment was that the cows from the supplemented line were ‘bigger’ than those from the non-supplemented line. Condition scores of cows were recorded in the later years of the trial (1988 to 1997), but these were separately scored by numerous technicians, and preliminary analyses revealed little variation. Hence weights at four stages of the year, perceived to have important effects on fertility, were studied in the post-crossover phase:

a) Minimum body weight (measured at the end of the dry season in October);

b) Body weight at the start of the mating season (December for the S and February for the NS environments respectively);

c) Body weight at the end of the mating season (March for the S and May for the NS environments respectively); and

d) Peak body weight (measured at the end of the growing season in May).

In addition to the above weights, total weight gain (peak weight less minimum weight) and weight gain over the mating season were also investigated. The weights and weight gains of heifers (three-year-olds) and mature cows (five to ten year olds) were analyzed separately to account for the different physiological status of the breeding females (growing *vs.* mature).

All weights and gains were analyzed using the GLM procedure of SAS (1985). Fixed factors affecting weights considered in the analyses were line, environment, year of mating, pregnancy status and for cows dam age as a linear and quadratic covariate and previous lactation status. All possible two-way interactions were considered and retained in the final model if significant ($P<0.05$).

5.3 RESULTS AND DISCUSSION

5.3.1 Cow fertility

A summary of the data description after final editing is given in Table 5.1. The relatively low incidence for CS of 68% out of 8862 matings is in accordance with estimates reported in literature (Table 1.1) and compares favourably with a value of 61% for field data for Afrikaner cattle obtained in South Africa for the period 1976 to 1998 (Rust & Groeneveld, 2002).

Table 5.1 Incidence and number of records (including censored data) used for analyses

	Calving success	Abortions and stillbirths	Calf loss	
			Trait of the cow	Trait of the calf
Incidence (SD), %	68.1 (46.6)	3.8 (19.2)	7.9 (27.0)	7.9 (26.9)
Records	8862	3047	5726	6818
Cows	1545	807	1290	-
(records per cow)	(5.7)	(3.8)	(4.4)	-
Sires	193	134	171	214
(records per sire)	(45.9)	(22.7)	(33.5)	(31.9)
Dams	889	522	799	1578
(records per dam)	(10.0)	(5.8)	(7.2)	(4.3)
Service sires	212	120	209	-
(records per service sire)	(41.8)	(25.4)	(27.4)	-
Line-Year-Environment	114	-	-	-
Year-Environment	-	30	71	80
Dam age-previous lactation status	9	7	9	9

A total of 193 sires and 889 dams were represented in the analyses of CS and CD (Table 5.1). Variance ratios for all random effects were low (<10%: Table 5.2). The direct heritability estimates for CS (nonlinear model) was similar to that of CD. However, repeatability estimates (repeated measurements on the cow) for CD were higher than those for CS. Service sire contributed to model fit but variance ratios were very low (0.01-0.02). Heritability estimates for the analyses of both CS (nonlinear) and CD within heifers (mated to calve at 4 in the pre-crossover or at 3-years of age in the post-crossover phases) and cows were the same as for the combined datasets (not presented); however, estimates of service sire variance were 0.05 for the heifer dataset in both analyses.

Table 5.2 Variance ratios (expressed as a proportion of phenotypic variance) for measures of fertility

	Calving success		Calving date	
	Nonlinear	Linear	Without SY[1]	With SY[1]
Log likelihood	-	-	-36134.0	-36127.6
Direct heritability	0.08+0.019	0.05+0.013	0.09+0.019	0.08+0.019
Repeatability	0.10±0.017	0.07±0.012	0.17±0.016	0.17±0.013
Service sire	0.02+0.006	0.01+0.004	0.01+0.004	0.01+0.004
Sire x year	-	-	-	0.02±0.006
Intraclass correlation coefficient (t)				0.81

[1] Sire x year interaction

As expected, a lower estimate of direct heritability was obtained for CS analyzed with a linear model. Transformation of the estimate to the underlying normal scale as proposed by Lush *et al*. (1948) by the equation $h_n^2 = h^2(1\text{-p})p/z^2$, where h_n^2 is the heritability on the underlying normal scale, h^2 is the heritability on the observable binomial scale, p is the population frequency of the trait and z is the normal ordinate for p, increased the estimate to 0.09.

The heritability and repeatability estimates for CS and CD in this study concur with more recent literature estimates (0.02 to 0.11 and 0.02 to 0.11 for CS; 0.03 to 0.39 and 0.10 to 0.26 for CD, respectively) (Rust & Groeneveld, 2001; Meyer & Johnston, 2003). In their linear analyses of 209,000 records of field data for Afrikaner cattle in South Africa, Rust & Groeneveld (2002) found no evidence of additive genetic variation for CS, in contrast to the nonlinear analyses of CS in a selected data set (sires used in more than four herds with more than 75 offspring), where a heritability estimate derived from sire variance components of 0.27 was reported.

Across years a marked variation (P<0.001) between lines and environment for CS was evident (Figure 5.1). The dramatic fluctuations immediately post-crossover could be attributed to a number of factors. Firstly, the crossed lines would either experience an increased (S/NS) or decreased (NS/S) inter-mating period for the first year of mating post-crossover (1977). Secondly, the mating season from 1977 to 1982 was decreased from 90 day to 65 day, and thirdly, the supplementation regime was altered significantly (see Section 2.2 and 2.3).

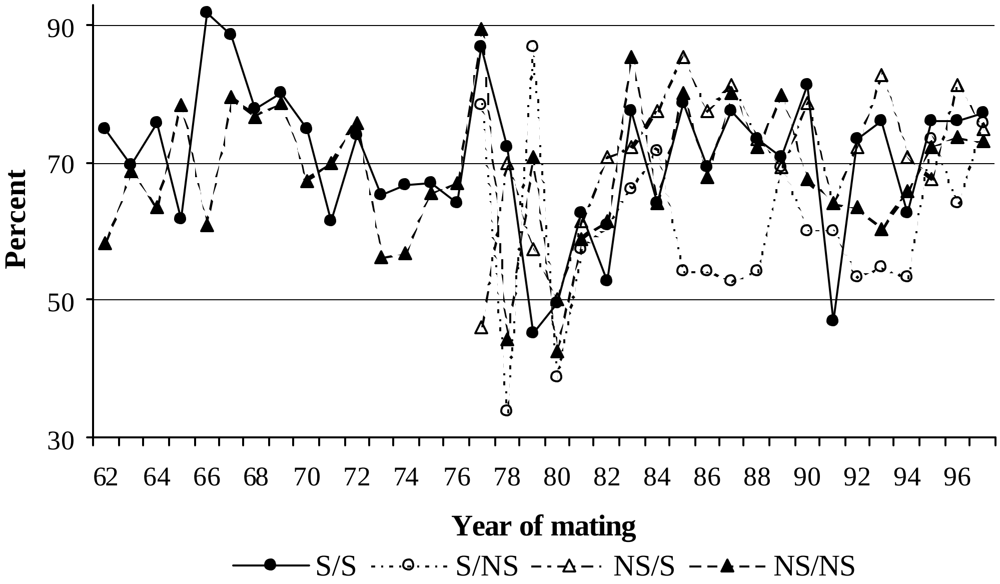


Figure 5.1 Yearly trends for calving success (%)

The higher CS of the S line in the pre-crossover phase presumably reflects the very high dry season supplementation regime (9kg maize silage and 1kg jack-bean hay) (Figure 5.2). All the lines responded adversely to the reduced length of mating season immediately post-crossover and showed an average CS of 60%, which corresponds well with the CS of 56% reported by Moyo (1990) for Afrikaner cows subjected to a 70d-mating season in a similar environment. A classic genotype x environment interaction occurred ($P<0.05$) upon reverting to a 90d mating season with the NS/S line showing the greatest response in CS of 16 percentage units, followed by the S and NS control lines with a 12 and 10 percentage units increase respectively. However, S line cattle reared in the NS environment only responded by two percentage units and in addition, appeared to be more sensitive than the other sub-lines to the droughts experienced in 1985 and in 1992 to 1994 (Figures 2.1b & 5.1).

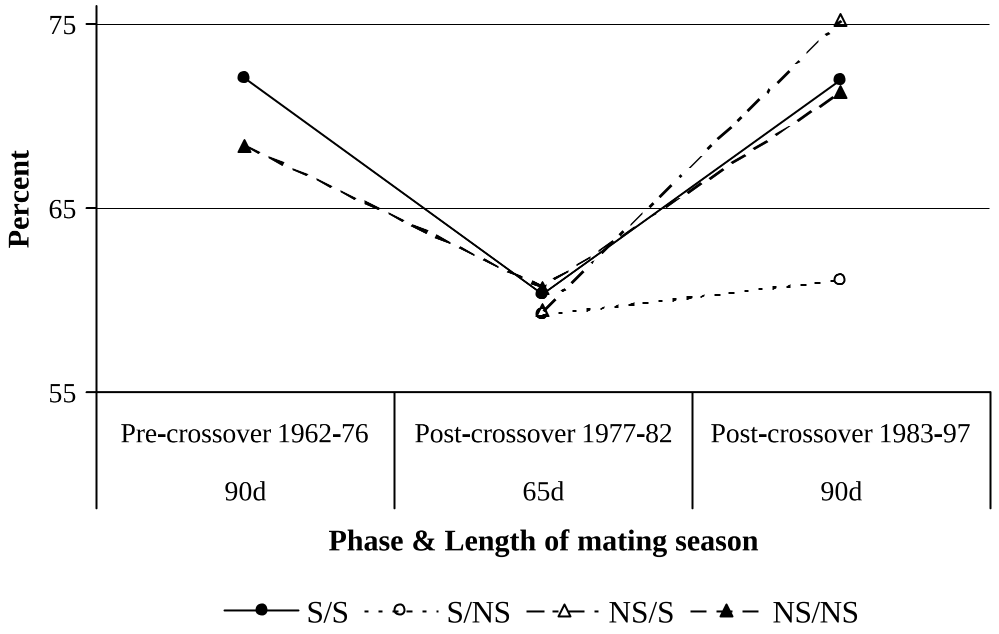


Figure 5.2 Effect of experimental phase and length of mating season on calving success

The average CD in the NS environment ranged from 51 to 58 days later than the S environment, despite the fact that cows in the NS environment are joined 65 days later (Table 5.3). This was due to different calving patterns (Figure 5.3), where presumably, a larger proportion of cows in the NS environment would have been gaining weight for several months, and would therefore be more receptive to the bull at the start of their mating season in mid-February, compared with their S counterparts. The effect of assigning a penalty value to non-calvers resulted in marked bimodal distributions, while calving period for the S line in the pre-crossover extended well beyond expectation as discussed in section 2.5.

Table 5.3 Effect of experimental phase and length of mating season on calving date (days) prior to assignment of values to non-calvers

		Experimental phase		
		Pre-crossover	Post-crossover	
		1962-76	1977-82	1983-97
		Length of mating season		
Line	Environment	90 days	65 days	90 days
S	S	72	60	76
NS	S		63	74
S	NS		117	125
NS	NS	126	121	126
Difference between environments		54	58	51

Age of dam-previous lactation status was the most important fixed effect affecting CS and CD, the effect being similar to that shown for calf growth traits (Chapter 3) where CS increased with dam age peaking at 5 to 7 years, before declining for dams older than 10 years (Figure 5.4). The effect of suckling a calf in the previous season was most pronounced for first calvers (four-year-old cows) of 51 percentage units and was also marked for older cows (24 to 27 percentage units). The performance of heifers was lower than that of 'dry' cows between four to ten years, while the performance of 'dry' cows greater than 10 years declined by 15 percentage units. Similar effects of PLS were reported by Hetzel *et al.* (1985). In their report on a selection experiment for pregnancy rate in the tropics, Davis *et al.* (1993) found a marked effect of PLS of 19 and 39 percentage units on first calvers (3-year-old cows) in the 'Low' and 'High' lines, respectively. Frisch (1989) found that the detrimental effect of PLS increased when CS was low – the latter being described as an indicator of environmental stress. In contrast, Archer *et al.* (1998) reported 8 percentage units higher pregnancy rates for cows that had calved in the previous year, and while the pregnancy rate of first lactation cows and older cows were lower than that of other age groups, the differences were only 10 percentage units.

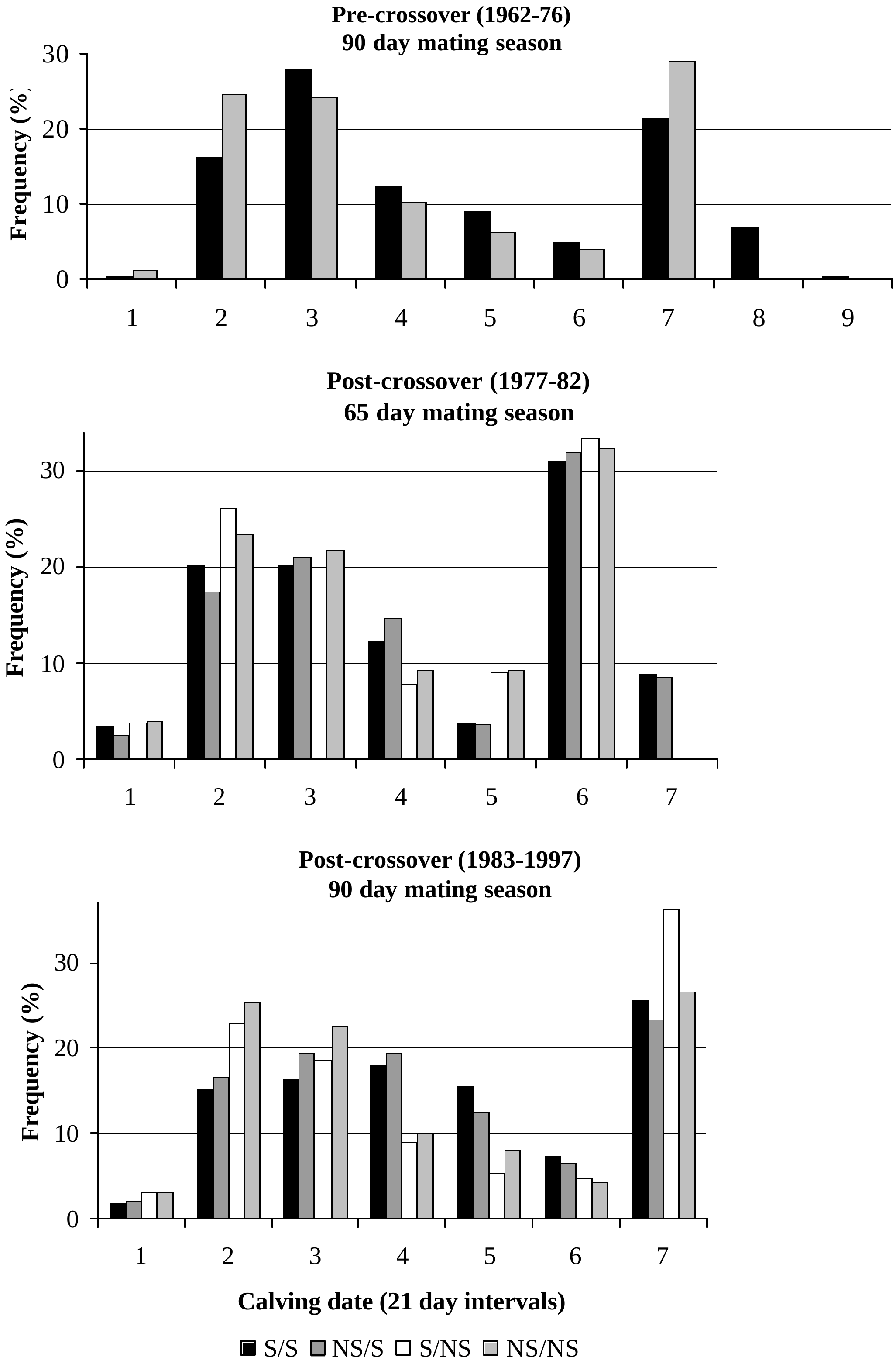


Figure 5.3 Calving distribution by crossover phase and length of mating season

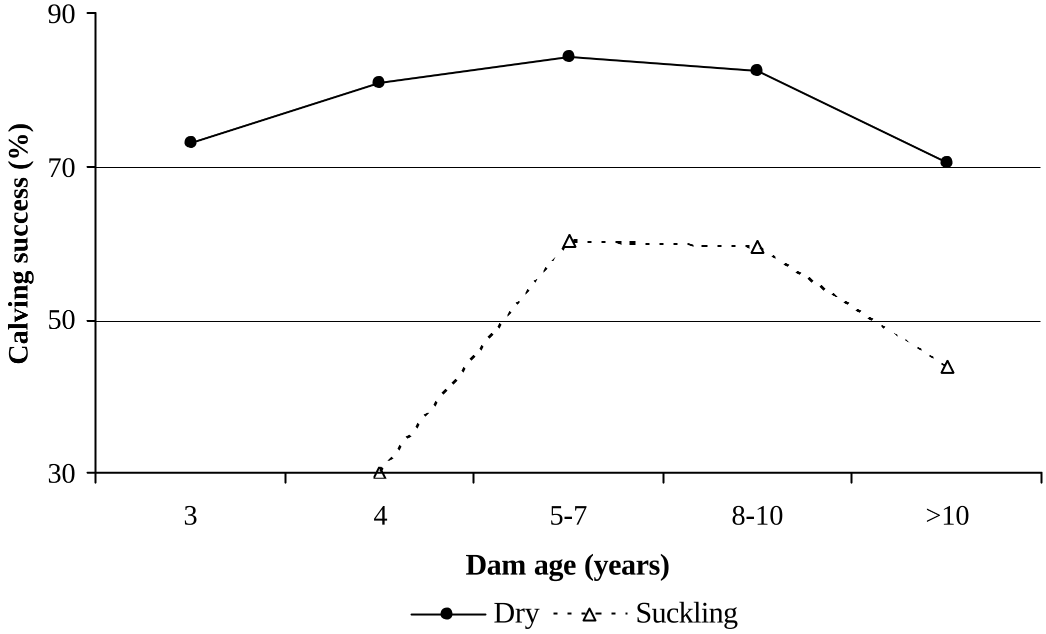


Figure 5.4 Effect of age of dam and previous lactation status on calving success

5.3.2 Calf survival

Calf losses within the first 24h of 3.8% (Table 5.1) in this study compares favourably with literature estimates for both beef (3.0-4.9%) (Morris *et al.*, 1992; Goyache *et al*, 2003) and dairy cattle (5.4-7.0%) (Weller *et al.*, 1998; Harbers *et al.*, 2000; Meyer *et al.*, 2001). Pre-weaning calf loss of 8% (of calves born alive) was disconcertingly high (Table 5.1), compared with 3.7% reported by Goyache *et al.* (2003) for field data of the Asturiana de los Valles beef breed in Spain and 4.1% reported by Morris *et al.* (1992) in growth selection experiments with Angus and Hereford cattle in New Zealand. However, similar rates of loss of 6.7% were reported by Patterson *et al.* (1987) in range beef cattle over a period of 15 years in the United States.

Moyo (1990) also reported similar losses to the current study of 6.3% between birth and 90 days, and 2.2% between 90 days and weaning (at 240 days) in a study at Matopos Research Station involving over 5000 calves from a wide range of purebred and crossbred cows evaluated over a period of eight years, while Trail *et al.* (1977) reported calf losses to one year of age in Afrikaner cattle in Botswana of 8.7%.

Prayaga (2004) reported a total pre-weaning loss of 10% among a range of breeds in a tropical environment in Australia.

The variance ratios for the measures of calf losses were low (Table 5.4). The direct heritability estimate for STIL was within the range reported in the literature for beef (0.01 to 0.15) (Koots *et al.*, 1994, Goyache *et al.*, 2003; Eriksson *et al.*, 2004; Tarrés *et al.*, 2005) and dairy (0.004-0.08 in heifers and 0.001-0.12 in cows) (Weller *et al.*, 1998; Harbers *et al.*, 2000; Meyer *et al.*, 2001). Koots *et al.* (1994) reported weighted average maternal heritability estimates of 0.15 for both heifers and cows in beef cattle, compared with estimates ranging from 0.002 to 0.02 in dairy cattle (Meyer *et al.*, 2001) and of 0.03 in beef cows (Goyache *et al.*, 2003), in contrast to the apparent lack of variation due to maternal genetic effects in this study. Much lower estimates of repeatability are reported in the literature for beef (0.008 to 0.02: Goyache *et al.*, 2003) and dairy (0.05-0.06: Niskanen & Juga, 1997). Weller *et al.* (1988) reported significant service sire effect in dairy cattle quoting a 0.08 variance ratio. Buddenberg *et al.* (1990) found the service sire accounted for a significantly higher amount of variation than sire of dam in Hereford cattle, noting that variance among service sires is a source of phenotypic variance.

Table 5.4 Variance ratios (as a proportion of phenotypic variance) for measures of calf losses

	Abortions and stillbirths	Calf survival Trait of the cow	Trait of the calf
Heritability	0.15+0.069	0.02±0.017	0.07±0.033
Service sire	-	0.03±0.025	-

There are remarkably few genetic studies of calf mortality between birth and weaning. In their study of late calf mortality between birth and weaning expressed as a trait of the dam, Goyache *et al.* (2003) reported a low direct heritability (0.01) and relatively large ratio (0.10) due to repeated measurements. In contrast to the results in the current study, these authors found the genetic affects on perinatal survival and late mortality to be similar and recommended, on the basis that survival to weaning was an economically important trait, that both be included in a composite trait in beef cattle improvement programmes.

Both the effects of year-environment and dam age-PLS were important (P<0.01) in the analyses of STIL. Heifers had a greater loss compared with older dams of either previous lactation status (Figure 5.5). Interestingly, four-year old cows which had not reared a calf to at least 90 days as heifers also had higher calf losses than older cows. The greater losses in heifers concur with majority of literature reports of perinatal calf losses in both the beef and dairy industry.

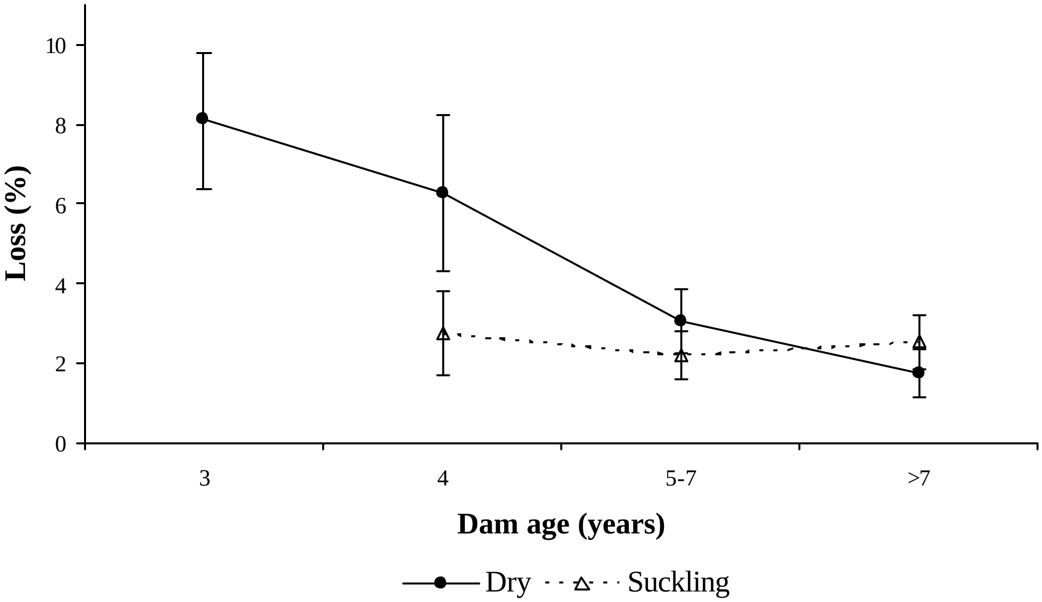


Figure 5.5 Effects of age of dam and previous lactation status on abortions at term (>8 months) and stillbirths

Linear and quadratic effects of birth weight were the most important sources of variation for SURV. Mortality was lowest for calves with average birth weights between the mean and two standard deviations above the mean (32-42kg) and increased sharply for weights below one standard deviation of the mean (<27kg: Figure 5.6). Similar effects of low birth weight on increased calf mortality were reported by Tomo *et al.* (2000), where mortality increased by 12 percentage units for Angoni calves less than 18kg at birth, while Prayaga (2004) noted higher mortalities for calves with birth weights outside 1.5 to 2 standard deviations of the mean. The effect of sex did not interact with birth weight; however, contrasts indicated mortalities were 1.7 percentage units higher among male calves, with which literature concurs (Patterson *et al.*, 1987; Luo *et al.*, 1999; Goyache *et al.*, 2003). In contrast to these results, Hetzel *et al.* (1989) found that PLS affected calf survival where cows that had suckled a calf in the previous season displayed a 10% increased calf survival rate. The lowest incidence of mortality about the mean birth weight suggests that birth weight is a fitness trait influenced by stabilizing selection towards the mean (Mather, 1973; Falconer, 1989).

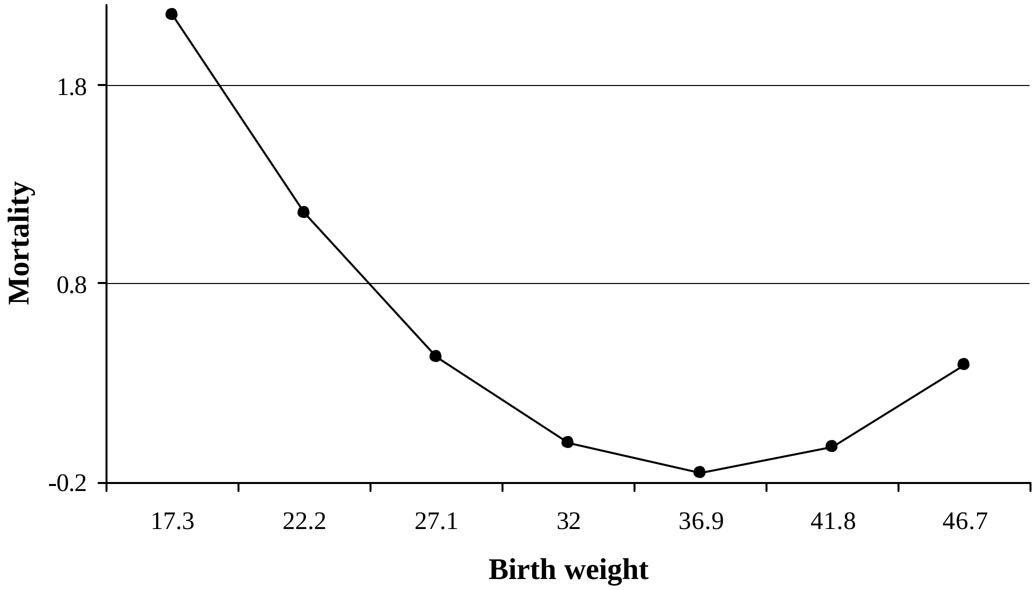


Figure 5.6 Effect of calf birth weight on calf mortality expressed in units of the underlying scale

Analyses of calf loss post-crossover did not reveal any consistent (P>0.10) line, environment, or line x environment effects (Figure 5.7). The experimental trial was under stable and constant management for the period 1978 to 1988 and thereafter underwent several management changes and together with the droughts experienced in 1992 to 1994 could be reflected in the high calf mortalities for the period 1992 to 1997 (Figure 5.7b).

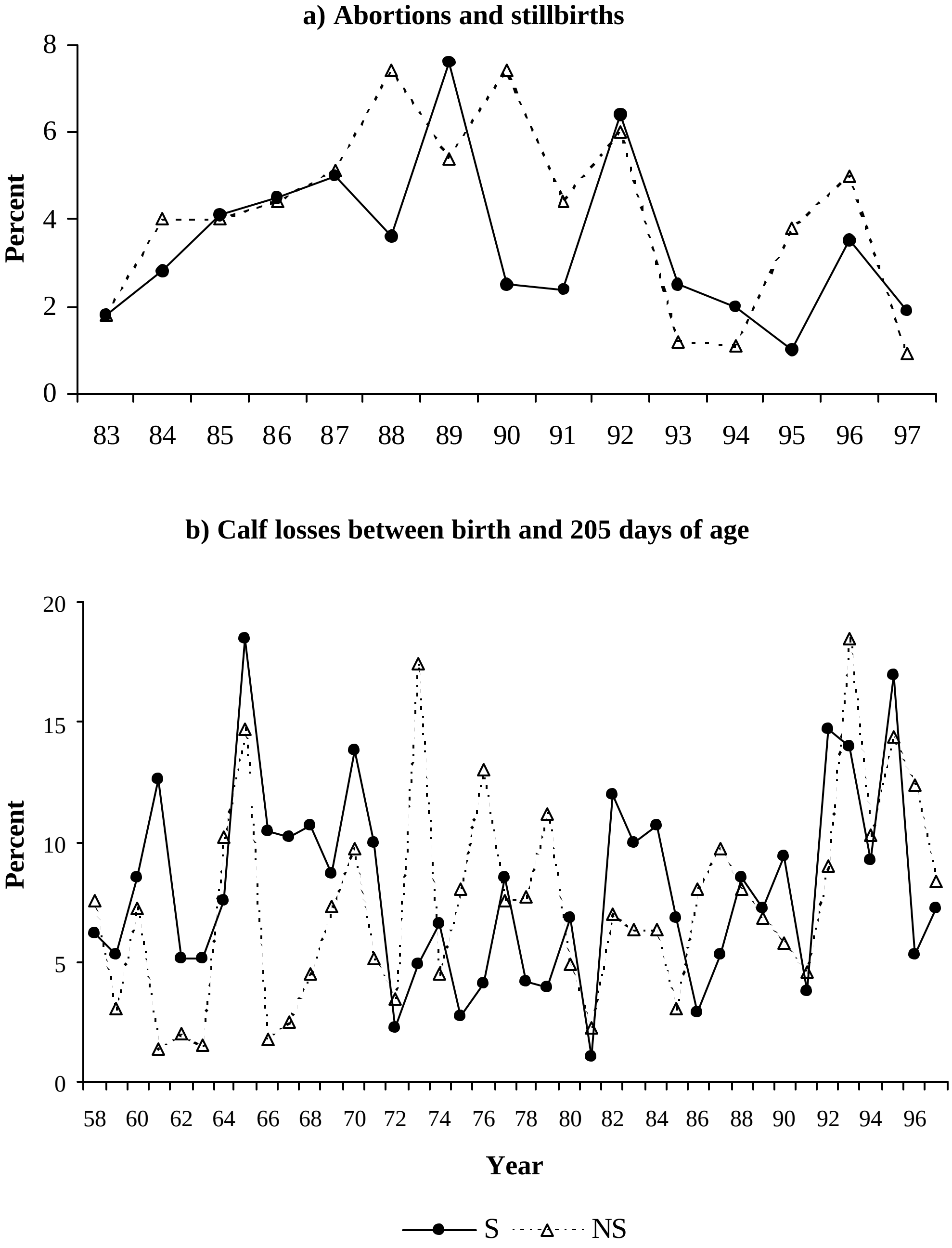


Figure 5.7 a) Abortions and stillbirths (1983-1977) and b) calf losses between birth and 205 days (1958 to 1997) within environment

5.3.3 Estimated breeding values

Estimated genetic trends for CS and CD were mirror images of each other (Figure 5.8). Base population (generation 0) estimated breeding values (EBVs) suggest that the average genetic merit of the S line for both CS and CD was markedly lower than the NS line. The genetic trends for transformed EBVs of CS for the lines differed ($P<0.05$) with the S line showing an improvement of 1.2±0.14%/generation ($P<0.01$) as against 0.8±0.13%/generation ($P<0.01$) for the NS line. However there were no line differences for CD and a favourable genetic trend of -0.8±0.09 days/generation ($P<0.01$) for both lines was shown. These results contrast to the absence of significant correlated trends for measures of female fertility in growth selection experiments in cattle (review Mercadante *et al.*, 2003). In a divergent selection experiment for pregnancy rate, Davis *et al.* (1993) reported a similar genetic trend for pregnancy rate of 0.15±0.06%/year compared with correlated trends for calving success in the current study of 0.21±0.022 and 0.13±0.022%/year for the S and NS lines respectively.

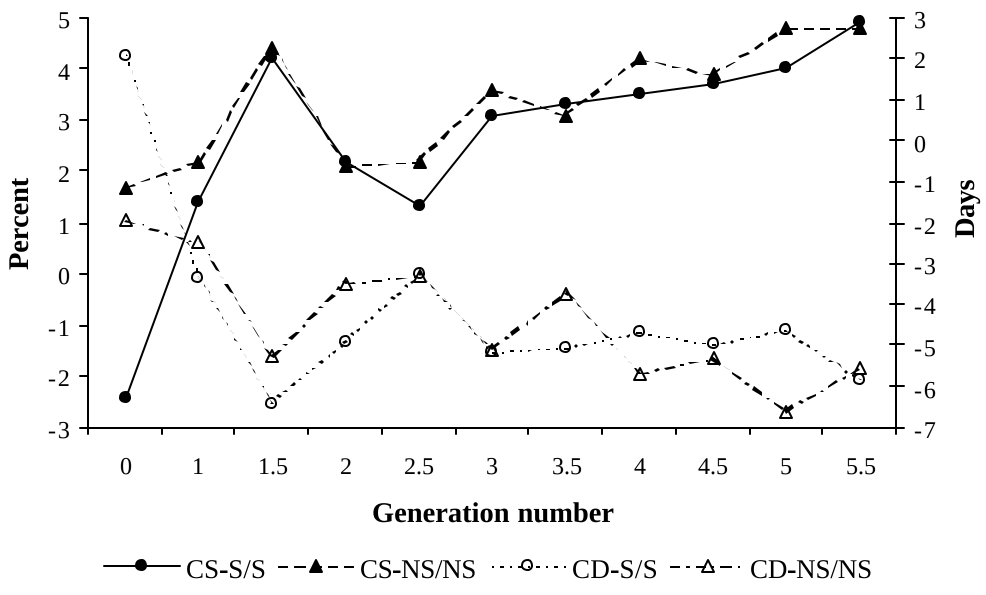


Figure 5.8 Estimated genetic trends for calving success (CS) and calving date (CD)

The correlation of sire solutions (51 sires with more than 10 daughters with mating records) from the analyses of CS with nonlinear and linear models were greater than 0.99 indicating that while the assumption of normality is clearly violated in the linear analysis, the results from the two methods are essentially the same. Similarly, correlation of sire solutions from the analyses of CS (nonlinear and linear) and CD was –0.90, while the genetic correlation from the bivariate analysis of CS (linear) and CD was –0.95 indicating that the two traits measure the same genetic variance. However, the major advantage of CD over CS is the higher repeatability estimate. Similar correlations of CS and days to calving EBVs of –0.96 and –0.99 were reported by Johnston *et al.* (2001) and Donoghue *et al.* (2004b), but their genetic correlation estimates were lower (-0.66 and –0.73, respectively). These results indicate that the higher probability of CS is associated with shorter days to calving interval. The regression coefficient for CD EBV was –1.0+0.07%/day, thus a one-day improvement in CD EBV is associated with a 1% increase in CS EBV (Figure 5.9). A similar relationship of –0.6%/day was reported by Johnston *et al.* (2001).

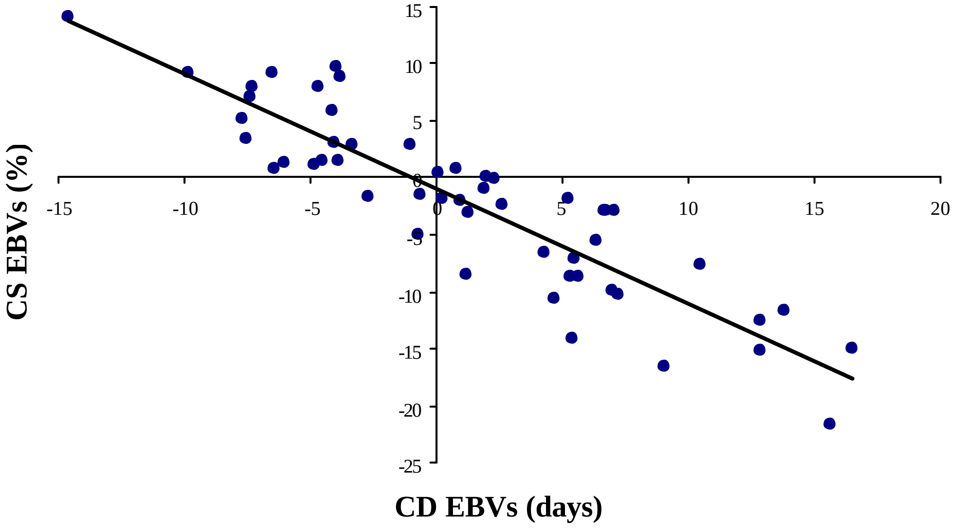


Figure 5.9 Relationship of estimated breeding values (EBVs) for calving success (CS) and calving date (CD) for 51 sires with more than 10 daughters with fertility records

The correlation of breeding values of sires (with more than 10 daughters with fertility records) between measures of cow fertility and growth traits was not significantly (P>0.05) different from zero (Table 5.5). However, in all cases the correlation was unfavourable (negative with calving success and positive with calving date) and concurs with the findings of Johnston & Bunter (1996)

Table 5.5 Correlations (and probability of estimate different to 0) of estimated breeding values of sires (with more than 10 daughters with fertility records) between measures of cow fertility and growth traits

		Calving success	Calving date
Birth weight	Direct	-0.16 (0.25)	0.17 (0.23)
	Maternal	-0.25 (0.07)	0.23 (0.10)
Weaning weight	Direct	-0.19 (0.19)	0.12 (0.38)
	Maternal	-0.05 (0.71)	0.07 (0.64)
18-month weight	Direct	-0.16 (0.26)	0.09 (0.53)
Pre-weaning daily gain	Direct	-0.26 (0.06)	0.27 (0.05)
	Maternal	-0.01 (0.95)	0.00 (0.99)
Post-weaning daily gain	Direct	-0.18 (0.20)	0.15 (0.28)

5.3.4 Influence of cow weight on calving success

Of interest is the fact that the CS of heifers displayed very similar response to that of mature cows to the length of the mating season post-crossover (Table 5.6). The low CS (63%) of heifers with a 65-day mating season is surprising given that heifers were only considered for selection if their body weight exceeded 265kg (there were a few exceptions in the drought years for the lines in the supplemented environment). The weights of all the heifers and those of selected heifers at the end of their second dry season at approximately two years of age are given in Table 5.7. Although the S line heifers were marginally heavier than their NS line counterparts, the line differences within environment were remarkably small (=4kg). Davis *et al.* (1993) also found that heifer weights in their 'High' and 'Low' pregnancy rate selection were the same, despite the higher pregnancy rate and earlier calving date of the 'High' line. On average, only 57% of the heifers were selected as replacements. However, the replacement rate was 69% for the S/NS sub-line compared with 50 to 58% for the other sub-lines. Similarly, the selection intensity was only 0.29 for the S/NS sub-line, but ranged from 0.43 to 0.53 for the other sub-lines. Referring to Afrikaner field data in South Africa, Rust *et al.* (2004) reported that only 54% of daughters of sires entered the breeding herd. As noted by Mercadante *et al.* (2003), the potential selection intensity for females in the tropics is lower given the low rates of reproduction.

Table 5.6 Effect of length of mating season on calving success (%, number of observations in parentheses) in heifers and mature cows (1977-1997)

Length of mating season[1]	Overall	Line/Environment S/S	S/NS	NS/S	NS/NS
		Heifers			
65 days	62.7 (300)	66.0 (94)	64.8 (71)	64.1 (67)	54.4 (68)
90 days	78.3 (747)	80.6 (186)	66.5 (191)	86.6 (187)	80.0 (183)
		Cows (5-10 years)			
65 days	64.7 (1148)	65.0 (297)	60.8 (250)	63.4 (265)	68.4 (336)
90 days	73.0 (2614)	75.6 (651)	64.5 (674)	76.5 (643)	75.7 (646)

[1] Mating season was 65 days for the period 1977-82 and 90 days for the period 1983-97.

Table 5.7 Heifer body weights[1] (kg), proportion selected (p), and selection differential (SD) and intensity (i) (1983-1997)

Sub-line[2]	Number	All heifers mean±sd[3]	p (%)	Selected heifers mean±sd[3]	SD (kg)	i
Overall	1309	258±37.7	57	269±34.3	10.5	0.39
S/S	338	277±34.7	55	292±29.6	14.8	0.53
S/NS	276	241±29.5	69	248±24.1	7.8	0.29
NS/S	373	272±35.7	50	287±29.7	14.5	0.53
NS/NS	322	237±31.0	58	248±25.3	10.3	0.43

[1] Taken at the end of second dry season in October at approximately two years of age;

[2] Leading symbol denotes line, trailing environment post-crossover;

[3] Standard deviation.

At the start of the mating season heifers on average weighed 325kg (70% of mature weight), gained 20% (63kg) over the mating season and were 80% of mature weight at the end of the mating season (Table 5.8). The difference between weight at the end of the mating season and peak weight was small (11kg); however, these weights were recorded at the same time for cows in the NS environment. There were no interactions between line and environment for all the heifer weights considered. Environment effects were the most important, reflecting a two-month difference in age (for minimum and peak) or different stages of the wet season (for start and end of mating). Heifers in the supplemented environment were 23kg lighter at the start of mating and 11kg heavier at the end of mating and therefore had greater weight gains of 32kg over the mating period than their NS counterparts. Line differences were small, although heifers from the S line were consistently heavier (4-7kg) than NS line heifers. Interestingly, there were no effects of pregnancy status on weights in the supplemented environment, however in the non-supplemented environment, pregnant heifers were consistently 12 to 15 kg heavier ($P<0.01$) than their non-pregnant counterparts. There were no effects on weight gains due to pregnancy status.

Table 5.8 Heifer and cow weights and weight gains (kg: 1983-1997)

		Weight				Weight gain	
	No	Min[1]	Start mating[2]	End mating[3]	Peak[4]	Total[5]	Mating[6]
Heifers	697	269	325	388	399	130	63
Cows (5-10 years)	2569	426	459	504	505	79	45

1 Minimum weight taken in October (end of second dry season) at approximately two years of age;
2 Weight taken at the start of the mating season (December for S environment and February for the NS environment);
3 Weight taken at the end of the mating season (March for S environment and May for the NS environment);
4 Peak weight taken in May (end of third wet season);
5 Total weight gain over the wet season (peak -minimum); and
6 Weight gain over the mating season.

Lowest weight of mature cows was 426kg and peaked at 505kg, also representing a 20% gain over the grazing season (Table 5.8). There were no line x environment interactions. Cows in the S environment were 24kg heavier at the worst time of the year (October), but gained less weight over the wet season than NS cows. Part of the difference in minimum weight may have been due to stage of pregnancy; however, pregnancy status did not interact with environment. For weights at the start of the mating season, the line difference was 5kg greater in the S environment, while NS line cows gained marginally more weight over the mating season. Cows in the S environment were 35 to 40kg lighter, but gained 43 to 49kg more than NS cows with the differences being greater for the NS line.

Pregnant cows that had suckled a calf in the previous season were 5 to 13kg heavier and gained 4 to 6kg more weight than empty cows, whereas effect of pregnancy status for cows that had not suckled a calf were varied across weights and weight gains. These results are consistent with findings reported in the literature where body weight is positively related to conception (Ward, 1968; Lammond, 1970; Richardson *et al.*, 1975; van Niekerk, 1982). In an experiment with Simmental cows, van Niekerk (1982) found that pregnant cows were significantly heavier than empty cows and the difference in weight decreased as body condition improved.

As discussed previously, stockmen looking after the experiment were of the impression that S line cattle were larger than the NS line. As the interaction became apparent in the mid 1980's, data on body condition score was collected against the hypothesis that the poor reproductive performance of S line cattle in the NS environment was due to their body condition being at or below a threshold necessary for successful conception. In both the analyses of heifer and mature cows weights and weight gains there was no evidence of systematic effects due to line and environment on weights that could explain the poor reproductive performance of the S/NS sub-line. However, these measures do not adequately describe the cows' body condition or frame size. The poor conception of the S line heifers in the NS environment is also difficult to explain after evaluating the weights of the groups at mating. Holness *et al.* (1978) reported that ovarian activity ceased after Afrikaner cows lost 19% of their body weight compared with Mashona cows (recognized for their higher fertility) (Moyo, 1990) which ceased ovarian activity after losing 33% of their body weight.

Morris *et al.* (1993) reported that cows of large frame size, as influenced by breed, were not adapted to less favourable environments and this was most clearly reflected in lowered reproduction. This was presumably due to larger cows being unable to sustain body conditions prerequisite for maximum fertility. However, literature estimates of effect of frame size within breed are scarce. Olson *et al.* (1989) found that smaller framed Brahman cows tended to have superior fertility. Furthermore, Kadarmideen & Wegmann (2003) reported a positive correlation between body condition score and sire breeding values for measures of fertility in dairy cattle.

The interaction serves to reinforce the commonly held principle that cattle, and in particular breeding cows, be reared in a similar environment in which selection takes place. Jinks & Connolly (1973) and Falconer (1989; 1990) reported that in general, upwards selection in a poor environment, termed 'antagonistic' selection, is advocated. Antagonistic selection has been found to decrease environmental sensitivity and improve overall selection response. Findings in this study concur with the above where, in terms of CS, the S line responded adversely to droughts in the NS environment and the mean performance of the NS sub-lines was superior to the S sub-lines.

5.4 CONCLUSIONS

A significant outcome was the manifestation of a large line x environment interaction for calving success: an overridingly important economic trait. NS line cattle reared in the S environment showed 3 percentage units higher incidence of CS to the S line controls, while S line cattle reared in the NS environment showed a 10 percentage lower incidence of CS than the NS controls (61 *vs.* 71%, respectively). While both lines showed superior incidence of CS in the S environment, suggesting that the S environment was superior for the expression of the trait, it is difficult to reconcile the large reduction in performance of the S line in the NS environment with the actual difference between environments.

A common notion held by stock handlers was that the S line cattle were ‘bigger’ than their NS counterparts and that the poorer fertility of the S line was due to certain threshold(s) not being attained for successful conception. This would be in line with the work of Holness *et al.* (1978) who reported that Afrikaner cows were anovulatory after the loss of only 19% body weight compared to 33% weight loss in Mashona. Furthermore, evidence suggests that large framed animals have poorer fertility. The analysis of cow body weight and weight gains did not provide any information towards the understanding of the poor reproductive performance of the S line. These results support literature findings that environmental sensitivity is reduced and mean performance across environments is improved by antagonistic selection, i.e. upward selection in a poor environment.

Given the low additive genetic variation for measures of reproduction, the low incidence of calving success and the apparent unfavourable genetic correlation with weaning weight (the primary selection trait), it is noteworthy that concomitant genetic improvement for measures of fertility was achieved. Similarly, in spite of the relatively small dataset and the binomial nature of survival traits, some degree of additive genetic variation was expressed for both calf survival at birth and for survival after birth. While a low heritability is taken to mean additive variation is low, Philipsson *et al.* (1997) provides evidence of large variation among sire estimates of dystocia and stillbirths in the dairy industry with incidences ranging from 2 and 27%. The very large effect of birth weight on calf survival suggest that this is a fitness trait under the influence of stabilizing selection towards the mean.

The results from the analyses of fertility and calf survival data in this study support the need to include these measures, together with birth weight and frame size, in routine genetic evaluations, breeding objectives and selection indices. There is also an urgent need to implement data collection strategies to ensure that all calving activities are comprehensively recorded, not least the adequate definition of contemporary groups.

CHAPTER 6

GENERAL CONCLUSIONS

Several factors detracted from the ability to extract useful information from this experiment. In the 'creation' of two environments, the supplementation regime was totally confounded with the mating/calving season. Secondly, the low cumulative selection differentials suggest that emphasis was placed on secondary traits and consequently very low direct selection responses in the lines were obtained for calf weights at weaning, the primary selection trait. However, central to the design was that selection within two lines subjected to different environments would establish lines adapted to their respective environments. Thirdly, the rate of supplementation in the pre-crossover phase was unsustainable and well outside normal practice. Fourth, after the initiation of the crossover, only sires were 'crossed' over environments, while replacements heifers were generated within sub-line. Therefore only half the 'genetics' was tested in the new environment, while heifer selection within heifer sub-line catered for any element(s) of adaptation.

It is important to appreciate the dramatic differences in production environment both within and across seasons in the sub-tropics, being principally determined by the quantity and distribution of rainfall. The large within season variation, compounded by the long calving season, complicated the analyses of performance data in this study. The imposed environmental treatments had a marked effect on calf growth and cow fertility. No effects were apparent for birth weight, however calves in the NS environment manifested poorer calf weights and weight gains from birth to 18-months of age and late born calves in the NS environment were on average 90kg (33%) lighter than their early S counterparts at 18 months. These results highlight the need to match management systems with the production environment to ensure superior cow fertility and calf growth rates. A recommendation is to mate animals to calve prior to the onset of the rains in semi-extensive rangelands as experienced at Matopos research station.

There were no indications of line x environment interaction for all the growth traits; however, and central to the stated objective of the experiment, an important line x environment interaction was manifested for the incidence of calving success due to the poor performance of S line cows in the NS environment. A significant line effect for calving success took place in spite of the low selection pressure and response for weaning weight. While the analyses of cow weights and weight gains did not assist with the identification of reason(s) for the dramatically poorer performance of S line cattle reared in the NS environment, it is presumed that these cows were unable to attain certain threshold(s) for successful conception and calving. However, body weight *per se* is a poor indicator of frame size and body condition. An apparent conclusion from the foregoing is that maximum cow fertility is dependant on the relation between cow size and environment. In spite of the commonly advocated mating period of 45 days, it is noteworthy that a mating period of 65 days imposed in this study suppressed the incidence of calving success to 60% for all lines. The interaction serves to reinforce the commonly held principle that cattle, and in particular breeding cows, be reared in a similar environment in which selection takes place.

While no sire x environment interactions were manifested, significant sire x year interactions were found for all the growth traits and for CS, which serves to highlight the tremendous seasonal differences experienced in the sub-tropics. Therefore there is a need to consider selection for genotypic stability, particularly for the more extensive farming environments. These results also support the notion that reduced environmental sensitivity and improved mean performance is best achieved by ‘antagonistic’ selection, i.e. upward selection in a poor environment.

With the exception of birth weight, all genetic parameters were similar to commonly published estimates as well as those for Afrikaner cattle in South Africa. In this study direct heritability for birth weight was lower. There was no apparent direct-maternal genetic relationship and genetic correlations with other traits were variable and often close to zero. This could be an artifact of the data or could reflect the very pronounced maternal behaviour of the Afrikaner cow. Similarly, the genetic properties of calf weight gains between birth, 90, 150 and 205-days of age were erratic and direct and maternal heritabilities were low, in contrast to calf weights at 90, 150 and 205-days which displayed very similar genetic properties to weaning weight.

Despite an apparent unfavourable genetic relationship between measures of calf growth and cow fertility, this study revealed that concomitant genetic improvements in both growth and fertility were attainable. Furthermore, genetic variation, albeit very low, was exhibited for measures of calf survival at birth and between birth and weaning. It is therefore recommended that fertility and survival be included in routine breed evaluations. However, procedures need to be urgently put in place that ensures that all calving activities are comprehensively recorded, not least the adequate definition of contemporary groups. The most efficient way to improve the average genetic merit is through a selection index that not only incorporates fertility and survival traits, but also takes into account optimum birth weight and frame size.

The remarkable stability of the performance of the Afrikaner across production environments is probably related to many generations of selection under harsh environmental conditions. It is however regrettable that the popularity of recent (less stable genotypes) has led to the demise of the Afrikaner in Zimbabwe, even in the extensive production areas.

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Appendix 1 Number, means and standard deviations (SD) for calf weights (kg)

		Pre-crossover: 1958-76		Post-crossver: 1977-97			
				Line: S		Line: NS	
Variable	Statistic	Line:S	Line: NS	Envr: S	Envr: NS	Envr: S	Envr: NS
Birth weight	Number	1494	1326	1036	892	1069	1001
	Mean	33.8	31.3	32.6	32.5	30.8	31.4
	SD	4.81	4.64	4.61	4.97	4.80	4.86
90 day weight	Number	1402	1265	965	828	1000	933
	Mean	108	96	106	102	104	101
	SD	16.2	15.7	16.4	16.0	16.3	15.4
150 day weight	Number	1452	1272	953	820	985	924
	Mean	150	133	152	141	149	139
	SD	21.7	19.9	21.1	21.7	22.0	20.9
205 day weight	Number	1449	1265	948	821	984	917
	Mean	180	152	181	159	177	156
	SD	27.3	23.6	26.0	25.7	26.2	25.0
Weaning weight	Number	1446	1270	946	822	981	921
	Mean	192	152	193	158	189	155
	SD	33.3	26.1	30.8	27.5	30.9	26.4
Age at weaning	Mean	247	201	249	198	250	196
	SD	28.1	22.8	26.4	22.9	25.9	23.0
12-month weight	Number	1342	1178	816	812	956	793
	Mean	198	154	189	159	187	152
	SD	34.3	26.2	27.6	26.0	29.4	23.6
Age at 12-month weighing, days	Mean	339	292	344	293	345	290
	SD	28.6	23.1	26.3	22.9	25.6	23.6
18-month weight	Number	1221	1049	755	745	898	733
	Mean	285	237	289	262	289	251
	SD	39.1	32.4	34.9	35.5	37.2	29.7
Age at 18-month weighing, days	Mean	551	504	554	504	556	500
	SD	28.3	22.9	26.5	22.6	25.7	23.0

Appendix 2 Number, means and standard deviations (SD) for calf weight gains (g/day)

		Pre-crossover: 1958-76		Post-crossver: 1977-97			
				Line: S		Line: NS	
Variable	Statistic	Line:S	Line: NS	Envr: S	Envr: NS	Envr: S	Envr: NS
Gain 0-90days	Number	1380	1239	964	828	998	932
	Mean	815	716	816	768	813	770
	SD	153.2	154.9	142.0	140.2	143.9	139.3
Gain 90-150days	Number	1399	1260	953	818	985	923
	Mean	742	610	758	648	744	635
	SD	210.5	186.2	197.7	188.4	203.1	185.1
Gain 150-205 days	Number	1448	1265	948	820	984	917
	Mean	542	347	535	331	518	303
	SD	230.1	197.3	209.7	182.4	196.6	191.5
Pre-weaning gain (0-205days)	Number	1425	1239	947	821	982	916
	Mean	716	588	724	617	715	607
	SD	129.1	113.3	121.2	122.4	122.0	121.8
Early post-weaning gain (WW-12 months)	Number	1342	1177	816	812	956	792
	Mean	86	30	7	14	-15	14
	SD	166.8	115.1	121.9	102.5	110.4	94.3
Post-weaning gain (12-18 months)	Number	1221	1045	754	744	897	732
	Mean	413	403	483	489	484	472
	SD	103.2	91.2	95.0	94.0	96.9	86.1

Appendix 3 Proportion of variance accounted for by the fixed effects models for calf weights (kg) and weight gains (g/day)

	Calf weight at:						
Effect	Birth	90 days	150 days	205 days	Weaning	12 months	18 months
Model (R^2)	30.3	39.7	38.9	50.1	64.1	58.9	60.4
Line-Year-Environment	13.7	15.0	21.0	31.9	40.6	42.7	43.1
Sex	6.2	4.3	5.0	4.2	2.9	2.5	6.1
Dam Age-PLS[1]	4.3	6.0	5.9	5.0	3.6	2.8	1.5
Birth date-Linear	4.6	0.2	1.4	4.6	10.3	6.4	6.5
Birth date-Quadratic		0.5	0.3	0.1			
Age-linear		14.7	4.5	1.1			

	Calf weight gain between:					
	0-90 days	90-150 days	150-205 days	0-205 days	WW-12 months	12-18 months
Model (R^2)	25.1	42.1	48.7	51.1	49.4	50.8
Line-Year-Environment	17.9	23.8	35.0	33.1	42.6	43.9
Sex	2.5	2.6	0.5	2.8	0.3	4.6
Dam Age-PLS[1]	5.2	1.6	0.7	3.9	0.6	0.2
Birth date-Linear	0.0	9.0	7.7	6.9	3.6	0.7
Birth date-Quadratic	0.7			0.1		

1. Previous lactation status

Appendix 4 Fixed effect solutions (±se) for calf weights (kg) and weight gains (g/day)

	Weight at:						
Effect	Birth	90 days	150 days	205 days	Weaning	12 months	18 months
BIRTH DATE-LINEAR	0.0472	0.0238	-0.1540	-0.3379	-0.9063	-0.4898	-0.5566
s.e.	0.00243	0.00800	0.01054	0.01165	0.01158	0.01285	0.01715
Birth date-quadratic		-0.0015	-0.0015	-0.0019			
s.e.		0.00022	0.00029	0.00032			
Age –linear		0.7274	0.5744	0.3291			
s.e.		0.01638	0.02180	0.02400			
Sex: male-female	2.49	7.0	10.3	12.0	12.5	12.6	21.9
s.e.	0.091	0.29	0.38	0.42	0.41	0.47	0.64
PLS[1]:dry-lactating	1.21	3.3	5.7	6.7	6.7	5.7	5.3
s.e.	0.131	0.43	0.57	0.63	0.62	0.70	0.94

	Gain between:					
	0-90 days	90-150 days	150-205 days	0-205 days	WW-12 months	12-18 months
Birth date-linear	-0.2274	-3.1890	-3.3335	-1.9009	1.237	-0.3925
s.e.	0.08346	0.10166	0.10843	0.05591	0.06253	0.05024
Birth date-quadratic	-0.0177			-0.0055		-0.0004
s.e.	0.00233			0.00154		0.00141
Sex: male-female	49	68	33	47	15	49
s.e.	3.8	3.8	4.1	2.0	2.4	1.9
PLS[1]:dry-lactating	24	43	28	27	-3	-8
s.e.	4.5	5.6	6.0	2.8	3.5	2.8

[1] Previous lactation status

Appendix 5 Parameters used in the derivation of standard errors for realised heritabilities after six generations of selection (Falconer, 1989, page 211)

	Supplemented								
Parameter[1]	BW	W90	W150	W150	WW	G1	G2	G3	ADG
ΔF	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014	0.014
Ne	35	35	35	35	35	35	35	35	35
M	145	133	133	132	132	133	133	132	132
$\sum S$	9.08	22.8	19.8	46.1	88.1	197	330	505	174
R	1.64	2.5	3.8	7.6	13.4	12	42	11	24
V_a	7.07	15.7	28.4	66.8	99.4	872	3358	1782	1347
V_P	18.00	180.3	349.5	493.0	565.6	18507	28221	32935	10783
V_d	1.20	2.7	4.8	11.3	16.9	148	571	303	229
V_e	0.12	1.4	2.6	3.7	4.3	139	212	250	82
V_R	1.33	4.0	7.4	15.1	21.2	287	783	553	311
h_R^2	0.18	0.11	0.19	0.16	0.15	0.06	0.13	0.02	0.14
se	0.13	0.09	0.14	0.08	0.05	0.09	0.08	0.05	0.10
h_a^2	0.39	0.09	0.08	0.14	0.18	0.05	0.12	0.05	0.13
se	0.07	0.04	0.04	0.05	0.05	0.03	0.05	0.04	0.05

	Non-supplemented								
Parameter[1]	BW	W90	W150	W150	WW	G1	G2	G3	ADG
ΔF	0.011	0.011	0.011	0.011	0.011	0.011	0.011	0.011	0.011
Ne	46	46	46	46	46	46	46	46	46
M	129	116	113	112	112	116	113	112	112
$\sum S$	5.84	7.3	30.8	64.8	64.2	16	384	609	291
R	2.25	2.3	5.4	9.3	10.0	6	40	12	29
V_a	5.09	14.4	68.7	75.6	80.3	858	3188	1326	1732
V_P	17.46	176.1	308.8	377.2	386.8	18928	22922	24992	8558
V_d	0.67	1.9	9.0	9.9	10.5	112	417	174	227
V_e	0.14	1.5	2.7	3.4	3.5	163	203	223	76
V_R	0.80	3.4	11.7	13.3	14.0	275	620	397	303
h_R^2	0.38	0.32	0.18	0.14	0.16	0.34	0.10	0.02	0.10
se	0.15	0.25	0.11	0.06	0.06	1.01	0.06	0.03	0.06
h_a^2	0.29	0.08	0.22	0.20	0.21	0.05	0.14	0.05	0.20
se	0.07	0.04	0.06	0.05	0.06	0.03	0.06	0.03	0.05

[1] ΔF is the inbreeding per generation; Ne is the effective number = $1/(2\Delta F)$; M is the number of observations at generation 6; $\sum S$ is the cumulative selection differential; R is the total response; V_a and V_P are the within line REML estimates of the additive and phenotypic variances; V_d and V_e are the variances due to random drift and measurement error; V_R is the variance of the realised heritability; h_R^2 is the realized heritability = $R/\sum S$ with se = $\sqrt{V_R}/\sum S$; h_a^2 is the REML estimate of the direct heritability

Appendix 6 Univariate model parameters for calf growth traits

Trait[1]/ Estimates[2]	*Model[1] (‘best’ model in bold italics[3])*					
BW	A	AC	***AM***	AMR	AMC	AMCR
Log L	25287.5	25203.0	***25143.9***	25142.4	25143.6	25142.1
h_T^2	55	47	***46***	47	47	47
h_a^2	55±2.5	47±3.1	***39±3.3***	36±4.2	40±3.4	36±4.2
h_m^2			***14±1.7***	13±2.0	13±2.4	12±2.5
r_{am}				15±12.4		15±12.7
c^2		9+1			1+1.4	1+1.4
e^2	45	47	***47***	49	47	49
s_p^2	18.67	18.31	***18.53***	18.47	18.48	18.43
W90	A	AC	AM	AMR	***AMC***	AMCR
Log L	38563.2	38141.9	38162.7	38159.7	***38100.5***	38100.1
h_T^2	36	13	24	21	***16***	15
h_a^2	36±2.7	13±2.4	8±2.0	10±2.5	***10±2.2***	11±2.5
h_m^2			32±1.9	36±2.9	***11±2.6***	12±3.1
r_{am}				-26+11.7		-12+17.5
c^2		26±1.6			***17±2.2***	17±2.3
e^2	64	61	60	59	***62***	62
s_p^2	180.3	172.3	187.5	187.1	***173.8***	173.8
W150	A	AC	AM	AMR	AMC	***AMCR***
Log L	42455.8	41791.9	41848.1	41839.3	41754.2	***41749.4***
h_T^2	43	16	32	25	20	***16***
h_a^2	43+2.7	16+2.6	11+2.2	15+3.0	14+2.5	***17±3.3***
h_m^2			41±1.9	48±2.9	11±2.7	***15±3.5***
r_{am}				-34±8.6		***-35±12.9***
c^2		32±1.6			23±2.4	***23±2.5***
e^2	57	52	48	46	52	***51***
s_p^2	342.2	326.8	374.9	371.8	330.1	***329.1***
W205	A	AC	AM	AMR	AMC	***AMCR***
Log L	43957.5	43017.0	43075.0	43063.4	42972.4	***42963.6***
h_T^2	47	15	36	29	21	***16***
h_a^2	47±2.5	15±2.5	11±2.0	15±2.8	14±2.4	***18±3.2***
h_m^2			50±1.7	58±2.8	14±3.1	***19±3.9***
r_{am}				-35±7.7		***-43±11.2***
c^2		40±1.6			27±2.7	***28±2.8***
e^2	53	45	39	38	45	***43***
s_p^2	457.9	438.2	526.9	519.7	444.0	***441.1***

Appendix 6 (cont)

WW	A	AC	AM	AMR	AMC	***AMCR***
Log L	44315.5	43102.9	43176.9	43157.1	43056.5	***43043.5***
h_T^2	50	15	39	29	22	***19***
h_a^2	50±2.4	15±2.4	11±1.9	16±2.8	14±2.3	***19±3.3***
h_m^2			56±1.6	66±2.7	15±3.2	***21±4.2***
r_{am}				-41±6.6		***-49±9.9***
c^2		45±1.6			31±2.9	***32±3.0***
e^2	50	40	34	31	40	***38***
s_p^2	490.6	470.3	587.9	579.0	477.5	***475.5***

W12	A	AC	AM	AMR	AMC	***AMCR***
Log L	41575.1	40599.6	40646.4	40623.6	40552.3	***40537.3***
h_T^2	49	15	37	26	22	***14***
h_a^2	49±2.6	15±2.6	10±2.0	16±3.1	13±2.5	***19±3.6***
h_m^2			53±1.7	65±2.9	17±3.5	***26±4.6***
r_{am}				-47±6.8		***-53±9.5***
c^2		42±1.7			27±3.0	***27±3.1***
e^2	51	43	37	34	42	***40***
s_p^2	546.2	518.7	632.0	621.5	531.5	***529.2***

W18	A	AC	AM	AMR	AMC	***AMCR***
Log L	39726.5	39469.8	39480.4	39474.2	39439.9	***39433.3***
h_T^2	52	32	39	35	34	***31***
h_a^2	52±3.0	32±3.8	25±3.5	32±5.3	28±3.8	***36±5.7***
h_m^2			28±2.1	34±3.3	11±2.8	***15±3.7***
r_{am}				-29±8.9		***-37±11.3***
c^2		21±1.7			14±2.3	***14±2.3***
e^2	48	47	47	43	47	***44***
s_p^2	755.4	725.2	777.6	776.7	734.0	***733.3***

G1	A	AC	AM	AMR	***AMC***	AMCR
Log L	38650.6	38258.5	38276.8	38266.0	***38218.4***	38215.4
h_T^2	28	6	18	12	***10***	8
h_a^2	28±2.7	6±1.8	3±1.4	6±2.0	***4±1.6***	6±2.0
h_m^2			30±1.8	37±2.9	***11±2.4***	14±3.3
r_{am}				-56±11.3		-39±17.6
c^2		25+1.5			***16±2.2***	15+2.2
e^2	72	69	67	65	***69***	68
s_p^2	18588	17832	19159	19137	***17962***	17983

Appendix 6 (cont)

G2	A	AC	AM	AMR	AMC	***AMCR***
Log L	40838.8	40657.4	40692.5	40686.2	40649.0	***40642.0***
h_T^2	27	11	19	14	12	***8***
h_a^2	27±2.7	11±2.3	10±2.3	13±3.0	10±2.3	***13±3.1***
h_m^2			18±1.8	24±2.8	4±1.9	***8±2.7***
r_{am}				-40±11.6		***-57±14.2***
c^2		16±1.4			12±1.9	***13±1.9***
e^2	73	74	72	71	74	***72***
s_p^2	26416	25356	26584	26507	25469	***25423***
G3	A	AC	AM	AMR	***AMC***	AMCR
Log L	41832.5	41753.3	41752.7	41748.6	***41739.9***	41736.4
h_T^2	15	4	8	8	***6***	5
h_a^2	15±2.4	4±1.6	3±1.6	5±2.1	***3±1.5***	5±2.1
h_m^2			10±1.4	14±2.3	***5±1.6***	7±2.4
r_{am}				-54±17.2		-57±19.5
c^2		10±1.2			***6±1.6***	6±1.6
e^2	85	86	87	86	***87***	86
s_p^2	28189	27490	27907	27915	***27566***	27589
ADG	A	AC	AM	AMR	AMC	***AMCR***
Log L	34279.0	33364.2	33425.0	33404.3	33322.8	***33307.1***
h_T^2	45	12	34	23	18	***10***
h_a^2	45±2.6	12±2.3	9±1.8	13±2.6	11±2.2	***15±3.0***
h_m^2			50±1.7	60±2.8	13±3.1	***21±4.1***
r_{am}				-48±7.5		***-57±10.1***
c^2		40±1.6			28±2.8	***28±2.8***
e^2	55	48	42	40	48	***46***
s_p^2	10084	9601	11519	11324	9723	***9667***
EPWG	A	***AC***	AM	AMR	AMC	AMCR
Log L	31934.7	***31903.9***	31905.4	31904.8	31905.4	31904.8
h_T^2	20	***13***	16	14	14	12
h_a^2	20±2.7	***13±2.6***	12±2.7	13±3.3	12±2.6	13±3.4
h_m^2			7±1.5	8±2.2	3±1.6	4±2.1
r_{am}				-17±18.6		-27±21.6
c^2		***6±1.3***			4+1.6	5+1.6
e^2	80	***81***	82	81	82	81
s_p^2	9006	***8842***	8935	8933	8935	8934

Appendix 6 (cont)

PWG	A	AC	***AM***	AMR	AMC	AMCR
Log L	26403.8	26396.2	***26378.3***	26375.0	26378.3	26375.0
h_T^2	32	29	***27***	26	27	26
h_a^2	32±3.1	29±3.3	***24±3.5***	29±5.2	24±3.6	29±5.3
h_m^2			***6±1.5***	9±2.4	6±1.8	9±2.9
r_{am}				-32±13.7		-32±13.0
c^2		3±1.2			0±1.5	0±1.6
e^2	68	68	***70***	67	70	67
s_p^2	5540	5499	***5469***	5498	5467	5498

1. See text for trait definitions and model descriptions;
2. Log L is the log likelihood; t^2 is the total heritability; h_a^2, h_a^2, c^2 and e^2 are the direct additive and maternal genetic effects, the maternal permanent environment and residual effects expressed as a percent of the phenotypic variance; r_{am} is the correlation between additive and maternal genetic effects (x100); s_p^2 is the phenotypic variance;
3. ‘Best’ model determined by $C^2_{.05}$=3.84 test of the difference of minus twice the log likelihoods.

Appendix 7 Genetic trends for calf growth traits by generation number[1]

	Direct		Maternal	
Trait[2]	Supplemented	Non-supplemented	Supplemented	Non-supplemented
BW	0.22±0.016**	0.44±0.014**	-0.02±0.007*	0.15±0.007**
W90	0.34±0.019**	0.61±0.018**	-0.13±0.020**	0.45±0.021**
W150	0.73±0.032**	1.26±0.036**	-0.43±0.029**	0.35±0.032**
W205	1.45±0.038**	1.92±0.043**	-0.63±0.040**	0.10±0.043*
WW	2.35±0.045**	2.22±0.047**	-1.07±0.046**	-0.15±0.047**
YW	1.38±0.034**		-0.88±0.053**	0.38±0.054**
W18	3.23±0.093**	2.88±0.094**	-0.82±0.054**	0.12±0.044*
G1	1.52±0.104**	2.33±0.114**	-0.74±0.206**	3.46±0.238**
G2	6.78±0.161**		-1.88±0.162**	-0.96±0.157**
G3	2.29+0.077**		2.35+0.161**	-0.21+0.157ns
ADG	4.98±0.150**	6.28±0.165**	-2.81±0.189**	-0.34±0.220ns
EPWG	1.81±0.181**	0.65±0.138**	-0.50±0.061**	0.13±0.050*
PWG	4.44±0.230**	2.01±0.221**	-1.46±0.104**	-0.21±0.079*

1 Regression coefficients (± standard errors) for calf weights (kg.generation^{-1}) and weight gains (g.generation^{-1}), either within line where significantly different (P<0.05) or pooled across line;

2 Trait definitions given in text and Table 3.1;

3 ns - non-significant; † - P<0.10; * - P<0.05; ** - P<0.01: probabilities of regression being different from zero;

Appendix 8 Annual genetic trends for calf growth traits[1]

	Direct		Maternal		Environmental	
Trait[3]	Supplemented	Non-supplemented	Supplemented	Non-supplemented	Supplemented	Non-supplemented
BW	0.04±0.002**	0.07±0.002**	-0.00±0.001ns	0.02±0.001**	-0.07±0.014**	
W90	0.05±0.003**	0.09±0.003**	-0.02±0.003**	0.007±0.003**	0.03±0.043ns	
W150	0.11±0.005**	0.20±0.006**	-0.07±0.005**	0.06±0.005**	0.14±0.060*	
W205	0.23±0.007**	0.31±0.007**	-0.10±0.007	0.02±0.007**	0.04±0.092ns	
WW	0.38±0.007**	0.35±0.007**	-0.17±0.007**	-0.01±0.008ns	-0.04±0.110ns	
YW	0.22±0.006**		-0.15±0.009**	0.07±0.009**	-0.17±0.122ns	
W18	0.52±0.015**	0.46±0.015**	-0.14±0.007**	0.02±0.008**	0.32±0.164†	
G1	0.24±0.017**	0.36±0.018**	-0.12±0.035**	0.58±0.037**	0.2±0.62ns	2.0±0.62**
G2	1.11±0.026**		-0.34±0.025**	-0.14±0.026**	1.5±0.70*	
G3	0.38±0.012**		0.37±0.025**	-0.02±0.026ns	-0.1±0.90ns	
ADG	0.79±0.026**	0.99±0.027**	-0.45±0.033	-0.01±0.033ns	0.7±0.046ns	
EPWG	0.26±0.026**	0.11±0.027**	-0.08±0.009**	0.03±0.009**	-4.1±1.15**	0.1±1.15ns
PWG	0.72+0.036**	0.32+0.037**	-0.24+0.015**	-0.04+0.015*	3.2+0.59**	

1 Regression coefficients (± standard errors) for calf weights (kg.y^{-1}) and weight gains (g.y^{-1}), either within line where significantly different ($P<0.05$) or pooled across line;

2 Trait definitions given in text and Table 3.1;

3 ns - non-significant; † - $P<0.10$; * - $P<0.05$; ** - $P<0.01$: probabilities of regression being different from zero.

Appendix 9 Mean genetic parameters (+ se of mean) derived from univariate and 12 bivariate analyses for calf weights and weight gains

	Parameter estimate[1]						
Trait[2]	h_T^2	h_a^2	r_{am}	h_m^2	c^2	e^2	σ_p
BW	0.47	0.36 ± 0.001	0.15 ± 0.003	0.12 ± 0.001	0.01 ± 0.000	0.48 ± 0.001	4.30 ± 0.001
W90	0.15	0.12 ± 0.003	-0.15 ± 0.021	0.13 ± 0.003	0.17 ± 0.002	0.61 ± 0.003	13.2 ± 0.01
W150	0.16	0.17 ± 0.006	-0.37 ± 0.022	0.15 ± 0.004	0.24 ± 0.002	0.50 ± 0.004	18.2 ± 0.01
W205	0.16	0.18 ± 0.005	-0.42 ± 0.014	0.19 ± 0.005	0.28 ± 0.005	0.43 ± 0.003	21.1 ± 0.02
WW	0.16	0.19 + 0.006	-0.45 + 0.032	0.22 + 0.007	0.31 + 0.006	0.38 + 0.003	21.9 + 0.02
W12	0.15	0.18 ± 0.003	-0.50 ± 0.015	0.25 ± 0.006	0.27 ± 0.004	0.41 ± 0.005	23.3 ± 0.06
W18	0.31	0.32 ± 0.009	-0.27 ± 0.031	0.13 ± 0.005	0.14 ± 0.001	0.46 ± 0.007	27.4 ± 0.08
G1	0.08	0.07 ± 0.002	-0.40 ± 0.017	0.14 ± 0.004	0.16 ± 0.002	0.67 ± 0.003	135 ± 0.2
G2	0.08	0.14 ± 0.003	-0.61 ± 0.014	0.09 ± 0.003	0.14 ± 0.003	0.71 ± 0.003	160 ± 0.2
G3	0.04	0.05 ± 0.001	-0.50 ± 0.012	0.07 ± 0.002	0.06 ± 0.002	0.85 ± 0.001	166 ± 0.1
ADG	0.11	0.15 ± 0.002	-0.56 ± 0.015	0.20 ± 0.002	0.28 ± 0.002	0.46 ± 0.001	99 ± 0.1
EPWG	0.13	0.13 ± 0.000	-0.25 ± 0.010	0.05 ± 0.004	0.04 ± 0.004	0.80 ± 0.001	94 ± 0.0
PWG	0.27	0.33 ± 0.007	-0.39 ± 0.012	0.09 ± 0.002	0.01 ± 0.001	0.64 ± 0.005	74 ± 0.1

1. h_T^2, h_a^2, h_m^2, c^2 and e^2 are the total heritability, direct and maternal genetic effects, the maternal permanent environment effect and residual variance; r_{am} is the correlation between direct and maternal genetic effects; σ_p is the phenotypic standard deviation;
2. BW=birth weight; W90, W150 and W205=weights at 90, 150 and 205 days, WW=weaning weight; W12 and W18=weights at 12 and 18 months; G1, G2 and G3=gain between birth and 90 days, 90 and 150 days and 150 and 205 days; ADG pre-weaning average daily gain between birth and 205 days; EPWG=early post-weaning gain between WW and W12; PWG=post-weaning gain between W12 and W18.

Appendix 10 Genetic and phenotypic correlations for calf growth traits (x100)

Direct genetic (r_{AxAy}) above diagonal and phenotypic (r_{PxPy}) correlations below

Trait[1]	BW	W90	W150	W205	WW	W12	W18	G1	G2	G3	ADG	EPWG	PWG
BW		82	67	58	58	56	46	47	15	-12	33	3	20
W90	43		88	85	86	75	57	90	44	27	71	-16	25
W150	38	86		99	96	83	73	83	81	59	92	-31	46
W205	34	78	91		99	88	81	84	86	71	96	-22	49
WW	33	76	87	94		95	79	83	81	73	94	-6	43
W12	19	74	84	89	93		84	67	67	75	82	22	39
W18	33	66	75	78	80	82		49	69	71	78	19	81
G1	11	94	81	73	71	71	60		43	36	82	-17	23
G2	13	23	69	64	62	60	52	21		68	88	-32	59
G3	3	10	11	49	44	44	38	10	15		78	44	27
ADG	14	72	87	98	91	86	74	74	63	52		16	47
EPWG	-3	-3	-2	-1	-1	37	20	-2	2	2	0		1
PWG	15	8	8	7	4	-4	54	3	4	0	3	-19	

Maternal genetic (r_{MxMy}) correlations

Trait[1]	BW	W90	W150	W205	WW	W12	W18	G1	G2	G3	ADG	EPWG	PWG
BW		27	19	19	21	23	28	-6	12	17	2	5	5
W90			96	96	96	93	82	95	75	82	94	25	-32
W150				99	99	97	92	94	92	86	99	39	-28
W205					100	97	93	91	94	90	99	36	-32
WW						99	93	90	92	89	98	43	-46
W12							91	88	91	88	96	61	-59
W18								70	91	83	90	23	0
G1									79	77	93	24	-44
G2										86	94	47	-35
G3											89	-7	-17
ADG												34	-31
EPWG													-67

[1] See Table 3.1 for trait definitions BW=birth weight; W90, W150 and W205=weights at 90, 150 and 205 days, WW=weaning weight; W12 and W18=weights at 12 and 18 months; G1, G2 and G3=gain between birth and 90 days, 90 and 150 days and 150 and 205 days; ADG pre-weaning average daily gain between birth and 205 days; EPWG=early post-weaning gain between WW and W12; PWG=post-weaning gain between W12 and W18.

cont/

Appendix 10 (cont):

Direct-maternal genetic (r_{AxMy}) correlations

Trait[1]	Maternal: BW	W90	W150	W205	WW	W12	W18	G1	G2	G3	ADG	EPWG	PWG
Direct:													
BW		10	2	2	0	-8	-10	5	5	14	-2	-32	-11
W90	36		-21	-32	-41	-46	-19	-25	-49	-20	-41	-16	16
W150	33	2		-37	-47	-53	-32	-12	-66	-34	-43	-40	12
W205	27	-25	-47		-45	-52	-35	-26	-69	-38	-51	-29	0
WW	13	-34	-50	-44		-54	0	-32	-63	-24	-51	-38	1
W12	2	-39	-46	-43	-49		-35	-32	-55	-36	-41	-47	12
W18	15	0	-16	-12	8	-17		6	-42	-8	-14	-23	-15
G1	45	-27	-35	-41	-51	-48	-17		-57	-27	-50	1	23
G2	17	-3	-28	-29	-38	-39	-22	-10		-25	-35	-36	8
G3	-14	-44	-53	-51	-52	-45	-43	-35	-48		-52	70	-35
ADG	23	-36	-55	-53	-57	-52	-39	-36	-74	-58		-21	9
EPWG	-19	-4	15	9	7	2	2	1	29	-18	12		11
PWG	24	19	-3	2	5	10	-11	15	-25	17	-1	1	

Permanent maternal (r_{CxCy}) above diagonal and temporary environment (r_{ExEy}) below

Trait[1]	BW	W90	W150	W205	WW	W12	W18	G1	G2	G3	ADG	EPWG	PWG
BW		100	85	82	75	59	76	100	36	46	88	15	100
W90	27		99	97	97	94	92	100	98	85	96	12	-100
W150	24	80		100	99	97	98	100	99	97	100	7	-100
W205	24	66	82		99	98	99	99	100	98	100	17	-100
WW	23	62	74	86		99	100	99	100	99	100	19	-100
W12	20	63	76	80	85		100	95	100	96	98	32	-100
W18	23	59	65	67	71	74		94	43	36	82	-17	23
G1	-3	95	74	60	57	61	54		100	90	98	13	-100
G2	9	-5	59	46	43	42	32	-7		100	100	100	-100
G3	3	-8	-18	39	29	29	23	-9	-4		99	7	-100
ADG	1	60	76	98	82	75	61	61	45	42		15	-100
EPWG	-2	-5	-1	-3	-11	45	19	-5	2	-5	-3		-87
PWG	11	13	8	6	3	-10	63	8	-2	1	3	-21	

[1] BW=birth weight; W90, W150 and W205=weights at 90, 150 and 205 days, WW=weaning weight; W12 and W18=weights at 12 and 18 months; G1, G2 and G3=gain between birth and 90 days, 90 and 150 days and 150 and 205 days; ADG pre-weaning average daily gain between birth and 205 days; EPWG=early post-weaning gain between WW and W12; PWG=post-weaning gain between W12 and W18.