A STUDY OF THE GROWTH AND MATERNAL PERFORMANCE OF NGUNI AND CROSSBRED BRAHMAN AND SIMMENTAL CATTLE IN SWAZILAND

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ABSTRACT

Growth data extracted from the calf (1832) and cow (1333) record files of the Data Processing Unit - Ministry of Agriculture and Co-operatives in Swaziland were analysed. The study considered records of calves born during the period 1975 to 1978 in three Government breeding stations: Mpisi (Station 1), Lowveld (Station 2) and Highveld (Station 3). Husbandry and management procedures employed on the stations have been standardised and cattle are raised on natural pastures.

The breeds and crossbreds involved were Nguni (N), Brahman (B), Simmental (S), and B x N, S x N crosses and grades. The breed groups were not represented in all stations. The calf-breed groups were:- Station 1 (444): N (108), B (121), $\frac{3}{4}$-B (114), and $\frac{7}{8}$-B (101). Station 2 (916): N (138), $\frac{1}{2}$-B (423), $\frac{3}{4}$-B (308), and $\frac{7}{8}$-B (47). Station 3 (472): N (155), S (182), $\frac{1}{2}$-B (46), $\frac{1}{2}$-S (45), $\frac{3}{4}$-S (17) and $\frac{7}{8}$-S (27).

The birth weight (BWT), weaning weight adjusted to 210-days (WWT), and 18-month weight adjusted to 540-days (18-MTH WT) of a total of 1832 animals were analysed within stations by least squares to investigate the effects of breed/cross, sire (within breed), breed of dam, year, month of birth, age of dam, sex, and breed x year, breed of dam x year, and sire x breed of dam interactions. The results indicated that breed of calf

had a highly significant effect on all the traits at each station, ($P < 0.01$). In Station 1, the breeds ranked: $\frac{3}{4}$-B, $\frac{5}{8}$-B, B, and N for the three weights. The crossbreds were up to 3.4, 29.1 and 32.5 kg heavier than the N, and 1.9, 14.0, and 11.5 kg heavier than the B in BWT, WWT, and 18-MTH WT, respectively. Straightbred B were 6 to 9 percent superior to the N in growth to 18 months. Breed x year interactions were non-significant.

In stations 2 and 3, the interaction of breed with year was important for all traits. Some rank changes occurred between the crossbreds in each of these stations, but the crossbreds were generally heavier than the straightbreds. In Station 2, the $\frac{1}{2}$-B were, on average, 4.3, 27.3, and 46.1 kg heavier than the N in BWT, WWT, and 18-MTH WT, respectively. The $\frac{3}{4}$-B were heavier ($P < 0.01$) than the $\frac{1}{2}$-B in WWT and there were no consistent differences among the crosses in 18-MTH WT. In Station 3, $\frac{1}{2}$-S were, on average, 3.6, 24.3, and 33.0 kg heavier than the N in BWT, WWT, and 18-MTH WT, respectively. Straightbred S and $\frac{7}{8}$-S were up to 10.6 kg (38%) heavier ($P < 0.01$) than the N at birth and $\frac{1}{2}$-S were up to 11 percent superior to $\frac{1}{2}$-B in growth to 18 months.

Sire effects were non-significant for BWT and WWT, but highly significant for 18-MTH WT in Station 1. In Station 2, sire effects were highly significant for

all traits. Breed of dam effects were significant for BWT and WWT in Station 1, and for WWT only in Station 2. Progeny of crossbreds were heavier ($P < 0.01$) than those of straightbreds. Breed of dam x year and sire x breed of dam interactions were not significant.

Results on the effects of the environmental factors have indicated that year, month of birth, age of dam, and sex are important sources of variation in growth to 18 months of age. A compact calving season and regulation of the breeding season to prevent cows from calving down after November was recommended.

Comparisons of the maternal performance of the cow-breeds indicated that crossbred cows were 7 to 25 percent superior to straightbreds in weight of calf weaned. Brahmans were 9 percent better than N cows. There were no significant differences between $\frac{1}{2}$-B and $\frac{3}{4}$-B cows.

Heritabilities and genetic correlations were estimated by the paternal half-sib method. Heritability estimates were in the range 0.06 to 0.29, 0.09 to 0.12, and 0.18 to 0.53 for BWT, WWT, and 18-MTH WT, respectively. Genetic correlations were all positive, but most of the values were greater than 1. Pooled phenotypic correlations were 0.27, 0.21 and 0.67 for BWT-WWT, BWT-18-MTH WT, and WWT-18-MTH WT, respectively.

Repeatability of WWT was estimated within cow-breed by the intra-class correlation (Station 1) and the regression of later on earlier records (Station 2) methods. The estimates ranged from 0.24 to 0.39.

Investigation of the feasibility of changing the performance testing age from 18 to 14 months in the breeding stations indicated that there was insufficient data on which reliable genetic parameter estimates could be based. More work is required to provide an answer to this problem.

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CHAPTER ONE

INTRODUCTION

Beef cattle development in Swaziland is based on the improvement of the environment in which beef cattle are produced and on the improvement of the genetic merit of the national herd. It has long been established that beef production is influenced by environmental (climate, diseases, nutrition and management) and genetic (breed, within breed genetic differences) factors. It is also abundantly clear that in most parts of the tropics and sub-tropics, environmental changes in feeding and health could increase the output of beef much more rapidly than genetic improvement (Williamson and Payne, 1978). In general, however, environmental modifications are costly, relatively temporary and their implementation is largely a function of the prevailing economic climate. While genetic gains may be more modest and slow, genetic improvement for a particular environment is relatively cheap, long lasting and cost saving (Frisch and Vercoe, 1978). Moreover, since lack of genetic improvement of stock is among the primary factors contributing to the low level of returns from cattle in Swaziland (see Butterworth and Presswood, 1978), improvement of the genetic potential of the cattle will ensure that as the environment improves, more productive animals are available to exploit it.

Growth rate in beef cattle is one of the objectives of the National Breeding Programme in Swaziland

(Butterworth and Presswood, 1978). Improving Swazi cattle through recording growth rate and other traits was officially initiated in 1975 on three Government ranches and a computerised data processing unit at the Ministry of Agriculture in Mbabane was established. The breeding programme is currently based on one indigenous breed, the Nguni, and two exotic breeds, the Brahman and Simmental. Its main aim is to provide superior performance tested bulls for distribution to the Rural Development Areas (RDAS). However, there are presently not sufficient straightbred Brahman and/or Simmental females to produce the anticipated bull requirements; hence some Nguni females are upgraded towards these two breeds. At the same time the potential of the recommended breeds and crosses is evaluated to find out which type of animal is most suited to the country's various climatic zones.

Genetic improvement of a population results from underlying changes in gene frequency and/or changes in the way in which the mating system in the population permits the genes to unite as the zygotes are produced (Lush, 1945, Falconer, 1960, Turner and Young, 1969). Selection; i.e. the method of choosing the parents of future generations, is the most commonly used method of changing gene frequencies. It is based on the accurate evaluation of differences between animals so that those with better genotypes are allowed to reproduce and poor genotypes are culled. The effectiveness of selection is dependent on the genetic superiority of the selected animals in relation to the mean of the population from which they come (i.e., the selection differential), this superiority being reflected in improved performance of their progeny.

An initial requirement in any genetic improvement plan is to determine the traits of economic importance. In beef cattle, economic traits are those that contribute to productive efficiency and quality or desirability of product and they include fertility, mothering ability, growth rate, efficiency of feed use, carcass merit, and longevity (Gregory, 1965, 1971, Rae and Barton, 1970, Willham, 1976).

Growth rate in slaughter animals appears to be most important from an economic point of view. Firstly, it has been established that growth rate is highly correlated with efficiency of feed conversion under feedlot conditions Gregory, 1965, 1971). Secondly, liveweight is a good index of carcass weight, there being little variation between animals in killing-out percentage. Thirdly, fast growth means that an animal has to be kept through fewer difficult and expensive winters before reaching a killable weight. It has been observed that high weight gains are positively correlated to lean growth and that the genes for rapid growth are not antagonistic to those for the production of desirable carcasses (Seifert and Rudder, 1976). Heritability estimates for postweaning growth have been found to be moderately high and responses to selection significant (Preston and Willis, 1974, Seifert, 1975 b).

Against these advantages, rate of gain has been found to be genetically and phenotypically positively correlated with birth weight and mature size (Preston and Willis, 1974, Seifert, 1975b). Hence, selection for fast growth could lead to herds of large cows with high maintenance requirements and increased dystocia due to heavy birth weights.

Mothering ability of a cow, which is commonly assessed by the weight of its calf at weaning, is another important trait in beef production. Although this measure of mothering ability includes the combined effect of a calf's potential for growth and its dam's ability to care for it, it also reflects to a large extent, the milk production of the dam. Under pastoral conditions where calves are reared singly on their dams, a cow's ability to produce calves regularly and to rear them satisfactory can be as economically important as the growth rates obtained by individual calves.

The basic requirement in genetic improvement of all traits of economic value is the measurement or evaluation of differences among animals. The purpose of the measurements is to provide an accurate estimate of the breeding value of an animal relative to others in a herd. However, genetic effects may be concealed by natural or induced factors which could confuse the breeder and reduce the accuracy of selecting animals having the greatest breeding value. To better estimate genetic differences between animals, environmental differences between records need to be removed or controlled. Some environmental influences can be adjusted statistically (e.g. sex, age of dam) and others can be controlled by standardising feeding and management. Statistical adjustment enables breeders to compare all animals on an equal basis assuming that the adjustment accurately equalises the means and the variances. For growth rate, there is accumulating evidence that among animals managed alike, differences in their live weights reflect real genetic differences reasonably well.

It is necessary to have reliable estimates of certain genetic and phenotypic parameters in farm livestock before breeding plans for optimum improvement can be made. The extent to which economic traits can be incorporated into a selection programme depends on knowledge of their heritability and the genetic correlations between them. It is indispensable to consider the heritability of a trait in any breeding programme because the opportunity for selection should be used on traits that will respond the most to selection. In addition, the heritability of a trait under selection has a major determing influence on the choice of the testing method. In traits of medium to high heritability, selection on individual performance (performance testing) is adequate whereas low heritabilities require consideration of progeny and sib testing. However, several economic traits of beef cattle that contribute to the productive efficiency and desirability of product have moderately high heritabilities (Preston and Willis, 1974). Performance testing is, therefore, the major selection method in breeding plans to improve traits like growth rate and feed conversion.

Genetic correlations are important in selection because they give an indication of the change which will occur in one trait when selection is applied to the other. They are useful in planning selection against undesirable correlated responses, and, although a particular trait may not be of direct economic value, it can be used as a basis for selection if it is genetically related to a criterion that is of direct economic value. Other important parameters in beef cattle are phenotypic correlations between traits and repeatability of cow performance with respect to growth rate of calves to weaning. All these parameters are discussed in detail in the next chapter.

In beef cattle, genetic improvement can be achieved through selection within existing breeds, choosing among breeds and crossbreeding designed either to exploit hybrid vigour or to combine the merits of different breeds (Preston and Willis, 1974, Bishop et al, 1975, Cundiff, 1980). However, effective selection is of fundamental importance whatever other improvement method is adopted.

Differences between breeds of cattle represent a valuable source of genetic variation which beef producers can exploit either by changing from one breed to another or by crossbreeding. The decision on choice of breed depends in part on the breeding objective, particularly on the relative importance attached to growth rate and cow performance; and in part on the suitability of different breeds under the particular farming environment. Crossbreeding on the other hand, allows for utilisation of heterosis and combining of desired characteristics in commercial cattle that would not be present in any parent breed alone. The genetic consequences of crossbreeding and the superiority of crossbred over straightbred animals have been well documented (Mason, 1966, Dickerson, 1969, 1973, Cundiff, 1970, 1980, Preston and Willis, 1974).

The major objective of the present study was to evaluate the growth and maternal performance of Nguni and Nguni crossbred cattle in Swaziland. The growth traits chosen for investigation were birth weight, weaning (210 days) weight and 18-month (540 days) weight. The weaning weights of calves were also used as a basis for evaluating the maternal performance of the cow "breeds".

The nature of the available data also made it possible to calculate estimates of heritability and genetic and phenotypic correlations of the growth traits, and to make estimates of the repeatability of weaning weight. The feasibility of lowering the age at which cattle are selected for breeding in the Swazi Government ranches from the current 540 days (18 months) to 14 months (420 days) was also evaluated.

CHAPTER TWO

REVIEW OF LITERATURE

2.1 Factors Influencing the Growth Performance of Beef Cattle

Growth is widely accepted as a most important characteristic in beef cattle. The growth cycle may be separated into two phases, namely, pre-natal and post-natal; the latter being further subdivided into a pre-weaning and a post-weaning phase (Hafez, 1963, Preston and Willis, 1974). The pre-natal growth phase involves changes in size between conception and birth and is usually measured as the birth weight of calves. Pre-weaning growth is a measure of post-natal growth while the animal is still under maternal influences, and post-weaning growth is a measure of independent growth. Most studies have dealt with the last two phases of growth and have measured growth as weight (and weight change) at various stages of the animal's life between birth and maturity.

The factors influencing any trait may be associated with a genetic and an environmental origin (Falconer, 1960, Preston and Willis, 1974). Variation in measures of growth are caused not only by breed or within breed genetic differences, but also by non-genetic factors such as climate, nutrition and management. The various factors influencing the growth traits of beef cattle are thus classified into genetic and non-genetic factors in this review and only those factors influencing the pre- and post-weaning traits are discussed under each category.

Literature on factors influencing the growth performance of cattle is extensive (Preston and Willis, 1974). However, in the main, such work has been confined to temperate climates and most studies have dealt with cattle maintained under feedlot conditions. There appears to be a relative dearth of information not only from the tropics and sub-tropics, but also from breeds other than the "European" and British beef breeds.

This review is confined to some of the available literature on factors influencing the growth traits of cattle in tropical and sub-tropical areas. It focuses on reports from studies carried out with cattle raised under grazing conditions.

2.1.1 Factors influencing pre-weaning growth traits

The pre-weaning performance of beef calves is commonly measured by birth weight, weaning weight, weaning weight per day of age, and gain or average daily gain from birth to weaning. Birth weight is an essential component of livestock production economics. It is an indicator of size and vigour of the calf at the beginning of post-natal development. Birth weight is also directly important through its influence on calving difficulty and is useful in determining the average daily gain of calves from birth to weaning and age-corrected weaning weight.

Calf weaning liveweight, adjusted for non-genetic factors, is used to measure the maternal performance of the dam. Weaning weight may also be used as a criterion for early screening or culling of bulls and heifers before their first winter feed shortage (see Carter, 1971). However, in cow-calf operations, weaning weight of the calf exerts a great influence on net income because it is directly related to the value of the calf at weaning.

Pre-weaning growth performance in cattle is a complex trait since it reflects not only the growth ability of the calf but also the maternal environment created for the calf by its dam. Calf growth rate prior to weaning is largely a reflection of its dam's mothering ability, especially her milk yield; the calf's own growth capacity plays a minor role at this stage. However, the various factors influencing the pre-weaning growth traits may be generally categorised into genetic and non-genetic influences.

(i) Genetic Factors

The effects of genetic factors on pre-weaning growth traits are well known. Differences in birth weight, pre-weaning daily gain and weaning weight due to breed of sire, breed of dam, sire lines or individual sire groups are all consequences of genetic influences. Heterotic as well as inbreeding effects on growth are also due to genetic sources of variation.

The existence of breed differences in pre-weaning growth is well established in the literature. Preston and Willis (1974) summarised the general ranking of the common beef breeds and concluded that some breeds were considerably larger at birth and weaning than others. In Table 2.1 are some birth weights of the indigenous breeds of Southern Africa, as well as other breeds commonly used in tropical areas. It is apparent from this table that there are breed differences in birth weight. However, there are very few reports in which the breeds are compared in the same environment. Some of the comparisons reported have been made using survey type data in which the various breeds were examined at different sites so that other factors confounded to some extent the comparison of breeds.

Maule (1973) reviewed some published comparative studies on the growth performance of indigenous and exotic breeds of cattle in Southern Africa and suggested apparent breed type differences in pre-weaning growth traits. He observed that most of the exotic breeds were superior in growth to the indigenous ones, with breeds like the Charolais weighing up to 106kg heavier than the indigenous Africander and Nguni at weaning (205 days). The review also revealed significant breed differences among the exotic, as well as between the indigenous breeds of cattle in growth rate to weaning and weaning weight.

In Botswana, Trail et al (1977) evaluated the productivity of the three locally available Sanga type breeds (Tswana, Tuli, Africander), using records collected

TABLE 2.1 The Birth weight of some Beef Cattle Breeds

Breed	Birth Weight (Kg)	Reference
Africander	32.3	Maule (1973)
	30.6	Preston and Willis (1974)
	29.9	Trail *et al* (1977)
Angoni	20.0	Preston and Willis (1974)
	21.1	Thorpe *et al* (1979)
Barotse	26.0	Maule (1973)
	24.0	Thorpe *et al* (1979)
Bonsmara	34.0	Maule (1973)
Boran	22.3	Preston and Willis (1974)
	25.7	Thorpe *et al* (1979)
Brahman	27.8	Preston and Willis (1974)
	28.1	DPU (1979)
Mashona	23.5	Maule (1973)
Nguni	26.0	Maule (1973)
	28.7	DPU (1979)
Santa Gertrudis	32.2	Preston and Willis (1974)
Simmental	42.7	Preston and Willis (1974)
	37.4	Joubert *et al* (1977)
	39.2	DPU (1979)
Tswana	30.7	Trail *et al* (1977)
Tuli	32.7	Maule (1973)
	28.8	Trail *et al* (1977)

over a 4-year period and reported significant differences in pre-weaning growth. They found that at birth, the Tswana (30.7kg) and Africander (29.9kg) calves were significantly heavier than the Tuli (28.8kg). The Tswana calves were also significantly better in weaning weight (174.6kg) than the Tuli (169.6kg) and the Africander (166.1kg) calves. Similar findings in Zambia have been reported by Thorpe et al (1979, 1980b), using different breeds of cattle (Barotse, Angoni and Boran).

A study of the efficiency of various breeds of cattle in a sub-tropical environment was undertaken by Venter et al (1980) in South Africa. The results of this study confirmed that breeds differed significantly in pre-weaning growth, with Simmental and Bonsmara calves having heavier weights at birth and weaning than Africander and Hereford calves. These reports are just a few examples of the many studies which confirm that breed differences in growth exist even within similar types of cattle.

The genetic factors that influence pre-weaning growth are of two sorts: direct genetic effects of the individual's own genotype, and maternal genetic effects controlled by the dam's genotype (Willham, 1963, 1972). The genotype of the dam apart from other influences, also affects the level of milk yield and consequently, the growth rate of the calf. Thus, although the genotype of the dam is to some extent confounded with the genotype of the offspring, it has the most important influence on pre-weaning performance.

Several studies have reported the importance of the dam in expressing breed differences in pre-weaning growth traits. Vorster (1954) reported on a long-term comparative study of beef producing abilities of different breeds of bulls when mated to "European" cross and "Native" cows in Zimbabwe. He found that, independent of breed of sire, the progeny of the European cross cows were significantly ($P<0.01$) heavier at birth and weaning than the offspring of the relatively small Native cows. In this study, the progeny of the European type cows were 14 kg heavier at weaning. Ellis et al (1965), working with straightbred and crossbred Brahman-Hereford cattle in the tropical areas of Texas observed that the genotype of the dam exerted considerably more influence on birth weight than did the genotype of the sire. Comparing the pre-weaning growth of the Simmental, Africander and Hereford breeds, Joubert et al (1977) found that Simmental calves were 40.6 kg and 42.1 kg heavier at weaning than the Africander and Hereford calves, respectively. They attributed this superiority to the differences in mothering ability of the three breeds.

Reports from the crossbreeding studies undertaken in Western Uganda by Trail et al (1971b) and Sacker et al (1971b, c) illustrated that breed of dam, breed of sire and breed of calf all have an important influence on pre-weaning body weights. These studies involved three introduced breeds; Angus, Red Poll and Boran; and two indigenous breeds: Ankole and East African Zebu. The reports have indicated that the birth weights of calves by Boran and Ankole dams were significantly heavier than those by Zebu dams. From 3 to 9 months (weaning), calves by Boran dams were also significantly heavier than those by Ankole and Zebu dams. Sire-breed influences in these studies indicated that the Boran and Red Poll sired significantly heavier calves at birth than the Angus sires. However, during the period 3 to 9 months, progeny of the Angus sires were in turn significantly heavier than those of Boran sires.

Trail et al (1977) compared four sire breeds, all mated to Tswana cows and reported sire breed differences in pre-weaning growth. They found that the progeny of Simmental and Brahman sires were significantly heavier at birth and weaning than progeny of Bonsmara and Tuli sires. Working with Africander dams as a basis, Mentz et al (1979a) also reported breed of sire differences in pre-weaning growth traits. The sire breeds compared in this study were Charolais, Simmental, Brahman and Hereford. Other workers who reported breed of sire and/or breed of dam differences in pre-weaning traits are Horak et al (1964), Harricharan et al (1976), Crockett et al (1979), and Paterson et al (1980a).

Crossbreeding brings about a favourable response in birth weight, pre-weaning gain and weaning weight, due no doubt to the superior viability and growth rate potential of the F_1 calf, and the superiority in maternal performance of the F_1 cow in the case of three-breed crosses or back-crosses. So far as the F_1 calf is concerned, the degree of heterosis manifest in these traits depends very much on the maternal performance of the straightbred cow. Different responses of reciprocal crosses for pre-weaning gain and weaning weight usually stem from variations in milk production and mothering ability.

The effect of crossbreeding on pre-weaning performance of calves has been confirmed by many reports. The crossing of different breeds has been found to result in increased birth weights and subsequent gain to weaning due to increased heterosis levels. Ellis et al (1965), reporting on the effects of heterosis on birth weight of Brahman-Hereford crosses found heterosis levels of 10.8% for first-cross calves, 5.5% for back-cross calves from first-cross cows, 8.2% for back-cross calves from straightbred cows and 2.0% for F_2 calves. The reports of Trail et al (1971b) and Sacker et al (1971b, c) indicated significant hybrid vigour effects on pre-weaning body weights of crossbred calves. In these studies, crossbred calves were heavier at birth, and at 3, 6 and 9 months than straightbred calves, and heterosis levels for these respective ages were 8%, 16%, 19% and 16%. The results from these reports also suggested that the effect of hybrid vigour on the mothering ability of F_1 dams was at least as great as on early growth of the F_1 crossbreds themselves.

In the sub-tropical areas of New South Wales, Barlow and O'Neill (1978, 1980) evaluated the growth performance of Hereford and crossbred Hereford calves to weaning. They found that crossbred calves grew faster than Hereford calves. The advantages in liveweight at weaning were 12.0kg for Brahman x Hereford, 15.1kg for Simmental x Hereford, and 16.3kg for Friesian x Hereford. These authors suggested that about half the superiority of the *Bos taurus* crosses would be attributed to heterosis and that most of the increases in birth weight and average daily gain among Brahman crosses could also be explained by the same phenomenon. Mentz *et al* (1979a) also found that crossbreds performed 11.1% to 11.8% better than Africander controls in weaning weight.

The Animal Production Research Unit (APRU) (1978) in Botswana reported on the comparative performance of crossbred Simmental, Bonsmara, Brahman and Tuli F_1 cows when mated to a third sire breed and noted significant differences in birth weight and daily gain to weaning of the three-breed cross calves. The calves by the Simmental cross cows were significantly heavier at birth and grew significantly faster than all the other breed crosses and the Tswana controls. The milk yield results revealed that the crossbred Simmental cows produced significantly more milk than all the other crosses during the pre-weaning period, providing further evidence that breed of dam differences in pre-weaning daily gain and weaning weight of calves are largely due to milk yield differences (Preston and Willis, 1974).

The effect of the sire on birth weight and weaning weight is to be anticipated in view of the moderate heritability estimates of these traits (Preston and Willis, 1974). The sire contributes a sample half of his genes towards the genetic make-up of the calf and therefore its genetic influence on measured calf performance is to be expected despite the very high influence of the maternal environment provided by the dam.

Most workers who have studied the effect of the sire on the pre-weaning performance of the calf have confirmed measurable sire effects. Significant differences between sires within breeds were reported by Bosman and Harwin (1966) who noted that sire differences were even more marked in the case of weaning weight than at birth. These authors reported a magnitude of differences among sires of up to 29 kg at weaning. In Sudanese cattle, Osman and Rizgalla (1968) found highly significant ($P<0.01$) sire effects on birth weight but non-significant effects on both pre-weaning average daily gain and weaning weight. They reported differences of up to 5 kg and 20 kg, respectively, for birth weight and weaning weight between the best and poorest sires. Similar findings were reported by Barlow and O'Neill (1978), who noted highly significant sire influences on birth weight, but non-significant effects on daily gain. These authors also illustrated that sires had a significant effect on the gestation length of their calves. Venkateshwarlu _et al_ (1972) reported significant sire effects on birth weights of 183 Ongole calves by 20 sires.

There appears to be breed differences in the magnitude of sire effects on pre-weaning growth traits of calves. Paterson et al (1980a), working with several breeds of cattle observed that the influence of sires within the Simmental breed was greater than sire influences within the Charolais and Hereford breeds for birth weight, pre-weaning average daily gain, and weaning weight. They noted an apparent large variation among the progeny of sires of the Simmental breed and less variation in Hereford and Charolais sires' progeny at birth and weaning. Similar results were obtained by Harricharan et al (1976) who observed that sires had a significant influence on birth weight in the Santa Gertrudis herd, but appeared to be less important in the Sahiwal and Brahman herds. However, these workers attributed the herd differences in sire effects to the different nutritional levels between herds and pointed out that the full potential effect of a sire on birth weight may not be manifested under poor nutritional conditions. They also observed that the effect of the sire on weaning weight became greater with increasing age at weaning.

In general, the evidence that variation in pre-weaning growth of calves due to sires exists, imply that selection of superior sires in terms of increased calf growth to weaning or reduced birth weight is possible. The measurable sire effects on gestation length and birth weight of calves are further evidence of the phenomenon that the calf controls its gestation period and plays a determining role in the initiation of parturition.

Inbreeding is also expected to have some influence on birth weight and subsequent growth of calves. The influence of the sire on pre-weaning growth is not only due to the relative genetic merit of a sire for growth, but also depends upon the degree of genetic differences between the sire and dam, which may give rise to either heterosis (between lines within a breed) or inbreeding depression. Alim (1964) working with Kenana cattle in Sudan reported that the degree of inbreeding of calves had a highly significant effect on birth weight. He found a regression coefficient which indicated that the inbreeding of the dam is unimportant in its influence on birth weight, but that the inbreeding of the calf is associated with depressed birth weights.

(ii) Non-Genetic Factors

The environmental factors affecting pre-weaning growth may either have a direct effect or act indirectly through their influence on the dam's milk yield. These include age of dam, weight and size of dam, the maternal environment and feeding, or the nutritional regime imposed on the dam. The sex of the calf as well as year and month of birth also play an important role in influencing pre-weaning growth.

The importance of the age of the dam in influencing birth weight, daily gain and weaning weight of calves is well established. A recent study by Jones and Hopkins (1980) on the effect of correction factors on response to selection have revealed that when the environmental effects of age of dam are not allowed for in selection for growth rate, the selection differentials and genetic responses to selection are reduced. Working with cows aged 2 to 8 years, these authors found that neglecting the dam-age effects reduced genetic gains by 15% when selection was for weaning weight.

Age of dam effects on pre-weaning performance are a measure of differences in the maternal environment of the dam ages. Progeny of young dams are usually lighter at birth and weaning and they tend to grow more slowly than those of older dams. Most studies have indicated an increase in production up to 5 to 8 years of age, followed by a gradual decline, though the peak period seems to vary between different breeds and types of cattle, most probably due to differences in age at maturity. The lighter birth weights of progeny of young dams may be partly due to the fact that in pregnant cows which are not yet mature, the growing foetus has to compete for resources with growth and development of the dam herself. Limitations due to the skeletal size of the dam in immature cows may also constrain the calf's growth during gestation and thus result in smaller calves at birth. The gradual decrease in calf birth weight and weaning weight as the cow age increases further is presumably due to a decline in maternal ability associated with old age.

There has been consistent reports on the reduction in performance of young cows compared with mature cows. Alexander <u>et al</u> (1960), working with 244 Herefords in a sub-tropical environment in Australia found that first calf heifers produced calves which were 1.8 times lighter at birth than those of mature cows. Bosman and Harwin (1966), dealing with several herds of cattle, reported highly significant age of dam effects on birth and weaning weights. Calves from 3-year-old dams averaged 10.5kg lighter at weaning than calves from mature dams (5 to 8 years) in their study. Those authors also noted that peak production appeared to be reached between 5 to 8 years of age in most herds, with the exception of the Africander herd which appeared to reach peak production at 10+ years.

In Western Uganda, Sacker <u>et al</u> (1971a) studied the effects of various environmental factors on body weights of crossbred cattle and reported significant age of dam effects. They found that 5-, 6-, and 7-year-old dams weaned the heaviest calves, older cows produced the lightest and the youngest cows varied greatly between years. Harricharan <u>et al</u> (1976) reported a 3.6kg and 5.9kg increase in birth weight as age of dam increased from 2.5 to 9 years in a Santa Gertrudis and Brahman herd, respectively.

Winks et al (1978) found that mature and aged cows (5 to 8 years and 9+ years) produced calves that were heavier at birth, grew faster and had heavier weaning weights than young cows (3 to 4 years). They, however, found no significant differences between calves from mature and aged cows. Similar results were obtained by Heyns (1960), working with cows aged 4 to 9 years. That author attributed the dam-age differences in pre-weaning growth to differences in milk production. Other workers who reported significant age of dam effects on pre-weaning performance are Alim (1964); Venkateshwarlu et al (1972) and Paterson et al (1980b).

On the contrary, Vilakati (1977), working with Nguni and Brahman crossbred calves, found a non-snigificant age of dam effect on weaning weight, presumably because the study involved only mature and aged cows (4 to 10+ years). Other workers who failed to find significant age of dam effects on some pre-weaning traits are Bosman and Harwin (1966), Rudder et al (1975) and Crockett et al (1979).

The parity of the dam and the previous parous state of the cow are also believed to have some influence on the pre-weaning growth of the calf. Ghosh et al (1978) found that birth weight increased from second, to fourth parity in female Holstein x Haryana calves and noted that parity effects were highly significant ($P<0.01$). A similar tendency of increasing birth weight with the advancement of parity was reported by Ray et al (1978). However, the effect of parity is partly dependent on the age of the dam at first calving and the interval between calves. With respect to previous parous state, calves raised by dams parous the previous year are generally lighter at birth and have a lower pre-weaning growth rate than calves from dams which were previously non-parous and thus rested the previous year. This trend has been confirmed by several reports (Koch and Clark, 1955a; Sacker *et al*, 1971a, Seifert and Rudder, 1976, Vilakati, 1977, DPU, 1979, Mentz *et al* 1979a, Thorpe *et al* 1980a), though in most cases the authors failed to find a significant and consistent effect of the dam's previous parous state. Besides, the previous parous state of the dam tends to be partially confounded with the age of the dam.

The weight of the dam has been found to be positively associated with the birth weight of the calf as indicated in Table 2.2. Although the correlation coefficients are not very high, they indicate that heavier cows tend to produce heavier calves at birth. The relationship between weight of dam and weaning weight is also not very strong, but is generally positive (Preston and Willis, 1974), indicating that the advantage established at birth continues to weaning.

Several reports have indicated that the weight and size of the dam affects the pre-weaning performance of the calf. Vorster (1954) observed that weights of calves at birth were closely related ($P<0.01$) to the size of their

TABLE 2.2 The Correlation between Weight of Dam and Birth weight of Calf

Breed	Correlation Coefficient	Reference
Ankole	0.28	Trail *et al* (1971a)
Angoni	0.19	Thorpe *et al* (1980a)
Boran	0.18 0.21	Trail *et al* (1971a) Thorpe *et al* (1980a)
Barotse	0.26	Thorpe *et al* (1980a)
Holstein x Haryana	0.39	Ghosh *et al* (1978)
Hereford	0.26	Alexander *et al* (1960)
Hereford	0.40	Tudor (1972)
"European"	0.23	Vorster (1954)
"Native"	0.29	Vorster (1954)

dams and concluded that within comparable groups of cows, the heavier animals produced the larger calves. Alexander et al (1960) found that the weight of the dam was significantly related to birth weight and was associated with about 6% of the variation in birth weight of the calf. They found that the regression of birth weight on cow weight was 0.019, indicating that for every 100kg increase in cow weight, calf birth weight was expected to be 1.9kg heavier. Singh and Tyagi (1970) reported that 3.28% of the variance in birth weight was attributable to dam weight.

Trail et al (1971a) found a correlation of 0.23 between the birth weights of all calves and the weights of their dams immediately after calving and a regression coefficient of 0.02kg. Reporting on the performance of Ankole, Boran, and Zebu cows, these authors found no evidence of differing relationships between calf birth weight and weight of cow at parturition among either cow age groups or cow breeds. A highly significant correlation of 0.24 between calf weaning weight and a regression of 0.127kg were also obtained. Thorpe et al (1980a) reported a regression of calf weaning weight on dam weight of 0.12kg, indicating that dams which were 50Kg lighter than average weaned calves which were 6kg lighter than average. A significant influence of pre-calving weight of the dam on calf performance was reported by Winks et al (1978), who also found correlation coefficients ranging from 0.31 to 0.39 between weight of cow pre-calving and growth rate (birth to weaning) and weaning weight (180 days) of calf.

The importance of maternal influence on the growth of young mammals has long been recognised (Koch and Clark, 1955a, Falconer, 1960, Koch, 1972). While the sire influences his offspring only through the sperm cell, the dam may influence her offspring through the environment provided as well as through the ovum. Although maternal effects are environmental in so far as their influence on offspring is concerned, they are also determined by genetic and environmental factors. The genetic maternal effects have already been discussed.

Maternal effects on birth weight refer to the differences in birth weight caused by differences in maternal environment provided by cows during gestation (pre-natal maternal influence). Brown and Galvez (1969) evaluated maternal and non-maternal influences on birth weight and reported that the effect of differences among individual cows on the birth weight of their calves accounted for 17.6% of the total variation in birth weight in Hereford and 9.3% in Angus. A review of the influence of maternal environment in beef cattle by Koch (1972) revealed that maternally-related variation accounted for 14 to 18% of the phenotypic variance in birth weight.

Since there is no direct measure of the influences included in the maternal environment, an estimate of total maternally-related variation and covariation is derived by comparing maternal half-sib with paternal half-sib correlations. Koch (1972) found an average correlation of 0.11 among paternal half-sibs for birth weight; whilst the maternal half-sib correlations among all calves was 0.25, and of adjacent calves, 0.29. The difference in relationship among the maternal and paternal half-sibs is due to the additional influence through the maternal environments provided during the pre-natal period. These correlations indicate that the maternal environment has a considerable influence on the birth weight of the calves.

However, there appears to be a fairly high negative genetic correlation between genetic ability and maternal ability for birth weight and gestation length. Koch (1972), after collation of data from several reports, found an average genetic correlation of -0.44 between individual and maternal effects on birth weight. The negative genetic correlation indicates an antagonism between genes for pre-natal growth and the genes conditioning the intra-uterine environment for heavier foetal weights (direct and maternal effects). Such an antagonism would be a balanced mechanism with the tendency to maintain birth weights in intermediate ranges (Brown and Galvez, 1969).

Evidence for the existence and extent of maternal environment from birth to weaning comes from experiments which measure known components such as milk production, by reciprocal crossing or cross-fostering among breeds or types and by the comparison of observed correlations with theoretical expectations for various kinds of relatives (Koch, 1972).

Milk yield has an overriding effect on calf growth rate from birth to weaning. Preston and Willis (1974) reported that milk yield can account for between 16 and 62% of the variation in weaning weight. Milk yield of dam has been shown by Richardson et al (1979) to account for 72 and 63% of the variation in calf growth during the first 98 and 150 days of life, respectively. A study of the weight gains of calves over the suckling period carried out by Walker (1964) showed that 70% of the weight differences at weaning are attributable to the differences at 12 weeks, indicating that differences in milk yield are particularly responsible.

Table 2.3 shows some published correlations of weaning weight and pre-weaning daily gain with the milk yield of the dam.

The various reports have indicated that the correlation between monthly lactational yield and monthly growth rates tends to decline as lactation progresses, as a result of the increasing dependence of the calf on pasture. Heyns (1960), working with 24 Africander cows, observed that up to the third and fourth months of lactation, the calf was highly dependent on the milk production of the dam, but that thereafter, the gain in

TABLE 2.3 Correlation of Calf Average Daily Gain and Weaning weight with Dam's Milk Yield

Breed	Average Daily Gain	Weaning Weight	Reference
Angus	0.54		Reynolds et al (1978)
Africander		0.64	Heyns (1960)
Africander x Angus	0.58		Reynolds et al (1978)
Brahman	0.51		Reynolds et al (1978)
Brahman cross	0.55		Holroyd et al (1978)
Brangus	0.60		Reynolds et al (1978)
N'Dama	0.93		Montsma (1960)
Sokoto	0.96		"
West African	0.98		"
Shorthorn			
Zebu	0.61	0.60	Lampkin and Lampkin (1960)

weight of calf did not seem to be affected to a great extent by the relatively low level of milk produced by its dam; suggesting that grazing ability makes the calf less dependent on the milk of its dam. In Ghana, Montsma (1960), working with three types of cattle, found high positive correlations between dam's milk yield and the calf's rate of gain and also noted a gradual decline in the importance of milk to the calf as it became more dependent on grass. He attributed the very high average correlation (0.96) between milk yield of dam and weight increase of calf at 8 weeks to the absence of pasture suitable for the calf.

The milk production in suckling cows is in turn influenced by plane of nutrition of the dam, calf birth weight and month of birth (Heyns, 1960, Montsma, 1960, Holroyd _et al_, 1979). A close relation between total lactation yield of suckling cows and the body weight of their calves at birth (r=0.75) has been reported by Heyns (1960) and this has been found to be at least partially independent of plane of nutrition of the cow (Walker, 1964, Richardson, 1979b).

However, a negative correlation between cow pre-weaning weight, and her calf's performance at weaning has been reported in several studies. Estimates of genetic correlations ranging from -0.28 to -0.70 have been reported by Koch (1972). This negative genetic correlation involving maternal ability has special concern with regard to the performance of the female offspring of high-producing dams. Selecting heifers superior in weaning weight would result in increased genetic value for growth response, but decrease milk production.

The nutritional environment provided for breeding cows throughout the year is of utmost importance because of the large influence of the dam on the pre-weaning performance of the calf. In general, low plane of nutrition prior to calving depresses birth weight and several reports confirm that the pre-calving nutritional effect of the dam is of approximately equal importance to post-calving nutrition, in so far as pre-weaning performance is concerned (Preston and Willis, 1974).

The importance of pre-calving levels of nutrition with respect to mothering ability and subsequent calf pre-weaning performance have been suggested by most workers in the tropics. In Zimbabwe, Ward (1968) carried out a study on the effect of supplementation of Mashona beef cows grazing on veld and reported that calves born to cows which had been supplemented with groundnut cake before calving were heavier at birth than those born to unsupplemented cows ($P<0.001$). He also noted an increase in weaning weight of 32% due to supplementation. Tudor (1972) investigated the influence of low and high plane of nutrition during pregnancy on calf birth weight in Hereford cows and found that the low plane of nutrition significantly ($P<0.01$) reduced calf birth weight. In that study, the calf birth weights of the low plane cows were reduced by 6.8kg or 21.9% compared with the high plane cows.

Richardson *et al* (1979) reported that an improvement in plane of nutrition led to an increase in weight of cow at the end of winter and after calving, and that this was associated with an increase in calf birth weight. In that study, cows given most concentrates produced significantly ($P<0.01$) heavier calves than those on veld alone. With respect to calf growth from birth to 150 or 240 days, the study indicated an increase in daily gain with an improvement in plane of nutrition of the dam, this being a reflection of the increase in milk production with improvement in plane of nutrition. Richardson *et al* (1979) also reported that cow weight change in winter had a significant and positive effect on calf birth weight, thus providing further evidence that cow weight change during pregnancy exerted an important effect on calf birth weight, apart from its action through increasing pre-partum cow weight. These results also support the hypothesis that plane of nutrition in late-pregnancy affects foetal growth. Generally, cows which tend to lose weight before calving will produce lighter calves than those which are fed in such a way that they gain weight (Preston and Willis, 1974).

The change in weight of the dam during lactation is also of major importance to pre-weaning growth. Most reports have indicated an inverse relationship between rate of cow weight gain and calf daily gain. Cows gaining the most under grazing conditions have been found to produce slower-gaining calves. Cows which gain a lot of weight during the suckling period do so at the expense of milk production and consequently wean lighter calves.

Lampkin and Lampkin (1960) observed that animals with higher milk yields lost more weight, or gained less weight during the lactation period than their lower-yielding contemporaries. They found a significant correlation of -0.28 between weight change and milk yield over the total suckling period. The regression coefficients obtained in their study indicated that for every extra kilogram of milk produced in the different 12-week periods of lactation, an additional loss in body weight of between 0.013 and 0.029kg was involved.

Trail et al (1971a) found a highly significant correlation of -0.15 and regression of -0.104kg per kg between calf weaning weight and gain (or loss) of dam's weight during lactation. Their results suggested that cows that came into milk in good condition tended to yield more, and heavier milkers made smaller gains as more of their nutrients were going into the production of milk than to building up body tissues. Similar results were obtained under Zambian conditions by Thorpe et al (1980a) who reported negative correlations between calf weaning weight and dam liveweight change measured over the major part of the lactation period, suggesting that the heaviest weaners were produced by the dams which lost most weight during lactation.

The sex of the calf is one of the important non-genetic factors influencing its pre-weaning performance. In almost all studies reviewed, the birth weights of male calves were reported to be significantly greater than those of female calves. Because of their advantage at birth, male calves also tend to grow faster to weaning and thus have heavier weaning weights than females. Since male calves are generally carried <u>in utero</u> for a longer period than females (Preston and Willis, 1974), part of the superiority of the male sex might be a reflection of a greater gestation length. For instance, Barlow and O'Neill (1978), evaluating the pre-weaning performance of first-cross calves found that gestation was 1.4 days longer for males than females and that males were in turn 2.2kg heavier at birth and they grew 0.06kg/day faster than females from birth to weaning. However, it is also contended that the differences in growth rate between the two sexes may be partly hormonal.

The analysis of birth weight records of 130 Haryana calves in 10 sire groups by Singh and Tyagi (1970) revealed that 9.38% of the total variance in birth was attributable to sex of calf. Alim (1964) reported that differences due to sex accounted for 6.9% of the total variance in birth weight. Males averaged 1.7kg heavier than females in this study, the difference being highly significant ($P<0.01$).

Bosman and Harwin (1966) reported a highly significant influence of sex on both birth and weaning weight. They found differences of 2.3 to 2.7 kg for birth weight and by weaning the differences between the 2 sexes were up to 12.7 in favour of the males. In a later study, Bosman and Harwin (1967) reported an average difference of 12.3 kg in weaning weight between bull and heifer calves. Harricharan et al (1976) found mean herd differences in favour of males of 0.9, 2.3 and 3.3 kg for calves of Santa Gertrudis, Sahiwal and Brahman breeding, respectively, these differences being significant. In Simmentals, Joubert et al (1977) reported that the average birth weight of bull calves exceeded that of heifers by some 11%. The long-term difference between the birth weight of male and female calves in their study was 4kg, while the weaning weight difference was 22.5kg. Others who have reported that males were superior to females in birth weight, average daily gain or weaning weight are Alexander et al (1960), Horak et al (1964), Osman and Rizgalla (1968), Kennedy and Chirchir (1971), Holroyd et al (1979), Mentz et al (1979a).

In most reports where castrated males were involved, steer performance have been placed above that of heifers and below that of bull calves. Sacker et al (1971a) found that male castrates were significantly heavier than females by up to 14.5 kg at weaning. Thorpe et al (1980a) reported significant differences between entire and castrated males in weaning weight, with bull calves having heavier weights than the castrated males.

Year and season (or month) of birth influences on the pre-weaning performance of calves have been well established. Year differences in pre-weaning growth of calves reflect the variation in general environmental conditions from year-to-year in a herd and are a normal expectation. When cattle live on the veld, the milk production of the cow depends to a large extent on the amount of grass available and thus gain from birth to weaning and weaning weight under such conditions is largely a reflection of rainfall in the current and previous season. Years of exceptionally high rainfall are usually accompanied by heavy birth and weaning weights of calves as a result of abundant grazing. However, abnormally large yearly fluctuations may also be a reflection of poor management or poor adaptability of cattle in a herd.

Differences between years for pre-weaning growth traits have been reported in many studies. Alim (1964) found that year effects accounted for 9.29% of the total variation in birth weight. Significant year effects on calf birth weight have been reported by Alexander et al (1960), Bosman and Harwin (1966), Kennedy and Chirchir (1971), Harricharan et al (1976), Joubert et al (1977), Paterson et al (1980a) and Thorpe et al (1980a). The major influencing factor in the study of Alexander et al (1960) appeared to be a drought year accompanied by an extremely low plane of nutrition imposed as a treatment. Joubert et al (1977) noted a close correlation between rainfall and resultant pasture conditions on the one hand and mean birth weight on the other. Their results revealed a decided tendency for improved nutrition to cause an increase in birth weight. However, most reports have conceded that birth weight seems to be little affected by environmental conditions unless they are extremely severe.

Significant yearly variations in pre-weaning daily gain and weaning weight have also been reported by several workers. Bosman and Harwin (1967) found differences of up to 34.5kg in weaning weight between the best and poorest years. Sacker et al (1971a) attributed the highly significant year of birth effects on body weight from three to nine months (weaning) to the very marked differences between years in pasture availability. Willis et al (1972) observed that weaning weight (90 days) tended to decline over the years of study due either to climatic conditions or to a general decline in the level of supplementation given to cows or calves. Paterson et al (1980a) found that although pastures were irrigated, rainfall of the previous year was related to the year effects on daily gain and weaning weight (210 days). Others who reported significant year effects on daily gain and weaning weight are Kennedy and Chirchir (1971), Joubert et al (1977), Mentz et al (1979a) and Thorpe et al (1980a).

The season of birth influences the birth weight of the calf indirectly through the pre-calving nutritional plane of the dam, and it can affect the weaning weight and gain in weight of the calf indirectly through its effect on milk production in addition to the direct effects of season. In Ghana, Montsma (1960) observed that calves born in the dry season and therefore developed *in utero* during the wetter part of the year, were 9% heavier at birth than calves born in the rainy season. Singh and Tyagi (1970) reported that 4.75% of the variance in birth weight was attributable to season of birth and that this effect was significant.

Bosman and Harwin (1967) found that spring-born calves had a superior growth rate to late summer calves and attributed this to the idea that early season calves and their dams have full advantage of the peak summer grazing period. These authors also found that in herds producing summer and winter calves, the latter calves were somewhat lighter at weaning than the early summer calves. In Cuba, Willis *et al* (1972) reported that seasonal effects showed a pronounced trend in both birth and weaning weight. They found that calves born at the beginning and end of the year tended to be lighter at 90 days (weaning) than those born in late spring and summer. They indicated that this was a reflection of the availability of grass which would begin to become plentiful in April or May with the onset of the rainy season and scarce towards the end of October.

Several authors have discussed the effect of time or date of birth, on birth weight as it operates during the calving season and have come to the conclusion that birth weight can be expected to increase as the season progresses. Alexander et al (1960) found that on average, birth weight increased by 0.43kg for each 10 days during the calving season resulting in a total average increase of 3.0kg for the 10-week calving period. Bosman and Harwin (1966) found that early-season calves were significantly (5 to 7kg) lighter in birth weight than calves born at the end of the calving season.

With respect to daily gain and weaning weight, calves born early in the season appear to grow faster and are heavier at weaning than late season calves. A study by Winks et al (1978) in the dry tropics of North Queensland revealed that although the birth weight of calves born late in the calving period were significantly heavier than those of earlier ones, early-born calves grew faster ($P<0.01$) and were heavier at weaning (180 days). Reports from Swaziland have also indicated that late-born calves (December) were generally heavy at birth, but that early born calves (September to November) were in turn significantly heavier at weaning (210 days) than late calves (Vilakati, 1977, DPU, 1979).

Richardson et al (1979) found that calf birth weight increased as the calving season advanced, but that the advantage of being born late was lost by the time the calves were 150-days old. They observed that calf weight gain from birth to 150 days declined as calves were born later in the season, even after correcting for the effects of milk yield and calf birth weight. These authors suggested that the negative relationship between growth to 150 days and date of birth was probably a reflection of the quantity and quality of grass available to suckling calves from 90 days of age onwards, when grass forms a substantial part of their diet. Mentz et al (1979a) found that calves born early in the calving season were significantly heavier at weaning than those born in the middle of the calving season and that these were in turn heavier than those born late.

The weaning weight of the calf is to some extent dependent on the age of the calf at weaning. The weaning age in beef cattle usually ranges from 180 to 250 days. The most frequently used ages being 180, 200, 205, and 210 days. The usual practise of weaning calves at a fixed time leads to age differences among calves which needs adjusting in order to make valid comparisons of weaning weights. The importance of correcting for calf age in selection experiments have been confirmed by Jones and Hopkins (1980) who indicated that if calves born within a period of 33 days were compared and calf age was neglected, the response to selection for weaning weight would be reduced by about 6%.

2.1.2 Factors influencing post-weaning growth traits.

Post-weaning growth in beef cattle can be measured by weight at suitably chosen ages, the weight gain over a specific period or the rate of gain in weight per unit time. Research has however indicated that post-weaning growth under grazing conditions is better measured by liveweight at specific ages about normal slaughter-age rather than by gain per day recorded over any shorter period (Carter, 1971, Seifert, 1975b). In cases where early mating is advocated, the yearling weight (12 to 14 months) of the animal is normally used as a measure of growth. Liveweight at 18, 20, and 24 months of age is said to be the main determinant of carcass weight and economic returns and is thus the most appropriate measure of response to selection.

The economic importance of post-weaning growth in beef production as already indicated in the introductory chapter, needs no further emphasis. The growth phase after weaning covers the larger proportion of the animal's life and is relatively free of maternal influences. Although post-weaning growth depends solely on the animal's genetic ability to grow, it is also subject to more environmental stress and consequently more variable than the pre-weaning phase. The various factors that influence post-weaning growth traits are also conveniently categorised into genetic and non-genetic factors. Knowledge of both the genetic and environmental influences on this period of the animal's life is of vital importance particularly under tropical conditions where most cattle have to cope with a wide range of environmental constraints.

(i) Genetic Factors

The importance of genetic factors in causing variation in post-weaning growth traits is apparent in view of the medium to high heritability estimates of such traits (Preston and Willis, 1974, Barlow, 1978). Breed and strain differences in post-weaning growth rate are well known, and genetic differences between sires within a breed and between individuals within a group, all contribute to the variation in post-weaning growth performance.

Most studies carried out under tropical and sub-tropical conditions have indicated significant growth performance differences between the different types of cattle (B. indicus Vs B. taurus) and within each type, breed differences are also well established. Cross breeding has also been widely reported to have a marked influence on post-weaning growth traits, particularly in cases where Zebu and European or British breeds are involved.

Several reports on the breed evaluation programme in Botswana have indicated significant differences in post-weaning growth among various breed groups and have also suggested an advantage in post-weaning growth to 18 months of age through crossbreeding (Trail et al, 1977, APRU, 1978). Trail et al (1977) found that straightbred Tswana and Tuli calves were significantly heavier at 18 months than straightbred Africanders. A comparison of the crossbred progeny of Tswana cows by Simmental, Brahman, Bonsmara and Tuli sires revealed that all the crossbreds were significantly heavier than the Tswana controls. The Simmental and Brahman sired crossbreds were significantly heavier at 18 months than the other crossbreds. Similar studies in Zambia (Thorpe et al, 1979, 1980b) based on different breeds also indicated significant breed differences in 12, 18, 24 and 36 month weight and have suggested some advantage in post-weaning growth performance due to crossbreeding, especially where *B. taurus* x *B. indicus* crossbreds were involved. Working with Brahman and Charolais cattle, Rudder et al (1975) showed that crossing Zebu with *B. taurus* in a tropical environment had a significant influence on post-weaning growth performance. They found that Charolais x Brahman cattle were 0.17kg heavier ($P<0.005$) per day of age than the straightbred Brahman and gained 0.13kg per day more during the post-weaning period.

Significant differences in growth performance due to breed of sire and breed of dam were illustrated by Trail et al (1971b), who found that from weaning to 24 months, progeny of Red Poll and Angus sires were significantly heavier than the progeny of Boran sires. At 24 months of age, progeny of the *B. taurus* sires were 9% heavier than progeny of Boran sires and calves by Boran dams were in turn 15% and 8% heavier at that age than progeny of East African Zebu and Ankole dams, respectively. However, these authors also reported significant genotype x year interactions, indicating the necessity of evaluating breed types over several years. A later report by Sacker *et al* (1971c) indicated significant hybrid vigour effects in crosses between Red Poll and Boran breeds. The average yearling weights of crossbreds were 26.4% superior to those of purebreds in this report.

A five-year evaluation study of F_2 and F_3 Africander, Brahman and British (Shorthorn x Hereford) crossbred cattle by Kennedy and Chirchir (1971) indicated that the Zebu crossbreds grew faster and were significantly heavier at 18 months than the British crosses. The average 18-month weights were 294.8kg, 282.8kg and 244.2kg for the Brahman, Africander, and British crossbreds, respectively. A similar study later undertaken by Seifert (1975b) has also suggested that Zebu crossbreds are superior to British crossbreds in the tropical areas of Australia. The latter study also revealed that among the Zebus, Brahman crossbreds were heavier ($P<0.01$) than the Africander crosses throughout the post-weaning period (up to 18 months).

A comparative study of the post-weaning growth performance of Zebu-sired crosses by Winks *et al* (1978b) has indicated that Sahiwal x Shorthorn crosses tended to have higher growth rates than Brahman x Shorthorn from weaning to 18 months and that the latter crosses have faster growth rates from 18 to 30 months. The authors suggested that the differences in growth rates during the various post-weaning periods could be a function of differences in rate of maturity in the two genotypes. In Guyana, Mahadevan *et al* (1972) also found that progeny of native cows by Sahiwal bulls were heavier as yearlings than those by Brahman bulls.

Other studies have indicated that genotype x environment interactions for post-weaning growth traits, as discussed in the reviews by Warwick (1972), and Preston and Willis (1974), exist. For instance, Mentz *et al* (1979b), evaluating the post-weaning growth performance of 342 steers out of Africander cows and by various sire-breeds under two systems of management reported a significant sire-breed x treatment interaction. They found that progeny by *B. taurus* sires (Charolais, Hereford and Simmental) performed strikingly better in a system of intensive fattening than those by *B. indicus* sires (Africander and Brahman). However, under the extensive production system, *B. indicus* progeny performed relatively better. Among the *B. indicus* sire-breeds, that study showed that the

Brahman crossbreds held no advantage over the straightbred Africander under intensive production system, but that the Brahman crosses outweighed the Africander control by 13.1% under the extensive production system. Among the *B. taurus* sire-breeds, the Simmental crossbreds performed relatively better than both the Charolais and Hereford crossbreds under extensive conditions.

The influence of the sire on post-weaning growth has also been established though most studies have been confined to evaluating breed of sire differences rather than individual sires within breeds. Working with Sudanese cattle, Osman and Rizgalla (1968) reported significant ($P<0.01$) sire effects on yearling weight and post-weaning average daily gain. They found differences of up to 40kg in average adjusted yearling weight between the best and poorest sires. An investigation of the genetic and environmental factors influencing growth traits of Holstein - Friesian x Sahiwal cattle by Naidu and Desai (1965) also indicated that differences among sire groups for yearling weight were highly significant. Significant sire effects on post-weaning daily gain of Africander cattle have been reported by Von La Chevallerie and Buys (1965).

(ii) Non-Genetic Factors

The importance of the environmental factors influencing beef cattle production is well known. While genetic improvement depends on the heritability of traits, the environment plays an important part in the expression of an animal's productive ability. Knowledge of the non-genetic factors influencing growth post-weaning is essential to make accurate assessment of the breeding values of animals for these characters.

The major non-genetic factors influencing post-weaning growth in cattle are climate, nutrition, management, the sex of the animal, the use of growth stimulants and disease and parasites (Preston and Willis, 1974, Williamson and Payne, 1978).

Climate may influence post-weaning growth directly through the animal's physiology in terms of its body temperature and respiration rate which in turn affect feed and/or water intake; or indirectly through its effect on the feed supply and health of the animal. The indirect effects of climate are of particular importance in areas where cattle are dependent on grazed pasture or crops for their food supply. In such areas, climatic factors, notably rainfall, temperature and solar radiation exert important influences on pasture production and hence the animals that graze that pasture.

Although the direct effects of climate on post-weaning growth have been studied extensively (Preston and

Willis, 1974, Holmes, 1979), this review gives a brief outline of the effects of high ambient temperature because they are of special importance to tropical and sub-tropical regions. In these areas, heat stress affects production of exotic, highly-productive breeds of cattle and, although the indigenous breeds are well adapted in terms of survival, they have low inherent growth potentials, by temperate standards (Frisch and Vercoe, 1978).

Research has indicated that very high temperatures depress growth in cattle through their effect on feed intake, water intake, and nitrogen metabolism. Reviews by Preston and Willis, 1974, Frisch and Vercoe, 1978 and Williamson and Payne, 1978) have indicated that daily gain decreases with increase in temperature from 23 to 33°C and that food intake also decreases at high temperatures. Kellaway and Colditz (1975), reporting on the effect of heat stress on growth and nitrogen metabolism showed that food intake and growth rate of cattle decreased at 38°C compared with 20°C and that cattle at 38°C showed evidence of disturbances in their metabolism. Feed efficiency is also affected adversely at high temperatures because the animal attempts to lower its heat load by reducing feed intake and this results in a decreased growth rate and hence poorer feed efficiency (Preston and Willis, 1974).

Nutrition is considered the most important single factor influencing beef cattle production. In most tropical and sub-tropical countries, beef production is based almost entirely on natural pasture. The major nutritional limitation to production in such places is thus a combined deficiency of energy and protein which normally arise from the poor quality herbage or roughage, which is the only food available to beef cattle during a long dry season. Reduced quantities of such food may be an additional limiting factor in particularly adverse drought situations (Topps, 1976). The low digestibility and protein content of the diet presented to cattle post-weaning imposes a severe physical restriction on the amount of food an animal is able to eat and this in turn reduces the growth rate.

Reports on the influence of nutrition on beef cattle growth in tropical and sub-tropical countries indicate that lack of protein in natural pasture is the major limiting factor. Pratchett <u>et al</u> (1977), investigating the factors limiting liveweight gain (post-weaning) of beef cattle on rangeland in Botswana, obtained results which indicated that liveweight change is influenced primarily by the crude protein content of the herbage selected. They found that crude protein content of fistula samples accounted for 54% of the variation in liveweight gain, while digestibility of the same samples accounted for 32%. Other workers who reported similar findings are Sutherland (1959), Topps (1962) and Van Niekerk (1974). The latter author stated that feeding of energy-rich, but protein deficient food gives poor responses in animal production and depresses forage intake. He concluded that energy is not the first limiting factor in the dry sub-tropical conditions of South Africa. On the contrary, reports from studies in temperate climates indicate that energy is the major limiting factor of post-weaning growth rate (Hodgson, 1968, Preston and Willis, 1974).

Seasonal influences on post-weaning growth are also well established. In a system of beef production based predominately on pasture, post-weaning growth changes with the seasons of the year, this being mainly due to the seasonal patterns of pasture production and availability. In a review of the factors affecting the performance of beef cattle on unimproved pastures in tropical Queensland, Sutherland (1959) concluded that the main problems of beef production in such an area were related to inadequate plane of nutrition provided at certain seasons of the year by unimproved pastures and its effect on the performance of cattle. The problem of periodic nutritional depressions caused by occassional drought conditions or by winter conditions in most parts of Southern Africa have also been long recognised (Naude, 1965, Ward, 1968, Butterworth and Presswood, 1978). Reviews by Payne (1970) and Williamson and Payne (1978) have each indicated severe post-weaning growth restrictions during the winter (or dry) period and faster growth rates during spring and summer (or wet season).

Post-weaning growth is also influenced by year and month of birth. Vorster (1954) noted that the advantage which animals born early within the calving season had at weaning was still apparent even at 3.5 and 4.5 years of age. Thorpe <u>et al</u> (1980a) reported that calves born 30 days later than average were lighter by 15 to 18kg at 12 months and by 18 to 20kg at 18 months. Sacker <u>et al</u> (1971a) emphasised the significance of taking period of birth into consideration in analyses of weight-for-age data in an environment where range conditions can change greatly from month-to-month. These authors also reported significant year effects on post-weaning growth; they found body weight differences of 26.8kg at 18 months and 19.1kg at 24 months between the best and worst years. Kennedy and Chirchir (1971) found significant differences of 43kg and 528kg for 13- and 18-month weights, respectively, between the best and poorest year. Significant year effects on post-weaning daily gain and yearling weight were reported by Straw and Jones (1977) and they also emphasised the importance of comparing post-weaning growth records of animals within year especially in areas where the environment is harsh.

Management has an important influence on growth and is a source of variation that the producer can attempt to control with some success. For instance, a comparison of two systems of management in Botswana by Rennie <u>et al</u> (1977) revealed that the productivity of indigenous cattle raised under a ranching within a fenced paddock system was superior to that of cattle raised under the traditional system of management on unenclosed communal grazing (Cattle Posts). These authors found productivity estimates of 188kg of 18-month old calf per cow per year for the ranch-raised animals while that for the cattle post-raised animals was 86kg. The animals maintained in the ranch for the whole period of study had a superior post-weaning gain (7 to 18 months) of 17.3kg or 20% over the cattle post-maintained animals.

The management aspects that influence growth post-weaning include feeding, supplementation, watering, modification of the environment (shade, shelter) and disease control. A detailed review of published work on these management factors has been made by Preston and Willis (1974).

Feeding as discussed here refers to the provision of dry matter or energy when total grazing is not sufficient to support the herd. This normally occurs in winter and/or during drought years, although the severity of nutritional stresses depends on stocking rate and regional restrictions of pasture production by climatic conditions. In general, the main idea behind feeding grazing animals is to equate the highly seasonal pattern of pasture production with the steadily increasing feed requirements of growing animals. Most reports from studies investigating the influence of feeding on post-weaning growth have indicated that grazing cattle fed with silage, hay or foggage during winter and/or the dry season, grew faster than non-fed animals (Sutherland, 1959, Naude, 1965, Topps, 1976, Williamson and Payne, 1978).

Closely associated with the effects of feeding grazing cattle is the frequency of grazing. This has an important influence on growth particularly in management systems where night kraaling is practised. It has been observed that during hot days cattle normally show a decrease in their grazing during the day, but a compensatory increase during the night when temperatures are cooler. Thus, if the management system is such that cattle have no access to grazing at night time, the effect of hot days on total food intake could be severe and thus growth rate would be reduced.

The provision of a nutritional additive to remedy deficiencies (in quality rather than quantity) in the diet of animals, i.e., supplementation, is another management factor with a marked influence on post-weaning growth. There is abundant evidence from the tropics and sub-tropics which indicate that the use of protein supplements to cattle grazing unimproved pastures during the dry season when the pasture available is of low feed value results in increased growth rates (Sutherland, 1959, Naude, 1965, Topps, 1976, Pratchett <u>et al</u>, 1977). The supplementation of minerals and vitamins to the diet of growing animals also increases their growth rates. For instance, the beneficial effects of phosphorus supplementation on live weight gain have been reported in most areas of Southern Africa where natural rangelands are deficient in this mineral (see Ward, 1968, Capper *et al*, 1977, APRU, 1978, Butterworth and Presswood, 1978).

In cattle, sex has a very strong influence on the growth rate of the young. Males maintain superiority from birth throughout life as have been shown by several studies that involved bulls and heifers or steers and heifers (Vorster, 1954, Osman and Rizgalla, 1968, Sacker *et al*, 1971a, Preston and Willis, 1974, Rudder *et al*, 1975, Winks *et al*, 1978, Thorpe *et al*, 1980a). Vorster (1954) observed that differences in weight between steers and heifers tended to widen during the growing season and that at 3.5 years of age, the steers were 11% heavier than the heifers. Osman and Rizgalla (1968) found that males were 9kg heavier than females at 12 months while Sacker *et al* (1971a) reported differences of up to 20kg at 18-months and 17kg at 24-months in favour of males. Winks *et al* (1978) found that steers outperformed heifers in liveweight gains, final liveweight and weight per day of age and were up to 31kg heavier at 800 days.

Obviously, any environmental penalties experienced by the animals up to weaning will carry-over to some extent. Some non-genetic factors influencing pre-weaning growth traits may thus be responsible for variation in post-weaning growth traits. Also, the fact that birth weight and weaning weight are positively correlated (see next section) with post-weaning weights would imply that the later weights depend, to some extent, on the level of weaning weight.

Correction factors are usually needed to remove handicaps against progeny of young cows. Jones and Hopkins (1980) found that neglecting the age of dam effects, reduced genetic gains by 11 to 7% when selection was at an age of 12 to 20 months. Straw and Jones (1977) found that age of dam had a significant effect on yearling weight and post-weaning daily gain, but that it was non-significant on corrected yearling weight. They noted that the adjustments made to weaning weight successfully removed the effect of age of dam on yearling weight, suggesting that yearling weight differences due to age of dam were reflections of the differences at weaning and that no significant compensatory growth occurred between weaning and yearling. Similar findings were reported by Sacker _et al_ (1971a). Several other studies have shown that age of dam effects on post-weaning growth traits are generally unimportant (Rudder _et al_, 1975, Vilakati, 1977, Winks _et al_, 1978 and Thorpe _et al_, 1980a).

2.2 Genetic and Environmental Relationships Among Some Beef Cattle Growth Traits

Improving the performance of economic characters in beef cattle through breeding depends on effective use of genetic variation. Pertinent to the effective use of genetic variability is a knowledge of the genetic and environmental relationships among the traits, as already indicated in the introductory chapter. These relationships include the heritability and repeatability of characters, as well as the genetic, environmental and phenotypic correlations among them. Estimates of such parameters for traits of economic importance are needed to formulate effective breeding plans.

Numerous estimates of the important genetic and non-genetic parameters for beef production have been published (Preston and Willis, 1974, Barlow, 1978). This present review is however, restricted to the estimates of genetic and phenotypic parameters for growth traits. The foregoing sections will focus on the available estimates from tropical and sub-tropical sources, especially those based on cattle populations raised under range conditions.

2.2.1 The heritability of growth traits.

Heritability is arguably the most important single concept in the application of genetics to animal breeding (Hill, 1974). The heritability of a trait has a predictive role in the measurement of the degree of correspondence between phenotypic values, which are directly measured, and breeding values, which influence the phenotypic values of the next generation (Falconer, 1960). Heritabilities are essential for planning breeding systems and predicting response to selection as well as for genetic evaluation programmes (Turner and Young, 1969, Dalton, 1979, 1980).

Various genetics and animal breeding textbooks have defined the two concepts of heritability and have also outlined the various ways in which the heritability of a character can be determined (Lush, 1945, Falconer, 1960, Turner and Young, 1969, Warwick et al, 1979, Dalton, 1980). The heritability concept referred to in this section is heritability in the narrow sense, i.e., the proportion of the observed differences among animals that is transmitted to their offspring. It is more useful in most aspects of animal improvement. The most widely used procedures for computing heritability in farm animals are the paternal half-sib correlation and the offspring-parent regression (Turner and Young, 1969, Preston and Willis, 1974, Warwick et al, 1979).

By definition heritabilities are applicable only to the data from which they were derived and it is thus strictly not accurate to take estimates made in one population for general application in another. However, characters can be generally classified as having high (>0.50), medium (0.25 to 0.50) or low (<0.25) heritability (Preston and Willis, 1974, Warwick et al, 1979). It must also be pointed out that heritability, being a function of genetic variance, could change its value with any change in gene frequency as a consequence of selection. The usefulness of periodic re-estimation of heritability for traits of economic importance particularly for herds under artificial selection have been stressed by Turner and Young (1969) and Dalton (1980). However, Hill (1974) indicated that gene effects have to be very large in relation to the phenotypic standard deviation before genetic variances are likely to change markedly in the first few generations. He stated that the general impression is that prediction based on present estimates are useful for up to five generations.

Numerous determinations of heritability have been made for economically important traits in cattle. The review of several reports on the estimation of heritability of a number of traits by Preston and Willis (1974) have indicated values ranging from below zero to over one, and yet the theoretical limits for estimates of heritability are zero and one (Lush, 1945, Falconer, 1960). This indicates the large sampling errors involved in the calculation of heritability estimates. Heritability estimates vary according to methods of estimation, sources of environmental effects and genetic variability of the population studied (Falconer, 1960, Preston and Willis, 1974, Warwick et al, 1979, Dalton, 1980). Some estimates of the heritability of certain pre- and post-weaning growth traits are summarised in the following sections.

(i) The Heritability of Pre-Weaning Growth Traits

Pre-weaning growth traits have been reported to have a medium level of heritability by various authors (see Warwick, 1968, Preston and Willis, 1974, Barlow, 1978). Median values of 0.38, 0.27 and 0.30 for the heritability estimates of birth weight, pre-weaning gain and weaning weight, respectively, were given by Preston and Willis (1974) after collation of a large number of heritability estimates. Table 2.4, 2.5 and 2.6 present some estimates of the heritability of birth weight, pre-weaning daily gain and weaning weight reported for cattle in the tropics and sub-tropics. The breed, method of estimation, and standard errors of the estimates are also indicated.

The heritability estimates in most studies are generally medium for all the growth traits. This indicates the scope of genetic improvement of pre-weaning growth traits through selection. The moderate to high heritability estimate of birth weight in relation to the other traits is an indication of the strength of the relationship which may be expected between the recorded birth weight of a sire and the birth weight of his progeny. Selection for sires with high birth weight would result in increased birth weight of calves and this could be undesirable since selecting for birth weight towards the extreme may increase the incidence of dystocia (Preston and Willis, 1974). The heritability estimate of pre-weaning daily gain is generally lower than that of weaning weight, indicating that pre-weaning gain is less reliable in mass selection than weaning weight and could profitably be excluded from a selection programme (Lombard, 1963, Berruecos and Robison, 1968, Preston and Willis, 1974, Barlow and O'Neill, 1980b).

Tables 2.4 and 2.5 also show considerable variation in heritability estimates reported in the literature. The large variations among reports may in part be due to the analyses of the data or the effectiveness of removing environmental variation (Barlow, 1978, Seifert, 1975b). Pattie _et al_ (1970) found that the heritability estimate of birth weight was lower (0.17) when using unadjusted data than when the data were adjusted (0.37) for variations due to year of birth. Seifert (1975b) also reported consistently smaller estimates of heritability on uncorrected data than among corrected data. He obtained heritability estimates ranging from 0.53 to 0.74 for birth weight, 0.05 to 0.64 for weaning weight for age and 0.06 to 0.60 for pre-weaning average daily gain, depending on the effects adjusted for in the data. Variation in the heritability estimates of some pre-weaning growth traits due to other factors such as sex (Pahnish _et al_, 1964, Francoise _et al_, 1973), strain/breed (Willis _et al_, 1972, Baharin and Beilharz, 1975) and pre-weaning environment (Barlow, 1978), have also been reported.

TABLE 2.4 Some Estimates of the Heritability of Birth Weight

Breed	Heritability Estimate*	Source and Method of Estimation
Kenana	0.18 ± 0.21	Alim (1964)-Paternal half-sib correlation
Unspecified	0.34	Baharin and Beilharz (1975)-Paternal half-sib correlation
Hereford and Crosses	0.56 ± 0.15	Barlow and O'Neill (1980b)-Paternal half-sib correlation
Brahman	0.41 ± 0.16	Berruecos and Robison (1968)-Paternal half-sib correlation
Holstein x Haryana	0.26 ± 0.07	Ghosh *et al.* (1978)-Paternal half-sib correlation
Haryana	0.40	Govindaiah and Singh (1980)-Paternal half-sib correlation
Santa Gertrudis	0.55 ± 0.16	Harricharan *et al.* (1976)-Paternal half-sib correlation
Sahiwal	0.13 ± 0.10	Harricharan *et al.* (1976)-Paternal half-sib correlation
Brahman	0.35 ± 0.25	Harricharan *et al.* (1976)-Paternal half-sib correlation
Africander	0.18 ± 0.07	Heyns (1977)-Paternal half-sib correlation
Hereford	0.35	Koch and Clark (1955a)-Paternal half-sib correlation

Table 2.4 continued

Breed	Heritability Estimate*	Source and Method of Estimation
Hereford	0.35	Koch and Clark (1955b) -Regression of offspring on sire
Hereford	0.44	Koch and Clark (1955b) -Regression of offspring on dam
Crosses	0.30	Lombard (1963)-Paternal half-sib correlation
Ngada	0.33 ± 0.17	Mahadevan and Marples (1961)-Intrasire regression of offspring on dam
Shorthorn x Zebu	0.23 ± 0.18	Marples (1964)-Intra-sire regression of offspring on dam
Red Dane	0.75 ± 0.27	Mehta _et al._ (1976)-Paternal half-sib correlation
Holstein x Sahiwal	0.15	Naidu and Desai (1965)-Paternal half-sib correlation
Sudanese	0.49	Osman and Rizgalla (1968)-Paternal half-sib correlation
Hereford	0.20	Pahnish _et al._ (1964)-Paternal half-sib correlation
Jersey x Haryana	0.16 ± 0.11	Ray _et al._ (1978)-Paternal half-sib correlation
Hereford	0.72	Shelby _et al_ (1955)-Paternal half-sib correlation

Table 2.4 continued

Breed	Heritability Estimates*	Source and Method of Estimation
East African Zebu	0.36 ± 0.13	Stobbs (1966) -Intra-sire regression of offspring on dam
Crosses	0.21 ± 0.09	Trail *et al* (1971b) - Paternal half-sib correlation
Ongole	0.33 ± 0.15	Venkateshwarlu *et al* (1972) -Intra-sire regression of offspring on dam
Ongole	0.56 ± 0.29	Venkateshwarlu *et al* (1972) -Paternal half-sib correlation
Charolais	0.25 ± 0.60	Willis *et al* (1972) - Paternal half-sib correlation
Santa Gertrudis	0.39 ± 0.30	Willis *et al* (1972) - Paternal half-sib correlation
Brown Swiss x Zebu	0.62 ± 0.40	Willis *et al* (1972) - Paternal half-sib correlation
Holstein x Zebu	0.09 ± 0.10	Willis *et al* (1972) - Paternal half-sib correlation

Range = 0.09 to 0.75

* with standard error

TABLE 2.5 Some Estimates of the Heritability of Pre-weaning Growth Rate (90 to 270 days)

Breed	Heritability Estimate*	Source and Method of Estimation
Angus	0.21 ± 0.38	Barlow and Dettmann (1978) -Paternal half-sib correlation
Hereford and Crosses	0.47 ± 0.15	Barlow and O'Neill (1980b) -Paternal half-sib correlation
Brahman	0.43 ± 0.17	Berruecos and Robison (1968) -Paternal half-sib correlation
Haryana	0.65 ± 0.16	Govindaiah and Singh (1980) -Paternal half-sib correlation
Brahman	0.63 ± 0.38	Harricharan *et al* (1976) -Paternal half-sib correlation
Santa Gertrudis	0.70 ± 0.19	Harricharan *et al* (1976) -Paternal half-sib correlation
Sahiwal	0.86 ± 0.39	Harricharan *et al* (1976)-Paternal half-sib correlation
Africander	0.19 ± 0.07	Heyns (1977) -Paternal half-sib correlation; 90-day weight
Africander	0.09 ± 0.05	Heyns (1977) -Paternal half-sib correlation; gain from birth to 90 days
Africander	-0.05 ± 0.03	Heyns (1977) -Paternal half-sib correlation; gain from birth to weaning

Table 2.5 continued

Breed	Heritability Estimate*	Source and Method of Estimation
Hereford	0.21	Koch and Clark (1955a) - Paternal half-sib correlation
Hereford	0.17	Koch and Clark (1955b) - Regression of offspring on sire
Hereford	0.07	Koch and Clark (1955b) - Regression of offspring on dam
Crosses	0.22	Lombard (1963) -Paternal half-sib correlation
Unspecified	0.11 ± 0.20	Mason <u>et al</u> (1970) - Regression of offspring on dam
Unspecified	0.05 ± 0.23	Mason <u>et al</u> (1970) - Intra-sire regression of offspring on dam
Unspecified	0.22 ± 0.22	Mason <u>et al</u> (1970) - Paternal half-sib correlation
Holstein x Sahiwal	0.44	Naidu and Desai (1965) - Paternal half-sib correlation; 19-week weight
Hereford	0.05	Pahnish <u>et al</u> (1964) - Paternal half-sib correlation
Zebu	0.38 ± 0.42	Torres (1962) -Paternal half-sib correlation; 90-day weight
Zebu	0.28 ± 0.38	Torres (1962) -Paternal half-sib correlation; Average daily gain-birth to 90 days

Table 2.5 continued

Breed	Heritability Estimate *	Source and Method of Estimation
Zebu	0.37 ± 0.41	Torres (1962) -Paternal half-sib correlation; Average daily gain-birth to 210 days
Zebu	0.33 to 0.40	Torres (1962) -Paternal half-sib correlation; Average daily gain - 90 days to 210 days
Crosses	0.14 ± 0.07	Trail *et al* (1971b) Paternal half-sib correlation; 3 month weight.

Range = 0.05 to 0.86

* with standard error

TABLE 2.6 Some Estimates of the Heritability of Weaning Weight (6 to 9 months).

Breed	Heritability Estimate*	Source and Method of Estimation
Angus	0.21 ± 0.38	Barlow and Dettmann (1978) -Paternal half-sib correlation
Hereford and Crosses	0.54 ± 0.15	Barlow and O'Neill (1980b) -Paternal half-sib correlation
Brahman	0.47 ± 0.18	Berruecos and Robison (1968) -Paternal half-sib correlation
Hereford	0.17	Blackwell *et al* (1962) -Paternal half-sib correlation
Angus, Hereford and Shorthorn	0.67; 0.18	Dunn *et al* (1970) -Paternal half-sib correlation
Crosses	0.29; 0.34	Dunn *et al* (1970) -Paternal half-sib correlation
Angus	0.72 ± 0.33	Francoise *et al* (1973) -Paternal half-sib correlation
Hereford	0.82 ± 0.12	Francoise *et al* (1973) -Paternal half-sib correlation
Haryana	0.67 ± 0.17	Govindaiah and Singh (1980) -Paternal half-sib correlation
Brahman	0.52 ± 0.34	Harricharan *et al* (1976) -Paternal half-sib correlation

Table 2.6 continued

Breed	Heritability Estimate*	Source and Method of Estimation
Sahiwal	1.33 ± 0.50	Harricharan *et al* (1976) -Paternal half-sib correlation
Santa Gertrudis	0.80 ± 0.21	Harricharan *et al* (1976) -Paternal half-sib correlation
Africander	0.05 ± 0.05	Heyns (1977) -Paternal half-sib correlation
Hereford	0.24	Koch and Clark (1955a) - Paternal half-sib correlation
Hereford	0.11	Koch and Clark (1955b) - Regression of offspring on dam
Hereford	0.25	Koch and Clark (1955b) - Regression of offspring on sire
Crosses	0.27	Lombard (1963) -Paternal half-sib correlation
Sudanese	0.10 ± 0.14	Osman and Rizgalla (1968) -Paternal half-sib correlation
Hereford	0.23; 0.05	Pahnish *et al* (1964) - Paternal half-sib correlation
Hereford	0.23	Shelby *et al* (1955) - Paternal half-sib correlation
East African Zebu	0.24	Stobbs (1966) -Intra-sire regression of offspring on dam
Zebu	0.28 to 0.38	Torres (1962) -Paternal half-sib correlation

Table 2.6 continued

Breed	Heritability Estimate*	Source and Method of Estimation
Crosses	0.08 ± 0.06	Trail *et al* (1971b) - Paternal half-sib correlation; 6 month weight
Crosses	0.13 ± 0.07	Trail *et al* (1971b) Paternal half-sib correlation; 9 month weight
Charolais	0.44 ± 0.80	Willis *et al* (1972) - Paternal half-sib correlation; 90 day weight
Santa Gertrudis	0.21 ± 0.20	Willis *et al* (1972) - Paternal half-sib correlation; 90 day weight
Zebu	0.11 ± 0.10	Willis *et al* (1972) - Paternal half-sib correlation; 90 day weight
Brown Swiss x Zebu	0.05 ± 0.10	Willis *et al* (1972) - Paternal half-sib correlation; 90 day weight
Holstein x Zebu	0.16 ± 0.20	Willis *et al* (1972) - Paternal half-sib correlation; 90 day weight

Range = 0.05 to 1.33

* with standard error

(ii) The Heritability of Post-weaning Growth Traits

Several reports on the heritability of post-weaning growth traits have been reviewed by Preston and Willis (1974). They gave preferred values of 0.52 and 0.70 for daily gain on test and final liveweight on test, respectively. However, most of the estimates reviewed by these authors were obtained from American sources and were based on data collected on cattle (mainly bulls and steers) tested on high-energy rations in confined areas for periods of 150 to 250 days. The average heritabilities for weights and gains of pasture-fed animals up to 24 months of age are generally lower than those under feed-lot conditions (Carter, 1971, Barlow, 1978, Hinojosa and Segura, 1980).

Table 2.7 presents a summary of some of the heritability estimates for certain post-weaning growth traits reported for cattle in the tropics and sub-tropics. Most of these estimates were extracted from reports on studies involving cattle generally grown on pasture with little or no supplementation.

Estimates of the heritability of post-weaning weight and/or gain are necessary to predict genetic gains and to formulate breeding plans, which are aimed at selecting animals on their own performance. The heritability estimates reported in most studies are generally medium to high for all the growth traits, indicating that selection for growth would result in progress at an appreciable rate (Warwick, 1968, Preston and Willis, 1974, Barlow, 1978). The heritability of actual weight for age is generally higher than that of post-weaning daily gain (Table 2.7), implying that it would be more appropriate in a genetic improvement programme to select animals on post-weaning final liveweight rather than the mean daily gain in the same period. For instance, a study of the effectiveness of selection for growth rate in Zebu x British crossbred cattle by Seifert (1975b) indicated that the heritability of post-weaning daily gain was the lowest of all estimates and ranged from 0.09 to 0.33. Estimates of the heritability of adjusted final weight per day of age (18-months) in that study were in turn larger than unity (1.42) and a realised heritability of 0.52 for this trait was obtained. After consideration of several other genetic and phenotypic parameter estimates for various growth traits, Seifert (1975b) remarked that weight per day of age at 18-months appeared to be the most efficient single trait to select beef cattle for increased growth rate. Hinojosa and Segura (1980), working with Brahman cattle fed only on pasture, also found that the heritability of final liveweight at 414 days was higher (0.51) than that of post-weaning daily gain (0.08). These two examples confirm the findings of several other reports which have indicated that under range conditions, actual weight is a more valid practical measure of growth than gain (see Carter, 1971 and Barlow, 1978). The relatively high heritability estimates of actual weight also imply that selection on individual performance i.e., performance testing, would be an adequate selection method in breeding plans to improve this trait.

The limited findings hitherto published on the comparison of heritability estimates of straightbred and crossbred populations appear to indicate that there are no significant differences between such estimates for post-weaning growth traits. Miquel and Cartwright (1963), Dunn _et al_ (1970) and Koger _et al_ (1975) have all reported that where sires of the same breed are mated to different breed groups of dams, half-sib heritability estimates obtained from within different groups are generally of the same order of magnitude. These findings suggest that selection for growth should be roughly as effective in crossbreds as in straightbreds.

The reported heritability estimates of post-weaning growth traits also show a wide variation between studies (see Table 2.7). This may be partly due to differences in the period over which post-weaning gain and/or the age at which post-weaning weights are recorded. The time of weaning and the nutritional regime over this period also vary considerably between studies and could thus be responsible for the variation in heritability estimates (Preston and Willis, 1974, Barlow, 1978).

TABLE 2.7 The Heritability Estimates of some Post-Weaning Growth Traits

Trait	Breed	Heritability Estimate*	Source, Method and Notes
(a) Yearling weight (12 to 15 months)			
	Haryana	0.81 ± 0.21	Govindaiah and Singh (1980) -Paternal half-sib correlation - 12-month weight
	Brahman	0.93 ± 0.49	Harricharan *et al* (1976) -Paternal half-sib correlation - 12-month weight
	Sahiwal	1.67 ± 0.54	Harricharan *et al* (1976) -Paternal half-sib correlation - 12-month weight
	Santa Gertrudis	0.74 ± 0.20	Harricharan *et al* (1976) -Paternal half-sib correlation - 12-month weight
	Brahman	0.51 ± 0.31	Hinojosa and Segura (1980) -Paternal half-sib correlation - 414 days
	Hereford	0.47	Koch and Clark (1955a) -Paternal half-sib correlation
	Hereford	0.43	Koch and Clark (1955a) Regression of offspring on dam
	Ngada	0.27 ± 0.26	Mahadevan and Marples (1961) -Intra-sire regression of offspring on dam. 12-month weight
	Holstein x Sahiwal	0.79 ± 0.31	Naidu and Desai (1965) - Paternal half-sib correlation - 365-days

Table 2.7 continued

Trait	Breed	Heritability Estimate*	Source, Method and Notes
	Sudanese	0.26 ± 0.26	Osman and Rizgalla (1968) -Paternal half-sib correlation - 365 days
	Crosses	0.08 ± 0.06	Trail *et al* (1971b) - Paternal half-sib correlation - 12-months
	Crosses	0.31 ± 0.14	Trail *et al* (1971b) - Paternal half-sib correlation - 15-months
(b) 18 to 24 months weight			
	Hereford	0.34	Blackwell *et al* (1962) - Paternal half-sib correlation - 18-months
	Hereford	0.70	Blackwell *et al* (1962) - Final weight
	Angus, Hereford and Shorthorn	0.71 S	Dunn *et al* (1970) - Paternal half-sib correlation. 550-day weight
	Angus, Hereford and Shorthorn	0.51 H	Dunn *et al* (1970) - Paternal half-sib correlation. 550-days
	Crosses	0.56 S	Dunn *et al* (1970) - Paternal half-sib correlation. 550-days
	Crosses	1.00 H	Dunn *et al* (1970) - Paternal half-sib correlation. 550-days

Table 2.7 continued

Trait	Breed	Heritability Estimate*	Source, Method and Notes
	Angus	0.18 ± 0.32	Francoise *et al* (1973) - Paternal half-sib correlation. 18-month weight/day of age
	Hereford	0.73 ± 0.13	Francoise *et al* (1973) - Paternal half-sib correlation. 18-month weight/day of age
	Haryana	1.02H± 0.35	Govindaiah and Singh (1980) -Paternal half-sib correlation. 18-months
	Haryana	0.93H± 0.33	"
	Ngada	0.34 ± 0.28	Mahadevan and Marples (1961) -Intra-sire regression of offspring on dam-18-months
	East African Zebu	0.31 ± 0.21	Stobbs (1966) -Intra-sire regression of offspring on dam- 1 to 2 years average weight
	East African Zebu	0.57 ± 0.17	Stobbs (1966) - 2 to 3 years average weight
	Crosses	0.11 ± 0.08	Trail *et al* (1971b) - Paternal half-sib correlation - 18-months
	Crosses	0.06 ± 0.07	Trail *et al* (1971b) - 21 - months
	Crosses	0.19 ± 0.11	Trail *et al* (1971b) - 24-months

Range (12 to 24 months) = 0.06 to 1.67

Table 2.7 continued

Trait	Breed	Heritability Estimate*	Source, Method and Notes
(c) Post-weaning gain			
	Unspecified	0.36	Baharin and Beilharz (1975) -Paternal half-sib correlation
	Hereford	0.32	Blackwell *et al* (1962) - Paternal half-sib correlation
	Angus	0.60 ± 0.39	Francoise *et al* (1973) - Paternal half-sib correlation
	Hereford	0.41 ± 0.11	"
	Brahman	0.08 ± 0.14	Hinojosa and Segural (1980) -Paternal half-sib correlation
	Hereford	0.39	Koch and Clark (1955a) - Paternal half-sib correlation
	Hereford	0.18	Koch and Clark (1955b) - Intra-sire regression of offspring on dam
	Sudanese	0.28 ± 0.20	Osman and Rizgalla (1968) - Paternal half-sib correlation
	Crosses	0.03 ± 0.06	Trail *et al* (1971b) - Paternal half-sib correlation (9 to 18 months)
	Crosses	0.34 ± 0.15	Trail *et al* (1971b) - 9 to 24 months.

Range = 0.03 to 0.60

* with standard error

S = steers H = heifers

2.2.2 The genetic and phenotypic relationships between beef cattle growth traits.

The relationship of growth made by cattle during different periods of development is of general significance to the beef cattle industry. Breeding animals must often be selected at a young age, and the success of selection depends largely on the cattle retaining the characteristic for which they were selected. The importance of being able to predict future gains from early growth in the production of animals for meat is obvious (Preston and Willis, 1974, Barlow, 1978).

Relationships between traits may be classified into genetic, environmental, and phenotypic correlations. However, it is not usually possible to measure all three types of relationship unless there is a large volume of data.

The genetic correlation is the correlation between the additive breeding values for two traits or between the sum of additive effects of the genes influencing these traits (Warwick et al, 1979). Genetic correlations are mainly an outcome of pleiotropic effects of genes, i.e., the capacity of a gene (or genes) to affect two characters simultaneously, and to a minor degree, of linkage or selection with varying emphasis on the different characters in many interbreeding groups of a population (Falconer, 1960, Turner and Young, 1969, Preston and Willis, 1974, Dalton,

1980). These correlations are of greatest interest to breeders because they are used in development of breeding plans to:
(1) Indicate what other characteristics are likely to change in future generations besides those under selection; (2) decide what counter-selection might be needed to prevent such change, and (3) decide whether an easily-measured character can be used as a selection criterion to obtain genetic gains in a trait which is more difficult (or expensive) to measure (Dalton, 1980).

Genetic relationships among beef cattle growth traits have not been studied nearly as extensively as heritability and estimates of genetic correlations are subject to larger sampling errors than are heritability estimates based on the same number of animals (Warwick, 1968, Preston and Willis et al, 1979). Like heritability, genetic correlations may change under selection, not only in degree (size), but also in direction (sign), as indicated by Turner and Young (1969). Genetic correlation coefficients are also specific to the population and environment in which they were obtained.

Phenotypic correlations, like the phenotype itself, arise from a combination of genetic and environmental effects. The phenotypic correlations between characters are not as important as the genetic correlations because they do not give a definite indication about expected changes in future generations in the course of selection.

They are useful indicators of the overall phenotypic relationships among traits, but offer little information on the magnitude of the genetic and environmental correlations. It is possible to have two traits which have a positive phenotypic correlation even though the genetic correlation between them is negative. There is therefore an obvious need to be cautious in interpreting and using phenotypic correlations until the size and direction of the corresponding genetic correlations are known.

Otherwise, phenotypic correlations are easy to obtain and the square of the correlation coefficient (i.e., the coefficient of determination) is used to measure the amount of variation in one trait that is accounted for by variation in a correlated trait.

The phenotypic and genetic relationships existing between various traits used as criteria for selection in beef cattle must be known in order to maximise the rate of progress in a selection programme and to devise the most efficient breeding plans.

This section summarises some of the published genetic and phenotypic correlation coefficients for growth traits of cattle raised under tropical and sub-tropical conditions. The reported correlation coefficients, especially the genetic correlations, show a wide range of variation, reflecting not only large sampling errors, but presumably also real genetic differences between the populations studied in terms of genetic and environmental components (Falconer, 1960). Most of the reported correlations among growth traits are, however, positive and they range from medium to high.

(i) The Genetic and Phenotypic Relationships between Pre-weaning Growth Traits

Table 2.8 and 2.10 presents a summary of some genetic and phenotypic correlation coefficients between pre-weaning growth traits. Variations in estimates of these correlations between studies exist, but generally medium to high levels of association have been reported. Part-whole genetic and phenotypic correlations (e.g., pre-weaning gain, and weaning weight) are the highest (see Table 2.10), as would be expected. Some of the genetic correlation coefficients are above +1 due to sampling error.

The magnitude of the phenotypic correlations between birth weight and weaning weight would suggest that heavier calves at birth are able to maintain their weight advantage through to weaning. The genetic correlations between birth weight and the other pre-weaning traits are positive, implying that many of the genes responsible for variation in pre-natal growth are also responsible for post-natal growth to weaning.

TABLE 2.8 Some Estimates of Genetic and Phenotypic Correlation of Birth Weight with Pre-weaning Growth and Weaning Weight

Correlated Trait	Correlation Genetic	Estimate Phenotypic	Source and Comments
(a) Pre-weaning growth (gain or average daily gain (ADG)	0.25	0.11	Barlow and O'Neill (1980b) -Hereford and crossbreds; Pre-weaning ADG.
	0.82	0.32	Berruecos and Robison (1968) - Brahmans Pre-weaning ADG
	0.68	-0.09	Heyns (1977) - Africander; gain to 90 days
	0.46	0.21	Koch and Clark (1955a) - Hereford
	0.30	0.20	Pahnish *et al* (1964) Hereford-Heifer data only; daily gain to 230 days
	0.17	0.12	Seifert (1975b) - Zebu x British; Pre-weaning ADG.
	-	0.28	Von La Chevallerie and Buys (1965) - Africander; daily gain to weaning
(b) Weaning weight	0.49	0.31	Barlow and O'Neill (1980b) -Hereford and crosses
	0.84	0.42	Berruecos and Robison (1968) - Brahmans

Table 2.8 continued

Correlated Trait	Correlation Genetic	Estimate Phenotypic	Source and Comments
	0.82	0.57	Govindaiah and Singh (1980) - Haryana; 4 month weight
	0.85	0.25	Govindaiah and Singh (1980) - Haryana; 8 month weight
	0.82	0.27	Heyns (1977) - Africander; 90-day weight
	0.79	0.21	Heyns (1977) - Africander; 210-days
	0.63	0.39	Koch and Clark (1955a) -Hereford
	-	0.42	Naude (1965) - Nguni
	0.42H 1.12B	0.42H 0.31B	Pahnish *et al* (1964) - Hereford; H=heifer data B=bull data
	0.86	0.35	Trail *et al* (1971b) Crosses; 6-month weight
	1.04	0.34	Trail *et al* (1971b) Crosses; 9-month weight
	0.47	0.27	Seifert (1975b) - Zebu x British
	1.00	0.26	Willis *et al* (1972) - Charolais; 90-day weight
	0.36	0.20	Willis *et al* (1972) - Santa Gertrudis; 90-day weight
	0.40	0.16	Willis *et al* (1972) - Zebu; 90-day weight

TABLE 2.9 Some Estimates of Genetic and Phenotypic Correlation of Birth Weight with Post-weaning Growth Traits

Correlation Estimate Genetic	 Phenotypic	Source and Comment*
-0.16	0.18	Govindaiah and Singh (1980) - Haryana; with 12-month weight
0.12	0.05	Govindaiah and Singh (1980) -Haryana; with 18-month weight; Heifers only.
0.67	0.07	Govindaiah and Singh (1980) -Haryana; with 24-month weight; Heifers only.
0.06	0.04	Koch and Clark (1955a) - Hereford; with post-weaning ADG
0.40	0.34	Koch and Clark (1955a) - Hereford; with yearling weight
0.82	0.21	Seifert (1975b) - Zebu x British, Post-weaning ADG.
0.59	0.34	Seifert (1975b) - Zebu x British, with 18-month weight.
1.12	0.36	Trail _et al_ (1971b) - crosses; with 12-month weight
0.79	0.36	Trail _et al_ (1971b) - crosses; with 15-month weight
0.81	0.36	Trail _et al_ (1971b) - with 18-month weight
0.58	0.35	Trail _et al_ (1971b) - Crosses; with 21-month weight

Table 2.9 continued

Correlation Estimate Genetic	Phenotypic	Source and Comment*
0.64	0.35	Trail <u>et al</u> (1971b) - Crosses; with 24-month weight
-	0.29	Vorster (1954) - European; with slaughter weight at 3.5 to 4.5 years.
-	0.18	Vorster (1954) - Native; with slaughter weight at 3.5 to 4.5 years.

* ADG = Average daily gain.

TABLE 2.10 Some Estimates of the Genetic and Phenotypic Correlation of Weaning Weight with Pre- and Post-weaning Growth

Correlated Trait	Correlation Estimate Genetic	Phenotypic	Source and Comment
(a) Pre-weaning gain or average daily gain (ADG).	0.96	0.97	Barlow and Dettmann (1978) -Angus; ADG; female data
	0.93	0.95	Barlow and O'Neill (1980b) -Hereford and crosses; ADG.
	0.92	0.99	Berruecos and Robison (1968) - Brahmans; ADG.
	1.04	0.86	Heyns (1977) - Africander; gain to 90 days.
	0.98	0.98	Koch and Clark (1955a) - Hereford; ADG.
	0.90H 1.70B	1.08H 0.94B	Pahnish <u>et al</u> (1964) -Hereford; gain to 230 days; H=heifer; B=bull
	0.97	0.98	Seifert (1975b) -Zebu x British; ADG.
(b) Post-weaning gain or ADG	0.61	-0.10	Blackwell <u>et al</u> (1962) - Hereford; gain to 18-months; heifer data
	0.12	-0.07	Francoise <u>et al</u> (1973) - Angus and Hereford; ADG.

Table 2.10 continued

Correlated Trait	Correlation Estimate Genetic	Phenotypic	Source and Comment
	-0.03	-0.33	Koch and Clark (1955a) -Hereford; ADG.
	0.71	0.09	Seifert (1975b) - Zebu x British; ADG.
	-0.18	-	Trail *et al* (1971b) - Crosses; gain to 18 months
	-0.23	-	Trail *et al* (1971b) - Crosses; gain to 24 months.

There are indications that genetic correlations between pre-weaning growth traits are generally higher than the corresponding phenotypic correlations. Selection for any of these traits would thus be expected to result in change in the others. Preston and Willis (1974) observed that the genetic correlations between birth weight and pre-weaning growth are mostly higher than the observed phenotypic correlations, indicating that selection for birth weight should increase subsequent gain. Trail *et al* (1971b) obtained genetic and phenotypic correlations of 0.86 and 0.35, respectively, between birth weight and 6-month weight; the respective estimates for birth weight and weaning weight (9 months) were 1.04 and 0.34. Seifert (1975b) also found that the genetic correlation between birth weight and weaning weight was higher than the phenotypic correlation.

(ii) The Genetic and Phenotypic Relationships between Pre-weaning and Post-weaning Growth Traits

The relationship between pre-weaning growth traits and weight or growth at later stages in cattle have been studied by several workers (Preston and Willis, 1974, Barlow, 1978). The genetic correlations between birth weight and post-weaning weights and gains are generally high (Table 2.9) and the phenotypic correlations between these traits are all positive and relatively low. For instance, Trail *et al* (1971b) found a genetic correlation of 0.81 between birth weight and 18-month weight, while Govindaiah and Singh (1980) reported a genetic correlation of 0.67 between birth weight and 24-month weight.

A study by Seifert (1975b) indicated that birth weight was more genetically correlated to post-weaning gains than to weights. The genetic correlation between birth weight and post-weaning average daily gain was 0.82 in his study, while that between birth weight and 18 month weight was 0.59. A high positive genetic correlation between birth weight and total gain to final weight was also reported, indicating that the same genes control pre- and post-natal growth. After citing many other workers who have found positive genetic correlations between birth weight and post-weaning gains, Seifert (1975b) stated that birth weight may be a useful indicator of an animal's genetic potential for growth.

Moderate to high genetic and phenotypic correlations between weaning weight and later weights have been reported in several studies. The reviews by Preston and Willis (1974) and Barlow (1978) have indicated that the genetic correlation between weaning weight and post-weaning weight is of the order of 0.6 to 0.7, although values outside this range are not rare (see Table 2.11). Pre-weaning gain is also positively correlated to post-weaning weights. Seifert (1975b) obtained a genetic and phenotypic correlation of 0.84 and 0.60, respecitvely, between pre-weaning average daily gain and final weight at 18 months of age. The genetic and phenotypic correlations between pre-weaning average daily gain and yearling weight reported by Koch and Clark (1955a) were 0.51 and 0.44, respectively.

Since pre-weaning growth is an integral component of post-weaning weight, it is not surprising that these traits should be highly and positively correlated. However, some authors (Koch and Clark, 1955a. Trail et al, 1971b) have observed that the genetic correlations between birth weight and post-weaning weights were as high as those involving weaning weight, even though birth weights were a smaller portion of the part-whole relationship.

The moderately high genetic correlations amongst pre- and post-weaning growth traits clearly indicate that the genes which are responsible for early body weight are also responsible for body weight at subsequent ages. A review by Barlow (1978) of the genetic parameters of several economic traits of beef cattle with a view of determining the likely consequences of selection for pre-weaning growth on the total herd or farm unit indicated that selection for either weaning weight or average daily gain to weaning will increase liveweight at all ages from birth to maturity. However, average daily gain to weaning was less highly correlated with weights at other ages than weaning weight and appeared negatively correlated with later gains, indicating that weaning weight would be a more efficient selection criterion than pre-weaning gain.

The relationship between weaning weight and post-weaning gain is in most cases low, and negative correlations are not uncommon (Table 2.10). This is explained by the fact that there are effects of compensatory growth in the post-weaning period. Trail et al (1971b) found negative genetic correlations between weaning weight and increase in weight to 18 months of age (-0.18) and between weaning weight and increase in weight to 24 months (-0.23). Francoise et al (1973) obtained low positive genetic correlations (0.12) and negative phenotypic correlations (-0.07) between weaning weight per day of age and average daily gain from weaning to yearling. They attributed the negative phenotypic correlations to compensatory gain effects.

Seifert (1975b) observed that even though the superficial relationship between pre- and post-weaning growth was small, there was a strong positive genetic relationship between the two stages of growth. The genetic correlation between pre- and post-weaning average daily gain was 0.66 in that study, while the phenotypic correlation was 0.08. This author noted that the low phenotypic correlation was as a result of the existence of a fairly strong negative environmental correlation (-0.40) between pre- and post-weaning average daily gain. Calves that are nutritionally or environmentally deprived during the pre-weaning growth period can often compensate during post-weaning growth with gains greater than they might otherwise have achieved.

(iii) The Genetic and Phenotypic Relationships between Post-weaning Growth Traits.

A summary of the relationship between post-weaning growth traits will give an indication of what should be expected of changes in one trait when selection is based on another during the post-weaning period. This is particularly important because breeders need to be able to predict trends in later traits when selecting earlier, so as to reduce the generation interval by assessing animals for inclusion in a breeding programme as early as possible. Table 2.12 summarises the genetic and phenotypic correlation estimates of some post-weaning growth traits arrived at in various studies. This table indicates a strong positive genetic and phenotypic relationship among post-weaning growth traits. The correlation between post-weaning gain and post-weaning weight is very high as expected since post-weaning gain is an integral component of post-weaning weights.

TABLE 2.11 Some Estimates of the Genetic and Phenotypic Correlation between Weaning Weight with Later Weights

Correlation Estimate Genetic	 Phenotypic	Source and Comment
0.10	0.70	Blackwell et al (1962) - Hereford; 7 month weight and 18 month weight; steer data
0.18	0.57	Blackwell et al (1962) - Hereford; 7 month weight and 18 month weight; heifer data
0.61	0.48	Francoise et al (1973) - Angus and Hereford; 240 day weight and 18 month weight
0.66	0.61	Govindaiah and Singh (1980) - Haryana; 8 month weight and 12 month weight
0.22	0.61	Govindaiah and Singh (1980) - Haryana; 8 month weight and 18 month weight; heifer data only
0.29	0.58	Govindaiah and Singh (1980) - Haryana; 8 month weight and 24 month weight; heifer data only
0.54	0.47	Koch and Clark (1955a) - Hereford; weaning weight and yearling weight
-	0.28	Naude (1965) - Africander; weaning weight and yearling weight
0.89	0.56	Seifert (1975b) - Zebu x British; weaning weight and 18 month weight
0.51	0.87	Trail et al (1971b) - Crosses; 6 month weight and 12 month weight

Table 2.11 continued

Correlation Estimate Genetic	Ihenotypic	Source and Comment
0.42	0.76	Trail <u>et al</u> (1971b) - Crosses 6 month weight and 15 month weight
0.55	0.80	Trail <u>et al</u> (1971b) - Crosses 6 month weight and 18 month weight
0.04	0.70	Trail <u>et al</u> (1971b) - Crosses 6 month weight and 24 month weight
0.87	0.91	Trail <u>et al</u> (1971b) - Crosses 9 month weight and 12 month weight
0.87	0.86	Trail <u>et al</u> (1971b); 9 month and 15 month weight
0.95	0.84	Trail <u>et al</u> (1971b); 9 and 18 month weights
0.89	0.79	Trail <u>et al</u> (1971b); 9 and 21 month weights
0.44	0.72	Trail <u>et al</u> (1971b); 9 and 24 month weights.

TABLE 2.12 Some Estimates of the Genetic and Phenotypic Correlation between some Post-weaning Growth Traits

Correlated Trait	Correlation Estimate Genetic	Correlation Estimate Phenotypic	Source and Comment*
(a) Post-weaning gain and post-weaning weight.			
	0.74	0.58	Blackwell *et al* (1962)-Hereford; gain and 18 month weight; steer data
	0.97	0.58	Blackwell *et al* (1962)-Hereford; gain and 18 month weight; heifer data
	0.66	0.73	Francoise *et al* (1973)-Angus and Hereford; gain and 18 month weight
	0.83	0.67	Koch and Clark (1955a)-Hereford; ADG and yearling
	1.05	0.76	Seifert (1975b) - Zebu x British; ADG and 18 month weight
(b) Post-weaning weights at various ages			
	0.67	0.65	Govindaiah and Singh (1980) -Haryana; 12 and 18 month weights; Heifer data
	0.48	0.52	Govindaiah and Singh (1980)- Haryana; 12 and 24 month weights; Heifer data only

Table 2.12 continued

Correlated Trait	Correlation Estimate Genetic	 Phenotypic	Source and Comment*
	0.96	0.64	Govindaiah and Singh (1980)- Haryana; 18 and 24 month weights; heifer data only
	0.91	0.87	Trail *et al* (1971b) - Crosses; 12 and 15 month weights
	0.89	0.90	Trail *et al* (1971b) - 12 and 18 month weights
	0.76	0.86	Trail *et al* (1971b) - 12 and 21 month weights
	0.31	0.79	Trail *et al* (1971b) - 12 and 24 month weights
	0.79	0.89	Trail *et al* (1971b) - 15 and 18 month weights
	0.88	0.84	Trail *et al* (1971b) - 15 and 21 month weights
	0.46	0.84	Trail *et al* (1971b) - 15 and 24 month weights
	0.87	0.91	Trail *et al* (1971b) - 18 and 21 month weights
	0.40	0.87	Trail *et al* (1971b) - 18 and 24 month weights
	0.42	0.88	Trail *et al* (1971b) 21 and 24 month weights

* ADG = average daily gain.

The relationships between the post-weaning weights at various ages are high and positive (Table 2.12), indicating that selection for weight at any age should result in correlated improvement in weight at other ages. Trail et al (1971b) obtained a genetic and phenotypic correlation of 0.89 and 0.90, respectively between 12 and 18 month weights. The respective correlations between 15 and 18 month weights in their study were 0.79 and 0.89. Govindaiah and Singh (1980) found that the genetic correlation between 12 and 18 month weights was 0.67 and that between 18 and 24 month weights was 0.96. The corresponding phenotypic correlations for these traits were 0.65 and 0.64. The estimates obtained in these two studies imply that selection for weight at 12 to 15 months of age would be generally as effective as selection for weight at 18 to 24 months of age, since the heritability of these weights is also relatively high (Section 2.2.1).

2.2.3 The repeatability of pre-weaning performance.

Repeatability is a concept closely allied to heritability and is useful for those traits which are expressed several times during an animal's lifetime such as lactation milk yield for dairy cows and weight of calf weaned for beef cows. It measures the extent to which differences between individuals depend on genetic and permanent environmental effects (Falconer, 1960, Turner and Young, 1969).

The various statistical techniques for estimating the repeatability of production traits have been outlined by Taylor et al (1960) and Turner and Young (1969). Repeatability can be computed as the regression of future performance on past performance and may also be derived from an analysis of variance as an intra-class correlation among successive records or observations on the same individual. Repeatability estimates may differ according to the genetic properties of the population and the environmental conditions under which the individuals are kept.

The repeatability of pre-weaning traits reviewed in this section is essentially a measure of performance of the dam, rather than of the calf. Clearly, traits such as birth weight and weaning weight occur only once in an animal's lifetime and are repeatable only when considered as a characteristic of the cow. The principal use of the repeatability estimate of pre-weaning traits in cattle is as a predictor of the future production of the cow. It is also necessary to know the repeatability of such traits in order to measure the effectiveness of selection for cow production. However, since the repeatability also contains non-hereditary differences between cows, it tends to over-estimate what can be gained in future generations by selection.

Several authors have estimated the repeatability of pre-weaning traits in cattle (Alexander et al, 1960, Alim, 1964, Cunningham and Henderson, 1965, Minyard and Dinkel, 1965, Trail *et al*, 1971b, Boston *et al*, 1975). The repeatability of weaning weight as a trait of the dam has been estimated as being generally greater than that for birth weight. For instance, Trail *et al* (1971b) obtained a combined (dam-breeds) estimate of 0.21 for the repeatability of birth weight compared with 0.42 for the repeatability of 6 and 9 month weight. Several other reports which have indicated that the repeatability estimate of birth weight was much lower than that of weaning weight were also cited by these authors. The review by Anderson (1977) indicated a range of reported repeatability values of -0.03 to 0.29 for birth weight. Reported estimates of the repeatability of weaning weight have been of the order of 0.3 to 0.5, with many values averaging 0.4 (see also Table 2.13). The influence of the milk-producing ability of the dam is probably an important factor in the repeatability of pre-weaning gain and weaning weight.

Culling of females on the basis of early performance under the assumption that maternal performance is a highly repeatable characteristic has become a common practice in most commercial beef herds. A survey of weaning weight repeatability estimates by several authors indicates that genetic and permanent environmental effects are important contributors to variation in maternal ability although the relative magnitude of components has varied in different studies (Table 2.13). Minyard and Dinkel (1965) considered repeatability estimates reliable enough to allow selection early in a cow's life. They stated that very low producers can be culled on the basis of the first records with little risk of culling good cows, since cows at both extremes (i.e., very high and very low producers) contribute much more to the repeatability of weaning weight than those near the average. Other authors who obtained results which have indicated that culling of cows on the basis of the performance of their first calves would be effective for increasing the average productivity of beef cattle are Cunningham and Henderson (1965), Sellers <u>et al</u> (1970), Trail <u>et al</u> (1971b), Bailey and Koh (1974), Boston <u>et al</u> (1975), Vanmiddlesworth <u>et al</u> (1977).

The repeatability estimates of pre-weaning traits are influenced by various factors. Breed differences in weaning weight repeatability estimates have been reported by Sellers <u>et al</u> (1970), Boston <u>et al</u> (1975) and Vanmiddlesworth <u>et al</u> (1977). These authors have all obtained lower repeatability values for Angus compared with Hereford cows. For instance, Boston <u>et al</u> (1975) obtained a repeatability value of 0.29 for Angus cows compared with 0.59 for that of Hereford cows. They suggested that the weaning records of a Hereford cow's early calves are a more accurate indicator of her future productivity than those of an Angus cow. They also

TABLE 2.13 Some Repeatability Estimates of Weaning Weight

Breed	Age at Weaning (days)	Repeatability Estimate	Source
Angus	-	0.27	Boston *et al* (1975)
Hereford	-	0.50	Boston *et al* (1975)
Hereford and Angus	210	0.48	Cunningham and Henderson (1965)
Hereford	182	0.34	Koch and Clark (1955a)
Angus	190	0.52	Minyard and Dinkel (1965)
Hereford	190	0.42	Minyard and Dinkel (1965)
Angus	165	0.26 0.25	Hohenboken and Brinks (1969)
Angus	205	0.19	Sellers *et al* (1970)
Hereford	205	0.27	Sellers *et al* (1970)
Zebu	210	0.13	Torres (1962)
Ankole	270	0.40	Trail *et al* (1971b)
Boran	270	0.50	Trail *et al* (1971b)
Zebu	270	0.39	Trail *et al* (1971b)
Angoni	210	0.63	Thorpe *et al* (1980a)
Barotse	210	0.47	Thorpe *et al* (1980a)
Boran	210	0.46	Thorpe *et al* (1980a)
Angus	205	0.24	Vanmiddlesworth *et al* (1977)
Hereford	205	0.34	Vanmiddlesworth *et al* (1977)

outlined the possible causes of the differences in repeatability estimates between these two breeds.

Degree of adjacency of records may also influence intra-dam relationships. Cunningham and Henderson (1965) have documented the tendency for repeatability based on likeness of adjacent records to be higher than repeatability based on likeness of non-adjacent or random chosen records. These authors remarked that the predictive value of early records for production in later life was not as great as is often assumed. They suggested that little emphasis should be given to repeatability estimates made on records more than two years apart. Studies by Sellers et al (1970), Boston et al (1975) and Vanmiddlesworth et al (1977) have also confirmed that early records may be a poor basis for prediction of performance more than two years removed. The results obtained by Boston et al (1975) indicated that progeny weaning weights were good indicators of a cow's subsequent productivity through 5 years, and that they were of limited predictive value beyond that time.

Nutritional conditions might also influence the repeatability of calf weight since progeny that are raised in areas of restricted feed supplies are more dependent on their dams than are those which are produced in a more optimal environment. Bailey and Koh (1974) found that the repeatability of weaning weight tended to be lower under more favourable feeding conditions (0.33) than under poor conditions (0.44) although the difference was non-significant. Similar results were obtained by Rollins and Wagnon (1956) in range herds operated under optimum and sub-optimum nutritional regimes.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Materials

3.1.1 The breeding stations

The data was collected at Government-owned breeding stations situated in the three main ecological zones of Swaziland. The Mpisi breeding ranch (Station 1) is located in the Middleveld region near Manzini whilst Station 2 is in the Lowveld (Big Bend) and Station 3 is in the Highveld region (Mahlangatsha). These stations are reasonable representative of the ecological conditions of the country. Table 3.1 presents some physical features of the three zones in which the ranches are located.

TABLE 3.1 Some Physical Features of the Three Main Ecological Regions of Swaziland *

	Lowveld	Middleveld	Highveld
Altitude (m)	150 - 500	350 - 1100	1000-2000
Annual rainfall (mm)	500 - 900	750 - 1150	1000-2300
Mean temperature ^{o}C	22	19.5	18.5
Grazing	Sweetveld with deciduous bush and Acacia	Mainly tall grassland	Generally poor sourveld

* After Butterworth and Presswood (1978).

In view of the important correlation between rainfall, pasture growth, and livestock producitivity, the monthly and annual precipitation during the years 1975 to 1978 for each station is given in appendix I.

The Government breeding stations breed the bulls needed for the genetic improvement of the national herd. The aim is to supply bulls that are genetically superior for the important performance traits (mainly growth) of beef cattle to the Rural Development Areas (RDA's) of Swaziland. A selection programme is maintained for each of the currently recommended breed types so that above average bulls can be distributed. In addition, the potential of these breeds and crosses is evaluated by performance recording.

On the Government ranches, performance tests are automatically carried out on all stock of both sexes. Evaluations of young stock are made at weaning (7 months) and at 18 months of age, when decisions on future use are made.

Husbandry and management procedures employed on all Government ranches have been standardised so as to minimise environmental differences between stations and also between herds within stations. In all ranches, calves remain with their dams from birth to weaning at 210 ± 15 days. There is no milking of beef cows. All calves are weaned by separation from their dams at the monthly weighing during the month when the calf is 7 months of age. Male and female weaners are separated as soon as convenient after weaning. All young stock of similar age and sex are run together irrespective of herd/breed. Weaned calves receive no special feeding being dependent on unimproved veld pastures. Animals suffer a severe check in growth at all stations during the dry winter months, achieving their gains in weight during the spring and summer seasons. However, some limited supplementary feeding is occassionally used during severe years, particularly in the Highveld (Station 3) where grazing conditions are generally poor.

All males are left entirely until the completion of the growth rate performance test at 18 months of age. After ranking, and field inspection, the bulls not selected for breeding are castrated and sent to the feedlot for finishing.

Breeding cows of all breeds and ages are run in one group except during the 90 day service period. There is only one breeding season each year and more than 90% of the cows are mated through natural service. The breeding season for natural service in Stations 1 and 2 is between November and February whilst that for Station 3 is from October to January. Artificial breeding and maiden heifer mating are normally commenced three weeks earlier.

Pregnancy diagnosis is carried out on all cows when their calves are weaned and cows which fail to conceive in two consecutive breeding seasons are usually culled. Heifers join the breeding herds each year, home-bred heifers being selected on their 18 month growth rate ranking and field inspections.

The cows also graze veld pastures and receive no special feeding except for a phosphate supplement in the form of bone meal and salt provided *ad libitum*.

3.1.2 Source of data - The data processing unit system.

The data were obtained from the Data Processing Unit (DPU) of the Animal Production Division (APD) in the Ministry of Agriculture and Co-operatives - Mbabane. This unit is involved in processing data from the National Beef Cattle Breeding Programme. The DPU system comprises a set of procedures for assembling, validating, analysing, and storing data. The processed data are made available by specially designed reports appropriate for each of the various levels of management. A detailed outline of the DPU information system is given by Butterworth and Presswood (1978).

The DPU collects data from the participating ranches by using three types of record books; the birth, weight and treatment record books. Entries in each book are made in triplicate by the ranch personnel. The main copy is sent to the DIU, the second to an officer in charge of the ranches, and the last copy remains on the ranch for its own records.

The birth record book is completed immediately after each birth at the station, whether the calf is born alive or is a stillbirth. The calf birth record contains: name of station, herd, calf identification number, date of birth, sex, breed, dam number and breed, sire number and breed, calf birth weight and date weighed, dam parturition weight and date weight, and description of the calf. A newborn calf and its dam are normally weighed within 24 hours. Completed calf birth record sheets are sent to the DIU weekly.

The weight record book contains all weights collected on the station. All cattle at each station are weighed at a similar time and/or date each month. The cattle are usually kraaled the night before weighing. Animal identification numbers and their weights are recorded in weighing order and a test weight is used to eliminate bias in the scales. This test weight is weighed before the first animal and after every 20 animals. The label of this weight and its weight are included in the weight record sheets. The DPU uses the actual weight of each test weight to adjust the weight records automatically if necessary. The weight record sheets are sent to the DPU after each weighing.

The treatment record book is used to report all other types of relevant information such as abortions, deaths, diseases, and pregnancy diagnosis.

When the record sheets reach the DPU, they are checked for completeness before being copied onto computer coding sheets. The cross-checkings are supported by enquiry questionnaires to the field and ultimately by validation programmes on the computer. The data from all the stations is processed on an ICL 2903 computer and records are stored on magnetic tape files.

There are three types of record files created and/or updated by the DIU each year; a calf record file, a cow reproductive performance file and an otherstock file (for bulls and castrates). This study is concerned with the first two files - the calf record file which covers the history of each calf from birth to 18 months of age and includes the basic information of identification number, date of birth, and sire and dam information; and the cow reproductive performance file which covers the complete calving history of each cow including the weaning weights and ratings of all its calves.

3.1.3 The data.

(i) Data Extracted from the Calf Record Files

Records of pre- and post-weaning growth were selected from record files of the three stations. While a few records were available from calves born before 1975, it was decided to limit the study to calves born in the period 1975 to 1978 (4 calf-crops) in Stations 1 and 2, and 1976 to 1978 (3 calf-crops) in Station 3.

Only those calves with birth, weaning, and 18 month weight records were included. The weaning (210 days) and 18 month (540 days) weights in these records were already adjusted for age by linear interpolation between their two closest monthly weight records. The following information was also available on each calf: year of birth, date of birth, sex, breed, dam age, dam breed, sire identification number, and sire breed.

Data for 1,832 animals were obtained. The total number of records extracted from each station and the distribution of data among the calf breeds are shown in Table 3.2.

TABLE 3.2 Number of Calf Records obtained from the Stations

Breed/Cross	Station 1	Station 2	Station 3
Nguni	108	138	155
Brahman	121	-	-
$\frac{1}{2}$ Brahman-$\frac{1}{2}$ Nguni	-	423	46
$\frac{3}{4}$ Brahman-$\frac{1}{4}$ Nguni	114	308	-
$\frac{7}{8}$ Brahman-$\frac{1}{8}$ Nguni	101	47	-
Simmental	-	-	182
$\frac{1}{2}$ Simmental-$\frac{1}{2}$ Nguni	-	-	45
$\frac{3}{4}$ Simmental-$\frac{1}{4}$ Nguni	-	-	17
$\frac{7}{8}$ Simmental-$\frac{1}{8}$ Nguni	-	-	27
Total	444	916	472

(ii) Data Extracted from the Cow Record Files.

Cow records were extracted for only two stations, namely, stations 1 and 2. The study only considered the weaning weight records of calves born during the period 1975 to 1978. Only cows which had weaned at least one calf during the period covered were included. The following information was available for each cow: identification number, breed, age, identification numbers of its calves, year of birth of each calf, sex and sire breed of each calf.

Records of a total number of 463 cows were obtained. The number of cows included in each station and the distribution of weaning weight records among the cow breeds are shown in Table 3.3.

TABLE 3.3 The Distribution of Data obtained from the Cow Record Files

Breed/Cross	Station 1		Station 2	
	Cows	No. of Records	Cows	No. of Records
Nguni	50	113	153	554
Brahman	68	125	–	–
½ Brahman-½ Nguni	42	115	93	324
¾ Brahman-¼ Nguni	57	102	–	–
	217	455	246	878

3.2 Statistical Methods

3.2.1 Analysis of growth records

(i) Introduction

The growth traits chosen for the major part of this study were birth weight, weaning (210 days) weight and 18 month (540 days) weight. However, some 14 month (420 days) weights were available and were used to study the feasibility of lowering the performance testing age in the Swazi Government ranches from the current 540 days to 420 days.

Preliminary analyses were carried out to check the records for connectedness (see Searle, 1971). The "breeds" were not represented in all the stations and all analyses were thus carried out within stations. The analyses were performed in three stages. The first stage compared the growth (birth, weaning, and 18 month weights) performance of the various breed groups and estimated the phenotypic correlations among the traits in each station. The second stage considered the influence of sires and dam breeds on the birth, weaning, and 18 month weight and estimation of some genetic parameters of these growth traits. Estimation of the heritabilities of and genetic and phenotypic correlations between the 14 month and 18 month weights were carried out in the third stage of the analyses in an attempt to evaluate the association between these two post-weaning growth traits. Since the Nguni sires were too few in numbers (≤ 3) and were only mated to Nguni cows in all three stations, it was decided to exclude them from the two latter stages of the analysis.

(ii) The Mathematical Models and Solutions to the Least Squares Equations.

The same general model was used for the analysis of all the weights considered in each stage of the analysis.

The mathematical model fitted for the first stage of the analysis was:

$$Y_{ijklmn} = \mu + t_i + b_j + (tb)_{ij} + c_k + d_e + f_m + e_{ijklmn}, \cdots \qquad (3.1)$$

where;

Y_{ijklmn} = the weight recorded on the n^{th} individual within the m^{th} sex category, l^{th} dam age group and j^{th} breed group; born during the k^{th} month and i^{th} year;

μ = a general mean;

t_i = the effect of the i^{th} year;

b_j = the effect of the j^{th} breed group;

$(tb)_{ij}$ = the effect of the interaction between the i^{th} year and the j^{th} breed group;

c_k = the effect of the k^{th} month of birth;

d_l = the effect of the l^{th} dam age group;

f_m = the effect of the m^{th} sex category;

e_{ijklmn} = the effect of the random error peculiar to Y_{ijklmn}. Residual effects were assumed to have mean = 0 and a constant variance, σ_e^2.

The subscripts and description of the factors in this model are shown in Table 3.4.

All effects in the model were regarded as fixed (except for the error term).

TABLE 3.4 Factor and Subscript Descriptions

Factor and Subscript	Level	Description of Factor Level		
		Station 1	Station 2	Station 3
Year i	1	1975	1975	1976
	2	1976	1976	1977
	3	1977	1977	1978
	4	1978	1978	-
Breed j	1	Nguni	Nguni	Nguni
	2	Brahman	$\frac{1}{2}$ Brahman	Simmental
	3	$\frac{3}{4}$ Brahman	$\frac{3}{4}$ Brahman	$\frac{1}{2}$ Simmental
	4	$\frac{7}{8}$+ Brahman	$\frac{7}{8}$+Brahman	$\frac{3}{4}$ Simmental
	5	—	—	$\frac{7}{8}$+Simmental
	6	—	—	$\frac{1}{2}$ Brahman
Month of k birth	1	September	September	August
	2	October	October	September
	3	November	November	October
	4	December	December	November+
Dam age l	1	2-3 years	2 years	2-3 years
	2	4-6 years	3 years	4-6 years
	3	7+ years	4-6 years	7+ years
	4		7+ years	
Sex m	1	Female	Female	Female
	2	Male	Male	Male

The mathematical model applied for the second and third stages of the anlysis was:

$$Y_{ijklmnp} = \mu+t_i+s_j+b_k+(tb)_{ik}+(jb)_{jk}+c_l+d_m+f_n+e_{ijklmnp} \quad \ldots \quad (3.2)$$

where the terms are as described in the previous model except the following:

$Y_{ijklmnp}$ = the weight recorded on the p^{th} individual within the n^{th} sex category, born during the l^{th} month and i^{th} year by a dam in the m^{th} age group and k^{th} breed group, and was sired by the j^{th} sire;

s_j = the effect of the j^{th} sire,
$j = 1,2,\ldots, 6$ in Station 1
$j = 1,2,\ldots,10$ in Station 2;

b_k = the effect of the k^{th} breed of dam,
$k = 1,2,\ldots, 4$ in Station 1
$k = 1,2$ in Station 2;

$(tb)_{ik}$ = the effect of the interaction between the i^{th} year and the k^{th} breed of dam;

$(sb)_{jk}$ = the effect of the interaction between the j^{th} sire and the k^{th} breed of dam.

All effects were regarded as fixed (except error). However, the s_j term was later regarded as random for the purpose of computing the genetic estimates (see Section 3.2.1 (IV)). Data from Station 3 were excluded from this part of the analysis due to incomplete sets of data.

These models (3.1 and 3.2) may be written in matrix notation as follows:

$$\underset{\sim}{y} = \underset{\sim}{X}\underset{\sim}{b} + \underset{\sim}{e} \quad \ldots \qquad (3.3)$$

where:

$\underset{\sim}{y}$ = a known Nx1 vector of observations;

$\underset{\sim}{X}$ = an Nxp incidence matrix of known values (p is the number of factors in the model);

$\underset{\sim}{b}$ = a px1 vector of unknown fixed effects comprising the general mean, factor level and interaction effects;

$\underset{\sim}{e}$ = an Nx1 vector of random error effects, assumed to have $E(\underset{\sim}{e}) = \underset{\sim}{0}$ and $E(\underset{\sim}{e}\underset{\sim}{e}') = \sigma^2 \underset{\sim}{I}_N$ where $\underset{\sim}{I}$ is an NxN identity matrix.

The method of least squares was used to estimate the b's. The principles of least squares analysis and the detailed steps used in the estimation process have been discussed by Kempthorne (1952) and Harvey (1975). Derivation of the least squares estimator of b follows minimisation of the sums of squares of the observations from their expected values.

Assuming that

$$\underset{\sim}{y} = \underset{\sim}{X}\,\underset{\sim}{b} + \underset{\sim}{e}$$

and

$$E(\underset{\sim}{e}) = \underset{\sim}{0},$$

then

$$E\,(\underset{\sim}{y}) \quad = \quad \underset{\sim}{X}\,\underset{\sim}{b}$$

and

$$\begin{aligned}\underset{\sim}{e}'\underset{\sim}{e} &= (\underset{\sim}{y} - E(\underset{\sim}{y}))'\,(\underset{\sim}{y} - E(\underset{\sim}{y}))\\ &= (\underset{\sim}{y} - \underset{\sim}{X}\underset{\sim}{b})'\,(\underset{\sim}{y} - X\underset{\sim}{b})\\ &= \underset{\sim}{y}'\underset{\sim}{y} - 2\underset{\sim}{b}'\underset{\sim}{X}'\underset{\sim}{y}+\underset{\sim}{b}'\underset{\sim}{X}'\underset{\sim}{X}\underset{\sim}{b}.\end{aligned}$$

Choosing as the estimator, $\hat{\underset{\sim}{b}}$ that value of $\underset{\sim}{b}$ which minimises $\underset{\sim}{e}'\underset{\sim}{e}$ involves differentiating $\underset{\sim}{e}'\underset{\sim}{e}$ with respect to elements of $\underset{\sim}{b}$ (Searle, 1966 and 1971). Equating the differential to zero and expressing the resulting equations in terms of $\hat{\underset{\sim}{b}}$, the normal equations are obtained:

$$\underset{\sim}{X}'\underset{\sim}{X}\hat{\underset{\sim}{b}} \quad = \quad \underset{\sim}{X}'\underset{\sim}{y}.$$

Provided $(\underset{\sim}{X}'\underset{\sim}{X})$ is of full rank, they have the unique solution for b of

$$\hat{\underset{\sim}{b}} \quad = \quad (\underset{\sim}{X}'\underset{\sim}{X})^{-1}\underset{\sim}{X}'\underset{\sim}{y}$$

If $(\underset{\sim}{X}'\underset{\sim}{X})$ is not of full rank, it has no inverse and no unique solution. However, if $(\underset{\sim}{X}'\underset{\sim}{X})^{-1}$ does not exist, a solution can be obtained by using a generalised inverse of $(\underset{\sim}{X}'\underset{\sim}{X})$ (Searle, 1971). An alternative method of obtaining a solution is by imposing restrictions on the equations. The various types of restrictions which may be imposed on the estimates of parameters to obtain a solution have been discussed by Harvey (1975).

In this present study, the equations were not of full rank. In order to obtain a solution, the restriction that for each factor in a model the sum of the constant estimates equals zero was applied. Inversion of the reduced matrix gave a generalised inverse from which sums of squares for each factor (and interaction) were computed. A generalised linear models programme - REG, was available for inverting the matrices and calculating the reduction in sums of squares due to fitting the factors in the model. The analysis of variance and the analyses for estimating the genetic parameters were all carried out by use of this programme.

The procedures used for constructing analysis of variance tables for unbalanced data using the reduction in sums of squares principle have been outlined by Searle (1971). It may be noted that the reduction in sums of squares accompanying the fitting of a factor in the model is dependent upon the order of fitting. This fact must be taken into account in the analyses of variance involving non-orthogonal data. In the present study, tests of significance were based on mean squares where the term being tested was fitted after all other terms included in the model.

Least squares means were computed for all the factors (and interactions) which were found significant ($P < 0.05$) in the first stage of the analysis (see model 3.1). Duncan's multiple range test was used to make pairwise comparisons among the least squares means (Duncan, 1955).

In all stages of the analysis, factors (and interactions) which were found to be non-significant were subsequently deleted from the model before any further analyses were carried out.

(iii) Estimation of Phenotypic Correlations.

Estimates of phenotypic correlations between the weights taken at the various ages were obtained within stations. The correlation coefficients were estimated by utilising the variance-covariance matrix derived from the residual (error) sums of squares and sums-of-cross products from the aforementioned analyses using the definition formula between random variables:

$$y1.y2 = \frac{Cov.y1.y2}{\sqrt{var.y1.var.y2}}$$

where,

y1 and y2 are the random variables (weights)

and

y1.y2 is the correlation coefficient between y1 and y2.

The correlation coefficients estimated from the three stations were later averaged by the Z-transformation method. The standard errors of the pooled correlation coefficients were also estimated (see Snedecor and Cochran, 1980).

(iv) Estimation of Genetic Correlations and Heritabilities.

The paternal half-sib correlation technique was adopted to estimate the genetic parameters (Falconer, 1960). Estimates of heritabilities (h^2) and genetic correlations (γ_g) were obtained for birth weight, weaning weight, 14 month weight and 18 month weight within each station. These estimates were later pooled over stations.

The heritabilities were estimated as:

$$h^2{}_1 = \frac{4\ \sigma^2_{s1}}{\sigma^2_{s1} + \sigma^2_{e1}}$$

and the genetic correlations as:

$$\gamma_{g_{12}} = \frac{\sigma_{s1s2}}{\sqrt{\sigma^2_{s_1} \cdot \sigma^2_{s_2}}}$$

where,

$h^2{}_1$ = the heritability estimate for trait 1,

$\gamma_{g_{12}}$ = the genetic correlation between trait 1 and trait 2,

$\sigma^2_{s_1}$ = the sire variance component for trait 1,

$\sigma^2_{s_2}$ = the sire variance component for trait 2,

σ^2_{e1} = the error (residual) variance component for trait 1,

and

$\sigma_{s_1 s_2}$ = the sire covariance component between trait 1 and trait 2.

The general theory involved in the use of least squares procedures with unequal subclass frequencies for the estimation of variance and covariance components with mixed models has been discussed by Henderson (1953). The variance and covariance components in the present work were obtained by following Henderson's method 3. This method is based on the method of fitting constants. It uses reductions in sums of squares due to fitting different subgroups of factors in the model. The estimation of variance components is done by equating each computed reduction to its expected value.

Since the inclusion of factors in the model used for studying genetic variation and covariation depend upon whether or not the terms included in the model are statistically significant; factors (and interactions) which were found non-significant in the previously mentioned analysis of variance were deleted from the model before the analyses for estimating the genetic parameters were carried out. After the exclusion of the non-significant year x dam breed and sire x dam breed interactions, the following general model for estimating the genetic parameters was applied:

$$y_{ijklmnp} = \mu + t_i + s_j + b_k + c_e + d_m + f_n + e_{ijklmnp} \quad .... \; (3.4)$$

where,

$y_{ijklmnp}$ = the weight recorded on the pth individual within the nth sex category, born during the 1th month and ith year by a dam in the mth age group and kth breed group, and was sired by the jth sire;

μ = a general mean,

t_i = the fixed effect of the ith year;

s_j = the random effect of the jth sire. Sire effects are assumed to have mean = 0 and variance = σ_S^2 ;

b_k = the fixed effect of the kth breed of dam;

c_l = the fixed effect of the 1th month of birth;

d_m = the fixed effect of the mth age of dam group;

f_n = the fixed effect of the nth sex;

$e_{ijklmnp}$ = the random residual effect peculiar to $y_{ijklmnp}$. Residual effects are assumed to have mean = 0 and variance = σ_e^2.

All the subscripts are as previously described.

This linear model (3.4) can be represented in matrix notation as:

$$\underset{\sim}{y} = \underset{\sim}{X}\underset{\sim}{b} + \underset{\sim}{Z}\underset{\sim}{a} + \underset{\sim}{e} \quad \ldots \qquad (3.5)$$

where,

$\underset{\sim}{y}$ = a known vector of observations;

$\underset{\sim}{X}$ and $\underset{\sim}{Z}$ = known incidence matrices;

$\underset{\sim}{b}$ = an unknown vector of fixed effects;

$\underset{\sim}{a}$ = an unknown vector of random effects, with mean zero and variance $\sigma_a^2 \underset{\sim}{I}$;

$\underset{\sim}{e}$ = an unknown vector of random residual effects, with mean zero and variance $\sigma_e^2 \underset{\sim}{I}$.

Cov (a , e) is assumed to be zero.

A set of normal equations which, when solved, produce least-squares solutions of the unknown vectors ($\underset{\sim}{b}$ and $\underset{\sim}{a}$) are:

$$\begin{bmatrix} \underset{\sim}{X}'\underset{\sim}{X} & \underset{\sim}{X}'\underset{\sim}{Z} \\ \underset{\sim}{Z}'\underset{\sim}{X} & \underset{\sim}{Z}'\underset{\sim}{Z} \end{bmatrix} \begin{bmatrix} \underset{\sim}{b} \\ \underset{\sim}{a} \end{bmatrix} = \begin{bmatrix} \underset{\sim}{X}'\underset{\sim}{y} \\ \underset{\sim}{Z}'\underset{\sim}{y} \end{bmatrix}.$$

The RMG programme was used for the computation of the variance and covariance components according to Henderson's Method 3. In the analysis, the factor for sires was fitted last in the model to enable the calculation of the reduction in sums-of-squares and sums-of-cross products due to this random (sire) effect, after adjusting for the fixed effects.

The error variance and covariance components were estimated by equating the error mean squares (MS_e) and error mean-cross-products (MCP_e) to their expectation:

$$E(MS_e) = \frac{\text{Error sums of squares}}{\text{Error degrees of freedom}}$$

$$= \sigma^2_e.$$

The sire variance and covariance components were estimated by equating the sire mean squares (MSs) and sire mean-cross-products (MCPs) to their expectation:

$$E(MSs) = k\ \sigma^2_s + \sigma^2_e$$

$$\sigma^2_s = \frac{MSs - MSe}{k}$$

where the k coefficient was computed using the equation:

$$k = \left\{ \text{trace } (\underset{\sim}{Z}'\underset{\sim}{Z}) - \text{trace } \left[(\underset{\sim}{X}'\underset{\sim}{X})^{-}\underset{\sim}{X}\underset{\sim}{Z}\underset{\sim}{Z}'\underset{\sim}{X}\right] \right\} \Big/ s-1;$$

where

$(\underset{\sim}{X}'\underset{\sim}{X})^{-}$ is a generalised inverse of $(\underset{\sim}{X}'\underset{\sim}{X})$

and

s is the total number of sires.

This procedure is the "indirect method" of computing k coefficients as described by Harvey (1975).

Estimates of the standard errors for the heritability estimates were ascertained by the method discussed by Swiger et al (1964). The following formula was used:

$$V(h^2) = \frac{32\ (N-1)\ (1-t)^2\ (1+\ (k-1)\ t\ )^2}{k^2\ (N-s)\ (s-1)}$$

where,

$V(h^2)$ = the variance of the heritability estimate,

s = the number of sires,

N = the total number of observations,

t = $\sigma_s^2 / (\sigma_s^2 + \sigma_e^2)$,

k = $\dfrac{N - \frac{\Sigma n_i^2}{N}}{s-1}$,

n_i = the number of observations in the i^{th} sire group.

The standard errors were then estimated as the square root of the variance of the heritability estimates. The limitation with this approach, however, is that a simple one-way random model is assumed.

The heritability estimates were pooled over stations by weighing the within station estimate by the inverse of its variance (w) thus:

$$\bar{h}^2 = \frac{\Sigma w_i h_i^2}{\Sigma w_i} \quad \ldots \quad (3.6)$$

where,

$\bar{h}^2$ = the pooled heritability estimate,

h^2_i = the heritability estimate for the i^{th} station, $i = 1,2$;

w_i = the weighing factor for the i^{th} station,

= $1/\mathrm{var}(h^2{}_i)$.

The standard error of the pooled estimate was calculated as:

$$\bar{h}^2_{S.E.} = \sqrt{\frac{\Sigma w_i^2 \; \mathrm{var}(h^2{}_i)}{(\Sigma w_i)^2}} \quad \ldots \quad (3.7)$$

where,

w_i^2 = $\left[\, ^1/\ \mathrm{var}\ (h^2{}_i) \,\right]^2$. Equation (3.7) was derived by equating the variance of the pooled heritability estimate (var ($\bar{h}^2$) (see equation 3.6)) to its expected value (Rae, Pers. Comm., 1981). It was assumed that cov $(h^2{}_1, h^2{}_2) = 0$.

The standard error of the genetic correlations was estimated by using the method of Tallis (1959):

$$\begin{aligned}
V(r_g) = & \Big[(1 + r_g^2)(1 + r_b^2)(1 + (k-1)t_1)(1+(k-1)t_2) \\
- & 2r_g r_b (t_1 t_2 (1+(k-1)t_1)(1+(k-1)t_2))^{\frac{1}{2}} \\
& ((1+(k-1)t_1/t_1) + (1+(k-1)t_2/t_2)) \\
+ & (r_g^2 (t_1 - t_2)^2 / 2t_1 t_2)\Big] \Big/ d_s k^2 t_1 t_2 \\
+ & \Big[(1+r_g^2)(1+r_w^2)(1-t_1)(1-t_2) \\
- & 2r_g r_w (t_1 t_2 (1-t_1)(1-t_2))^{\frac{1}{2}} \\
& (((1-t_1)/t_1) + ((1-t_2)/t_2)) \\
+ & (r_g^2 (t_1 - t_2)^2 / 2t_1 t_2)\Big] \Big/ d_i k^2 t_1 t_2,
\end{aligned}$$

where,

$V(r_g)$ = the variance of the estimate of the genetic correlation,

d_s = the sire degrees of freedom,

d_i = the error degrees of freedom,

k = $\dfrac{N - \dfrac{\Sigma n_i^2}{N}}{s-1}$,

t_1 = $\sigma^2_{s1}/(\sigma^2_{s1} + \sigma^2_{e1})$,

t_2 = $\sigma^2_{s2}/(\sigma^2_{s2} + \sigma^2_{e2})$,

r_b = $V_{12}/\sqrt{V_{11}+V_{22}}$,

r_w = $v_{12}/\sqrt{v_{11}+v_{22}}$,

V_{12} = the between sire covariance for traits 1 and 2,

V_{11} = the between sire mean square for trait 2,

v_{12} = the error covariance between traits 1 and 2,

v_{11} = the error mean square for trait 1,

v_{22} = the error mean square for trait 2.

The standard error was then estimated as the square root of $V(r_g)$.

Pooling of the estimates of the genetic correlations and calculation of the standard errors of the pooled estimates were carried out as for heritabilities.

3.2.2 Analysis of the cow records

The cow record analysis was restricted to evaluating the maternal performance of the cow breeds based on the weaning weight records of their calves. The repeatability of weaning weight was also estimated.

(i) The Mathematical Model and Analysis Procedures

Within each station the following fixed effects model was applied:

$$y_{ijklm} = \mu+t_i+a_j+b_k+(ta)_{ij}+(tb)_{ik}+(ab)_{jk}+(tab)_{ijk}+s_l+e_{ijklm} \quad \ldots \quad (3.8)$$

where,

y_{ijklm} = the weaning weight of the m^{th} calf in the l^{th} sex category, born by a dam within the k^{th} breed group and j^{th} age group during the i^{th} year;

μ = a general mean;

t_i = the effect of the ith year;

a_j = the effect of the j^{th} age of dam group;

b_k = the effect of the k^{th} breed of cow;

$(ta)_{ij}$ = the effect of the interaction between the i^{th} year and j^{th} age of dam group;

$(tb)_{ik}$ = the effect of the interaction between the i^{th} year and the k^{th} breed of cow;

$(ab)_{jk}$ = the effect of the interaction between the j^{th} age of dam group and the k^{th} breed of cow;

$(tab)_{ijk}$ = the effect of the three-way interaction of the i^{th} year, j^{th} age of dam group and k^{th} breed of cow;

s_l = the effect of the l^{th} sex;

e_{ijklm} = the random residual effect associated with y_{ijklm}. Residual effects are assumed to have mean = 0 and variance = σ_e^2.

The subscripts are as previously described.

The analysis of variance procedures used were as already described in the previous sections. All factors and interactions which were found non-significant were subsequently deleted from the model. Least squares means were computed for all significant factors and interactions. Duncan's multiple range test was used to make pairwise comparisons among the least squares means.

(ii) Estimation of Repeatability

Estimates of the repeatability (t) of weaning weight were computed within station and breed. Two techniques of estimating repeatability were adopted:

(a) The Variance Component Technique

In station 1, the repeatability of weaning weight was estimated by the variance component method (Falconer, 1960, Becker, 1967). In terms of the variance components, repeatability is the intraclass correlation among records of the same cow. The intraclass correlation repeatabilities were calculated from the variance components as the ratio:

$$t = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_e^2}$$

where,

t = the repeatability estimate,

σ_c^2 = the estimated variance components among average calf weaning weight records of different cows (between cows variance component);

σ_e^2 = the estimated variance components among calf weaning weight records within the same cow (within cow or error variance component).

Records of all cows including those with only a single weaning record were all included in the intraclass correlations.

Within each breed of cow, the following mathematical model was applied:

$$y_{ijklm} = \mu + t_i + a_j + s_k + d_l + e_{ijklm} \quad \ldots \quad (3.9)$$

where,

y_{ijklm} = the weaning weight record of the mth individual in the kth sex category born by the lth cow within the jth age group during the ith year;

u = a general mean;

t_i = the fixed effect of the i^th^ year;

a_j = the fixed effect of the j^{th} age of cow group;

s_k = the fixed effect on the k^{th} sex;

d_l = the random effect of the l^{th} cow. Cow effects are assumed to have mean = 0 and variance = σ_c^2.

e_{ijklm} = the random residual effect peculiar to Y_{ijklm}, assumed to have mean = 0 and variance = σ_e^2.

For details of the l^{th} subscript see Table 3.3 (section 3.1.3), all the other subscripts are as previously described.

The analysis of variance procedures involving a random (cow) variable were carried out in two steps. An initial analysis was performed using a model including years, sex, and age. The model for a second analysis included years, sex, age, and cows absorbed into the remaining equations. The cow sums of squares were then computed as the difference in error sums of squares of the two analyses.

The between cow component of variance (σ_c^2) was deduced by equating the mean square for cows to its theoretical expectation:

$$E\,(MS_{cows}) = \sigma_e^2 + k\,\sigma_c^2$$

$$\therefore\ \sigma_c^2 = \frac{\text{Mean square between cows-Error mean square}}{k}$$

where,

k = the coefficient of expected mean squares

$$= \left\{ \text{trace } (\underset{\sim}{Z}'\underset{\sim}{Z}) - \text{trace} \left[(\underset{\sim}{X}'\underset{\sim}{X})^{-}\underset{\sim}{X}\underset{\sim}{Z}\underset{\sim}{Z}'\underset{\sim}{X} \right] \right\} / d-1$$

and

$d-1$ = cow degrees of freedom.

The standard errors of the repeatability estimates were calculated using the method of Swiger <u>et al</u> (1964):

$$S.E._{(t)} = \sqrt{\frac{2(N-1)(1-t)^2 \quad 1+(k-1)t \quad ^2}{k^2(N-d)(d-1)}} ,$$

where,

$S.E._{(t)}$ = the standard error of repeatability estimate,

N = total number of observations,

d = the number of cows.

(b) The Regression Method

In station 2, the repeatability estimates for weaning weight were computed by the regression method as described by Cunningham and Henderson (1965). Only cows with at least two weaning weight records were included in the analysis. Within each breed of cow, the regression repeatabilities were obtained using pairs of maternal half-sib weaning records made by cows aged 10+ years and less.

The 210 days weaning weights were first corrected for sex, year, and age of dam using least squares constants from previous analysis (see Section 3.2.2(i)). Since some of the Nguni cows were mated to different sire breeds, the records from these cows were also adjusted for breed of sire. The repeatability was computed from the corrected records as:

$$t = \frac{Cov(y_2 y_1)}{Var\ (y_1)} ,$$

where,

y_1 is the earlier record of a pair and

y_2 is the later record of the same pair.

Separate estimates were computed for all possible pair combinations within a cow of each later, on each earlier calf record classified by age of dam in years, that is, for all pairs of weaning records made by the same cow at ages 2 and 3, 2 and 4, ..., 9 and 10+ years. Whereas the intraclass correlation repeatabilities considered all weaning records of a cow at once, each regression coefficient examined only the relationship between a specific pair of weaning records of the same cow.

All repeatability estimates were later pooled within and across breeds by weighing the estimates by the inverse of their variance as previously described for heritability estimates. The standard errors of the pooled estimates were also calculated in the same manner.

CHAPTER FOUR

RESULTS AND DISCUSSION

4.1 Environmental Influences on Birth Weight, Weaning Weight and 18 Month Weight.

The results of the analysis of variance for birth weight, weaning weight and 18 month weight are summarised in Table 4.1. Table 4.2 presents the effects of the various non-genetic factors on each trait for each station. These effects are discussed separately for each trait.

4.1.1 Birth weight

In station 2 and 3, year of birth had a highly significant ($P<0.001$) effect on birth weight, and was non-significant in station 1 (Table 4.1 a,b,c). The effects of years (Table 4.2 b,c) indicate significant differences ($P<0.01$) between all the years, with differences of about 6kg and 9kg between the best and worst years in station 2 and 3, respectively.

Month of birth effects on birth weight were highly significant at all stations (Table 4.1). In station 1, the effects (Table 4.2a) indicated a gradual increase in birth weight from September to December of about 1kg per month. The differences in birth weight between the months at this station were all highly significant ($P<0.01$). In station 2, there were no significant differences between the birth weight of calves born in September and

TABLE 4.1 Analysis of variance for Birth Weight, Weaning weight and 18 month Weight.

(a) Station 1

Source of variation	Degrees of freedom	Mean Squares		
		Birth Weight	Weaning Weight	18 Month Weight
Year	3	6.32 NS	6467.3***	21311.0***
Breed	3	241.9***	14501.7***	36587.3***
Month of birth	3	75.2**	4354.6***	5021.5**
Age of dam	1	171.1***	3678.9**	507.8NS
Sex	1	604.9***	35231.5***	21583.4***
Breed x year	9	11.0 NS	435.0 NS	1625.7NS
Residual	423	15.7	530.4	990.1

Table 4.1 continued

(b) Station 2

Source of variation	Degrees of freedom	Mean Square		
		Birth weight	Weaning weight	18 month weight
Year	3	272.2***	3202.5**	54097.0***
Breed	3	181.7*	7784.5***	16256.4***
Month of birth	3	699.5***	29487.4***	38635.3***
Age of dam	2	274.0**	14524.4***	59628.3***
Sex	1	1206.7***	52179.1***	182357.3***
Breed x year	9	80.9**	2474.8**	4383.6***
Residual	894	31.5	657.4	946.4

Table 4.1 continued

(c) Station 3

Source of variation	Degrees of freedom	Mean Square		
		Birth weight	Weaning weight	18 month weight
Year	2	2744.2***	17532.6***	11605.5***
Breed	5	1267.0***	16112.2***	23821.9***
Month of birth	3	816.5***	9065.2***	6564.2***
Age of dam	1	762.0***	11263.3***	7119.9**
Sex	1	402.6***	7480.6**	2141.2 NS
Breed x year	8	78.2*	1311.2[a]	1730.4*
Residual	451	34.9	779.1	837.4

[a] $0.05 > P > 0.10$

* = $P < 0.05$

** = $P < 0.01$

*** = $P < 0.001$

NS = non-significant.

October (Table 4.2 b), and November born calves were the highest. Calves born in December were the heaviest, being about 4kg heavier ($P < 0.01$) than November calves. Effects for month of birth in station 3 (Table 4.2 c) show a similar trend to that of station 2 in that calves born during the third month of the calving season (October) were the lightest; the heaviest calves were those born in November. However, there were no significant differences between late-born (November) and early-born (August) calves at this station.

Age of dam effects on calf birth weight were highly significant at all stations. Calves from 2- and 3- year-old heifers were significantly lighter (1 to 4kg) than calves from older dams in stations 1 and 3. In station 2, where it was possible to classify calves from 2- year-old and those from 3- year-old heifers into different groups (Table 4.2 b), it was found that calves from 2- year-old heifers were significantly lighter (27.8 kg) than those from 3- year-olds (29.1kg). Three- year-olds produced significantly lighter calves than older cows (30.8 kg). In all the stations, calves from 4-, 5- and 6- year-old dams were not significantly different in birth weight to calves from older dams.

The sex of the calf had a highly significant influence on birth weight (Table 4.1). The effects for sex (Table 4.2) indicate that males were about 2 kg (6 to 9%) heavier than females at birth in all stations.

TABLE 4.2 Effects of Non-genetic Factors on Birth weight, Weaning weight and 18 month weight. (deviation from Station Means)

(a) Station 1

	Birth weight (kg)	Weaning weight (kg)	18 Month weight (kg)
General mean	27.5±1.5*	165.1±1.5	253.7±1.5
Factors			
Year			
1975	0.32	6.07^{c}	4.49^{c}
1976	-0.33	-9.82^{a}	-21.24^{a}
1977	0.04	9.53^{d}	-1.96^{b}
1978	-0.03	-5.79^{b}	18.69^{d}
Month of birth			
September	-1.36^{a}	7.57^{c}	1.03^{b}
October	-0.32^{b}	5.59^{c}	8.62^{c}
November	0.32^{c}	-2.72^{b}	2.59^{b}
December	1.36^{d}	-10.46^{a}	-12.24^{a}
Dam age			
2- and 3- year olds	-0.62^{a}	-3.61^{a}	-1.46
4 to 6 years and 7+ years	0.62^{b}	3.61^{b}	1.46
Sex			
Female	-1.22^{a}	-9.17^{a}	-7.33^{a}
Male	1.22^{b}	9.17^{b}	7.33^{b}

Table 4.2 continued

(b) Station 2

	Birth weight (kg)	Weaning weight (kg)	18 Month weight (kg)
General mean	29.3±1.7*	170.3±1.7	261.3±1.7
Factors			
Year			
1975	3.47^{c}	-1.23^{b}	17.25^{c}
1976	-0.73^{b}	3.73^{c}	19.11^{c}
1977	-2.10^{a}	3.65^{c}	-5.49^{b}
1978	-0.64^{b}	-6.17^{a}	-30.88^{a}
Month of birth			
September	-0.27^{b}	4.19^{c}	-3.99^{b}
October	-0.32^{b}	10.90^{d}	13.21^{d}
November	-1.74^{a}	1.28^{b}	7.35^{c}
December	2.34^{c}	-16.37^{a}	-16.57^{a}
Age of dam			
2- year-olds	-1.32^{a}	-8.54^{a}	-6.18^{a}
3- year-olds	-0.16^{b}	-3.88^{b}	-2.24^{b}
4 to 6- and 7+ years	1.48^{c}	12.42^{c}	8.42^{c}
Sex			
Female	-1.16^{a}	-7.62^{a}	-14.24^{a}
Male	1.16^{b}	7.62^{b}	14.24^{b}

Table 4.2 continued

(c) Station 3

	Birth weight (kg)	Weaning weight (kg)	18 Month weight (kg)
General mean	32.0±1.7*	161.5±1.7	215.6±1.7
Factors			
Year			
1976	1.36^b	14.62^c	13.56^c
1977	-5.38^a	-11.98^a	-4.42^b
1978	4.02^c	-2.63^b	-9.14^a
Month of birth			
August	2.71^c	6.78^c	0.00^b
September	-1.74^b	6.19^c	4.78^c
October	-3.10^a	1.95^b	6.75^c
November +	2.13^c	-14.92^a	-11.53^a
Age of dam			
2- and 3- year-olds	-1.76^a	-6.75^a	-5.38^a
4 to 6 and 7+ year olds	1.76^b	6.75^b	5.38^b
Sex			
Female	-0.94^a	-4.06^a	2.17
Male	0.94^b	4.06^b	-2.17

* standard error

a,b,c,d Effects within the same column with different superscripts differ significantly ($P < 0.01$).

4.1.2 Weaning weight

In all stations, year, and month of birth had a highly significant effect on the weaning weight of calves (Table 4.1). In stations 1,2 and 3 respectively, differences between the best and worst years were about 19kg, 10kg and 27kg (Table 4.2). The effects for month of birth indicate that calves born early in the calving season were significantly ($P<0.01$) heavier at weaning than those born later. In station 1, calves born in September and October were significantly heavier in weaning weight than those born in November (162.4kg) which were in turn significantly heavier than December calves (154.7kg). There were, however, no significant differences between the September (172.7kg) and October (170.2kg) calves. On the other hand, October (181.2kg) born calves were significantly heavier than September (174.5kg) born calves at weaning in station 2. Late-born calves (November and December) were 10 to 27kg lighter than earlier-born calves at this station (Table 4.2b). Early-born calves in station 3 (August and September) were up to 22kg heavier ($P<0.01$) than late calves at weaning (Table 4.2c).

The influence of age of dam was more marked at weaning than at birth (Table 4.2). In general, 2- and 3- year-old dams weaned the lightest ($P<0.01$) calves and there were no significant differences between mature (4, 5 and 6 years), and old (≥ 7 years) dams. The difference between the weaning weights of calves from 2- and 3- year-olds and those from older dams in station 1 and 3 were about 7 kg and 11 kg, respectively. In station 2, calves from 2- year-old dams were about 13 kg lighter ($P<0.01$) than those from 3- year-old dams which were in turn 8 kg lighter ($P<0.01$) than calves from older dams (≥ 4 years). The difference in weaning weight between the 2- year age group and the 4-, 5- and 6- year group was about 21 kg.

Sex had a highly significant influence on weaning weight, male calves being 18 kg, 15 kg and 8 kg heavier ($P<0.01$) than females in station 1, 2 and 3, respectively.

4.1.3 18- month weight

Year and month of birth differences in 18-month weight were significant at all stations ($P<0.01$) and were larger than those of the pre-weaning traits. Differences in 18-month weight between the best and worst years in station 1, 2 and 3, respectively were about 40 kg, 50 kg and 23 kg. (Table 4.2). The effects for month of birth (Table 4.2) show that October-born calves performed significantly better than the calves born during the other months in all stations. Late-born calves were at the greatest disadvantage, being about 21 kg, 30 kg and 18 kg lighter than calves born during the best month (October) in stations 1, 2 and 3, respectively.

Age of dam had no significant effect on 18- month weight in station 1, but had a highly significant effect on this trait in station 2 and 3 (Table 4.1). At the latter stations, trends with respect to age of dam were similar to weaning (Table 4.2 b,c). In station 2, calves from 2- year-old dams were 10kg and 15kg lighter than calves from 3- year and those from older dams, respectively; calves from 3- year-olds were in turn 4kg lighter ($P<0.01$) than calves born to older dams (4,5 and 6 years and 7+ years). In station 3, the difference in 18-month weight between progeny of 2- and 3- year-old dams and those of older (≥ 4 years) dams was similar to that for weaning weight (11 kg).

Sex had a highly significant effect on 18- month weight in stations 1 and 2 (Table 4.1), with differences of 15 kg and 18 kg, respectively, in favour of males. In station 3, sex had a non-significant effect on weight at 18- months of age, and the females (217.8 kg) were even slightly heavier than the males (213.4 kg).

4.1.4 Discussion

The results of this study have indicated that year of birth effects were highly significant for birth weight, weaning weight and 18-month weight in all the stations (with the exception of birth weight in station 1), suggesting the importance of taking year of birth into consideration in analyses of weight records collected over several years. The variation between years in weight at birth, weaning and 18- months of age at these stations can be largely attributed to the range in quality and quantity of available pastures during the different years, since the cattle were raised entirely on natural pasture. The differences of 6 to 9 kg for birth weight, 10 to 27 kg for weaning weight, and 23 to 50 kg for 18- month weight between the best and worst years obtained here agree closely with those reported in the literature. Kennedy and Chirchir (1971), working with Zebu x British crossbred cattle reported a significant effect of year of birth on growth, with differences of up to 5 kg, 34 kg and 53 kg for birth weight, weaning weight and 18- month weight, respectively between the best and worst years. In Western Uganda, Sacker et al (1971a) reported highly significant year of birth effects on body weight of crossbred cattle from birth to 24 months of age. Results by Harricharan et al (1976), Joubert et al (1977) and Straw and Jones (1977) all confirm the significance of year of birth on growth traits.

The wide variation in birth weight due to month of birth is, presumably, a reflection of different pasture conditions during the last third of the gestation period when the foetus makes its greatest increase in weight. The results have indicated that late-born calves are generally heavier at birth than are calves born early in the calving season. This may be a function of better nutritional conditions during the last trimester of pregnancy for the late-calvers, as pre-calving nutrition has a significant effect on birth weight of calves (Tudor, 1972). Vorster (1954), Bosman and Harwin (1966) and Richardson et al (1979) reported that calf birth weight increased as the calving season advanced. A similar trend was obtained for the birth weight of calves in station 1. Winks _et al_ (1978) also showed that birth weight favoured late-born calves.

Month of birth effects on weaning weight support the widely held belief that early calves are heavier at weaning than late-born calves. Bosman and Harwin (1966), Winks _et al_ (1978) and Richardson _et al_ (1979) all found that early-born calves grew faster and were significantly heavier than late-born calves at weaning. Seifert _et al_ (1974) and Seifert (1975a) also recorded similar findings and suggested that older and, therefore, heavier calves could use the flush of milk which coincides with the break in the season and rapid pasture growth. In the present study, early-born calves were 18 to 27 kg heavier than late-born calves at weaning. Such variations in weaning weight due to month of birth may also be attributed to the fact that calves born early in the season have the full advantage of the growing season and would naturally tend to grow more rapidly than calves born later. The results of Mentz _et al_ (1979a) are similar to those obtained here in that early-born calves were significantly heavier than those born in mid-season, which were in turn significantly heavier than those born later in the calving season.

According to the results, weight at 18- months of age favoured calves born in October at all stations; calves born very late in the calving season (December (station 1 and 2), November (station 3)), being at the greatest disadvantage. The fact that at each station, calves born during the last month of the season were strikingly lighter (18 to 30kg) at 18- months than earlier calves has important practical implications in so far as the current 4- months breeding season is concerned. These findings tend to suggest regulation of the breeding season to prevent cows from calving down after November, in order to avoid the unfavourable consequences of seasonal variation on the calves born after that time. In Zimbabwe, a study by Vorster (1954) involving a 4- months breeding season indicated that late-born calves (March) were still significantly lighter than calves born early in the season (December to February) even at 3.5 and 4.5 years of age. The significant effect of month of birth on 18- month weight, however, generally highlights the importance of month of birth in making breed and crossbred comparisons as already pointed out by several authors (Sacker et al,1971a; Straw and Jones, 1977 and Thorpe et al, 1980b).

The highly significant influence of age of dam on birth and weaning weights, emphasise the importance of taking dam age into consideration in evaluating pre-weaning growth records. Jones and Hopkins (1980) found that when weaning weight records were not corrected for age of dam effects, the chance that progeny of 2- year-old dams were selected for this trait was only about one-fifth that of progeny of 5- year-old dams (0.015 and 0.080, respectively). The results from the present exercise indicated that calves born to heifers (2- and 3- year-olds) were up to 10 percent lighter at birth than those born to older cows. This is in agreement with most reports in the literature (see Chapter 2). Hafez (1963) attributed the lighter weights at birth of calves from young dams to the severe competition for the available nutrients between the growing dam and its foetus. The difference of 13 kg in weaning weight between calves from 2- year and 3- year-old dams obtained in station 2 suggest large differences in mothering ability (especially milk production) between these age groups. The weaning weight difference of 8 kg between calves from 3- year-old dams and those of older dams in station 2 agree closely with Bosman and Harwin (1967) who found that 3- year-old dams weaned calves which were on average 10.5 kg lighter than calves from mature dams (5 to 8 years). The non-significant differences in birth and weaning weights between calves from mature (4, 5 and 6 years), and those of aged (7 to 10+ years) dams indicated here is in agreement with findings from other reports in the literature. Winks _et al_ (1978) found non-significant differences in pre-weaning growth between calves of mature (5 to 8 years) and those of aged (9+ years) dams. Heyns (1960) also reported similar findings.

Age of dam effects were non-significant on 18-month weight in station 1. Non-significant age of dam effects on some post-weaning weights were also reported by Francoise _et al_ (1973), Rudder _et al_ (1975), Vilakati (1977), Winks et al (1978) and Thorpe et al (1980b). The significant age of dam effects for 18-month weight in station 2 and 3 suggest that correction factors are needed to remove handicaps against progeny of young cows during the post-weaning period. Similar findings were reported by DPU (1978) for these two stations. Sacker et al (1971a) and Straw and Jones (1977) obtained results which suggested that yearling weight differences due to age of dam were reflections of the differences at weaning. In general, however, it has been observed that the effect of age of dam on growth after weaning is small (Straw and Jones, 1977) so that smaller correction factors are needed as age at selection increases (Jones and Straw, 1980).

Male calves averaged consistently higher than females for all traits with the exception of 18- month weight in station 3. The weight differences between the sexes increased with age from about 2 kg at birth to 15 to 28 kg at 18- months of age in station 1 and 2. The 9 to 11 percent and 6 to 10 percent advantage of males in weaning weight and 18- month weight, respectively, are of the same order as those reported by Bosman and Harwin (1966, 1967), Osman and Rizgalla (1968), Joubert et al (1977) and Holyroyd et al (1979). The non-significant sex effect on weight at 18- months of age indicated in station 3 is inexplicable since bull and heifer calves at each station were raised under similar management systems during the post-weaning period.

4.2 Genetic Influences on Birth Weight, Weaning Weight and 18- Month Weight.

Results of the analysis of variance (Table 4.1) have indicated that the effect of breed of calf on all the traits was highly significant. The least squares means for the effect of the breeds and crossbreds on birth, weaning and 18- month weights are presented by station in Tables 4.3 to 4.6. In view of the significant breed x year (Table 4.1) interaction in station 2 and 3, the breed means are shown within years for these stations (Table 4.5 and 4.6). Analysis of variance results which comprise sire and breed of dam factors are presented in Table 4.7, and an outline of the effects of these factors on weight at birth, weaning and 18- months is given in Table 4.8. Results on the effects of all the above-mentioned genetic factors on the traits studied are reported separately for each station.

4.2.1 Station 1

Breed x year interactions were non-significant for all traits in station 1 (Table 4.1a). The least squares means in Table 4.3 indicate that there were significant ($P < 0.01$) differences between the breeds and crossbreds in birth, weaning and 18- month weights. It is apparent from this table that the Brahmans and Brahman x Nguni crossbreds were all significantly heavier than the straightbred Ngunis at all stages. Table 4.4 shows the

TABLE 4.3 Least Squares Means and Standard Errors for the Effect of Breed* on Birth weight, Weaning weight and 18- month weight — Station 1.

	Birth weight (kg)	Weaning weight (kg)	18-Month weight (kg)
General mean	27.5 ± 1.5	165.1 ± 1.5	253.7 ± 1.5
Breed			
Nguni	26.2 ± 0.4^{a}	154.1 ± 2.5^{a}	240.3 ± 3.4^{a}
Brahman	27.8 ± 0.4^{b}	169.2 ± 2.4^{b}	261.4 ± 2.9^{b}
$\frac{3}{4}$-Brahman	29.7 ± 0.4^{d}	183.2 ± 2.2^{d}	272.8 ± 3.0^{d}
$\frac{7}{8}$-Brahman	28.7 ± 0.3^{c}	176.2 ± 1.5^{c}	267.1 ± 2.0^{c}

* Note: The term "breed" has been used for convenience, as a criterion for comparison. This usage does not imply that a $\frac{3}{4}$-Brahman-$\frac{1}{2}$-Nguni crossbred, for instance, is considered a breed in a genetic sense.

a,b,c,d

Means within the same column with different superscripts differ significantly ($P < 0.01$).

TABLE 4.4 The Superiority in Birth weight, Weaning weight and 18-Month weight shown by the Brahman and Brahman Crossbreds over the Nguni - Station 1.

Breed/Cross	Weight above Nguni (kg)		
	Birth weight	Weaning weight	18-Month weight
Brahman	1.6 (6%)*	15.1 (9%)	21.1 (8%)
¾-Brahman	3.4(12%)	29.1 (16%)	32.5 (12%)
⅞-Brahman	2.5 (9%)	22.1 (13%)	26.8 (10%)

* Percentage superiority in parentheses.

magnitude of the weight differences between these breeds. It is of interest to note that the differences in weight between the straightbred Brahmans and the Ngunis (1.6 to 21.1 kg) were not as large as those between the Ngunis and the crossbreds (2.5 to 32.5 kg).

According to Table 4.3, the Brahman crosses were significantly heavier than the straightbred Brahmans at all stages. The $\frac{3}{4}$-Brahmans were 1.9 kg, 14 kg and 11.5 kg heavier than the purebred Brahmans at birth, weaning and 18-months, respectively. Differences in weight between the $\frac{7}{8}$-Brahmans and the straightbred Brahmans were 0.9 kg, 7 kg and 5.7 kg for birth, weaning and 18-months, respectively. These differences were all highly significant ($P < 0.01$).

The analysis of variance results in Table 4.7a indicate that sires had a non-significant effect on birth and weaning weights, and a highly significant ($P < 0.001$) effect on 18-month weight. The least squares constants (Table 4.8a) show that the effects due to sires increased from birth to 18-months. For instance, the effects associated with sire 6 were about +0.69 kg, +5.4 kg and +17.4 kg on birth, weaning, and 18-month weights, respectively. Progeny by sire 3 at this station were 1.2 kg, 1.6 kg and 27.1 kg below the general mean at birth, weaning and 18-months, respectively.

Breed of dam effects were significant for birth weight ($P < 0.05$), highly significant for weaning weight

($P < 0.01$) and non-significant for 18-month weight (Table 4.7a). Breed of dam x year and Breed of dam x sire interactions were all non-significant. The least squares constants for breed of dam (Table 4.8a) indicate that the heaviest calves at birth were those by $\frac{3}{4}$-Brahman dams (29.5 kg), followed by $\frac{1}{2}$-Brahman dams (28.7 kg) and then pure Brahman dams (27.9 kg). The differences in birth weight between calves by these dam breeds were all significant ($P < 0.05$). The heaviest calves at weaning were those by $\frac{1}{2}$-Brahman dams (3.18 kg above average), followed by $\frac{3}{4}$-Brahman dams (1.01 kg above average), purebred Brahman dams produced calves which had the lowest weight at weaning (4.19 kg below average).

4.2.2 Discussion

The results have indicated that breed x year interactions were not important at station 1. This is in agreement with Kennedy and Chirchir (1971) who reported that such interactions were not significant on weaning and 18-month weights of Zebu x British cattle. However, a highly significant ($P < 0.01$) breed x year interaction on birth weight was obtained in this latter study.

Straightbred Brahmans were 6 to 10 percent better than the Ngunis in weight at all stages. This agrees closely with the review of Maule (1973) which indicated that the growth performance of the Nguni breed was generally lower than that of the Brahman breed. One of the studies indicated that Nguni calves were about 50 kg lighter than Brahmans at weaning (205 days). In Botswana, the APRU (1978) also found that straightbred Brahmans were significantly heavier (305.0 kg) at 18-months of age than the local Tswana (300.6 kg), another Sanga type breed (Mason and Maule, 1960). However, weaning weight (210 days) differences between the Tswana and Brahman were non-significant and at birth, the Tswana calves were significantly heavier.

The most important results of this present study are those indicating the superiority of the Brahman crossbreds (10 to 19 %) over the Ngunis. These findings suggest an increase in growth performance due to crossbreeding the Ngunis with the Brahmans. Similar results have been obtained in Botswana (Trail et al, 1977, APRU, 1978) where Brahman sires were crossed with the local Tswana cows and in South Africa (Mentz et al, 1979a,b) where the exotic Brahmans were crossed with the local Africanders. It is apparent from the results that the crossbreds were also superior in growth to the straightbred Brahmans. The advantage of the crossbreds over the straightbreds (Nguni and Brahman) may be due to additive and non-additive gene effects (heterosis). Unfortunately, it was not possible to measure any heterotic effects here. However, sizeable heterotic effects would be expected in Nguni/Brahman crosses in view of the fact that the greatest heterosis in beef production traits occurs in crosses involving parent breeds of widely divergent sources (Cundiff, 1970, Preston and Willis, 1974).

Among the crossbreds, the ⅞-Brahman grades had significantly lower weights than the ¾-Brahmans probably because of reduced heterotic effects associated with upgrading (Ellis et al, 1965, Dickerson, 1973). The ⅞-Brahman crossbreds, which contain about 88 percent of the Brahman breed genes, were 3 to 4 percent heavier than the purebred Brahmans. The superiority of these high grade Brahmans may be partly due to improved adaptability associated with genes derived from the Nguni.

The non-significant sire effects on birth and weaning weights suggest that the sire genetic influences on these pre-weaning traits were masked by the high influence of the maternal environment provided by the three breeds of dams.

It is of interest to note, however, that although sire effects were non-significant for weaning weight, there were differences of up to 18 kg between the best and poorest sires for this trait (Table 4.8a). These results are in agreement with Osman and Rizgalla (1968) who obtained differences of up to 20 kg between sires for weaning weight, but found non-significant sire effects on that trait. In Australia, Barlow and O'Neill (1978) also found that the influence of the sire was not significant for pre-weaning gain and weaning weight. Non-significant sire effects on birth weight were reported by Harricharan *et al* (1976) in Sahiwal and Brahman herds, who also remarked that the full potential effect of a sire on birth weight may not be manifested under poor nutritional conditions. Ghosh *et al* (1978) found non-significant sire effects on the birth weight of Holstein x Haryana calves.

Results relating to the effects of the sire on 18-month weight indicate that variation in post-weaning growth of calves due to sires exist, suggesting that it would be possible to select superior sires in terms of increased progeny growth to 18-months of age. The differences of up to 44 kg in 18-month weight between progeny of the best (284.9 kg) and worst (240.4 kg) sires obtained here agree closely with results by Naidu and Desai (1965) in India, Osman and Rizgalla (1968) in Sudan and many other reports in the literature. The non-significant breed of dam x sire interactions indicate that the influence of the individual sires on the weights did not vary with breed of dam, suggesting that progeny testing of these sires within crossbred populations would be as effective as evaluating sires on the basis of straightbred progeny. Similar results were obtained by Dunn et al (1970) and Koger et al (1975).

The influence of breed of dam on birth and weaning weights is to be expected in view of the large maternal influence during the pre-weaning phase. The results have indicated that calves by crossbred dams had an advantage in birth and weaning weights over those by straightbred dams. These findings can be compared with those of Ellis et al (1965) who observed that the genotype of the dam exerted a significant influence on the birth weight of crossbred calves, and of Harricharan et al (1976) who found that in the Sahiwal and Brahman herds, the calves out of crossbred dams had an advantage in their birth weight over the purebred calves. The significance in birth weight between calves by ½- and ¾-Brahman dams in favour of the ¾-Brahman dams is in agreement with Vorster (1954) who reported that the birth weights of calves out of crossbred cows increased from the first to the second generation of grading up. The heavier weaning weight of calves by the half-bred dams compared to the straightbred and ¾-Brahman dams indicates the superiority of F_1 cows in maternal ability and suggests the possibility of maternal heterosis.

4.2.3 Station 2

The breed x year interaction was significant for all the traits at station 2 (Table 4.1b). Figure 1 illustrates the interaction between breed and year for birth weight, weaning weight, and 18-month weight. The least squares means for the breeds and crossbreds are shown within years in Table 4.5.

Least squares means for birth weight (Table 4.5a) indicate that Nguni calves were the lightest in all but one year (Year 1) during which the $\frac{7}{8}$-Brahmans had the least birth weight. The $\frac{7}{8}$-Brahmans were, however, the heaviest in all the other years and were up to 7kg, 2kg and 3kg heavier than the Nguni, $\frac{1}{2}$- and $\frac{3}{4}$-Brahman, respectively. There were inconsistent changes in rank between the $\frac{1}{2}$- and the $\frac{3}{4}$-Brahman crosses (Fig. 1a). The half-breds were significantly heavier than the $\frac{3}{4}$-Brahmans during year 2 and 3 (1976 and 1977) and the $\frac{3}{4}$-Brahmans ranked higher ($P < 0.01$) than the $\frac{1}{2}$-Brahmans during year 1 and 4 (1975 and 1978).

The weaning weight means (Table 4.5b) show that the Nguni calves were the lightest ($P < 0.01$) at weaning throughout the four years. Half-bred Brahmans were significantly lighter than the $\frac{3}{4}$-Brahmans at all times (Fig. 1b) and had lower weaning weights ($P < 0.01$) than $\frac{7}{8}$-Brahmans in years 3 and 4. In year 1, the half-breds were significantly heavier than the $\frac{7}{8}$-Brahmans and, year 2 indicated no significant differences in weight

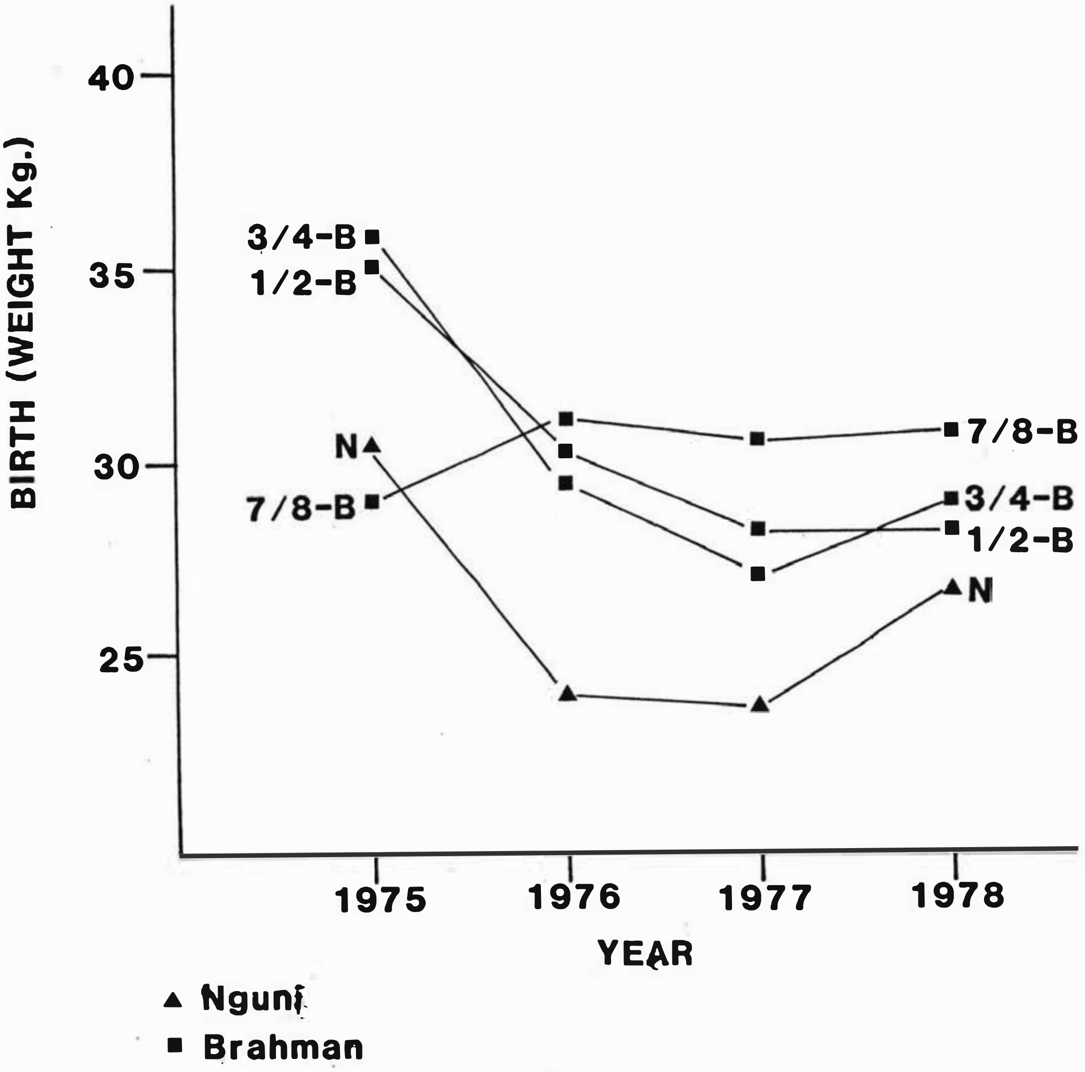

Fig. 1a : Interaction between breed and year for birth weight - station 2.

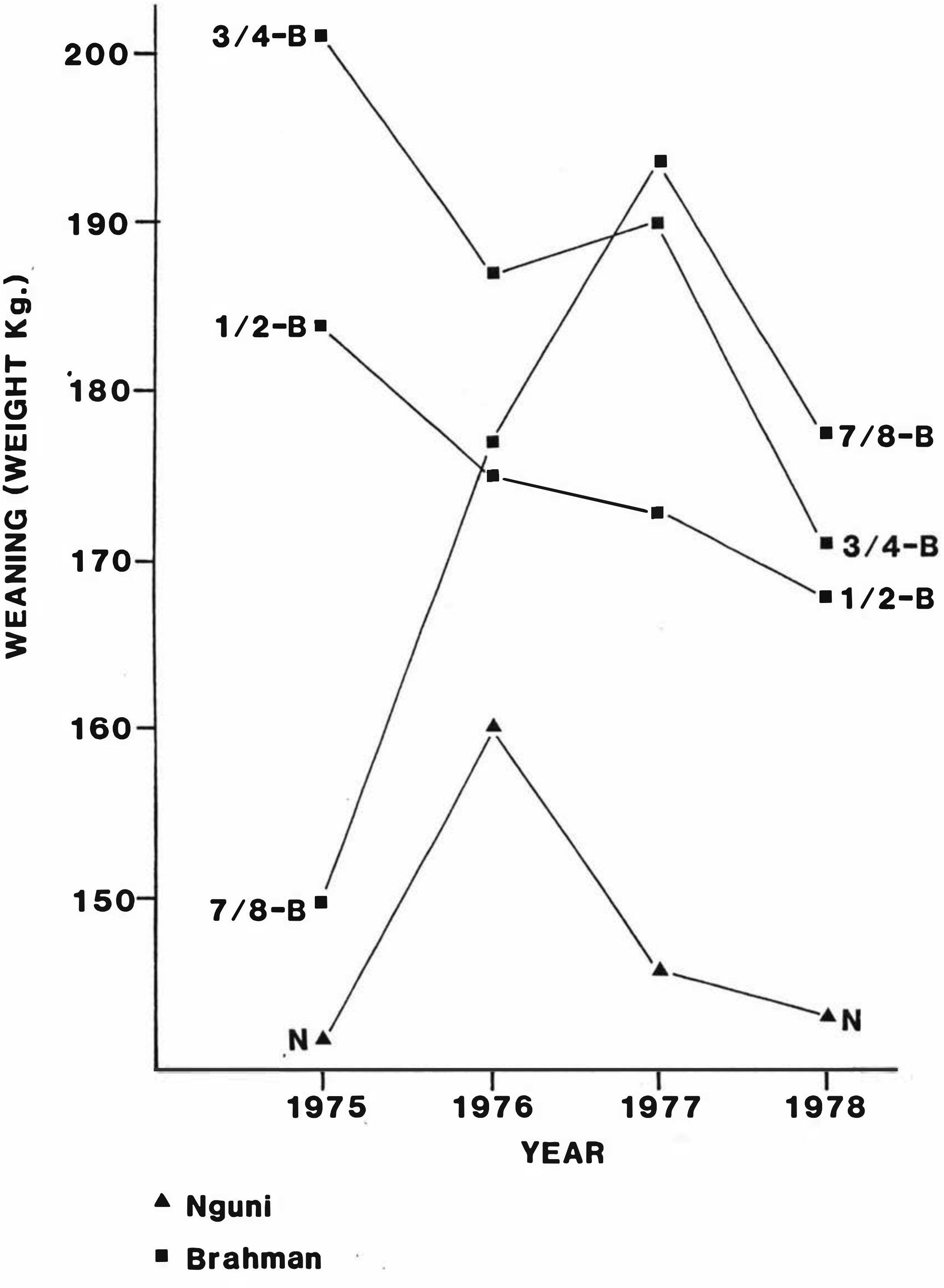

Fig. 1b : Interaction between breed and year for weaning weight - station 2.

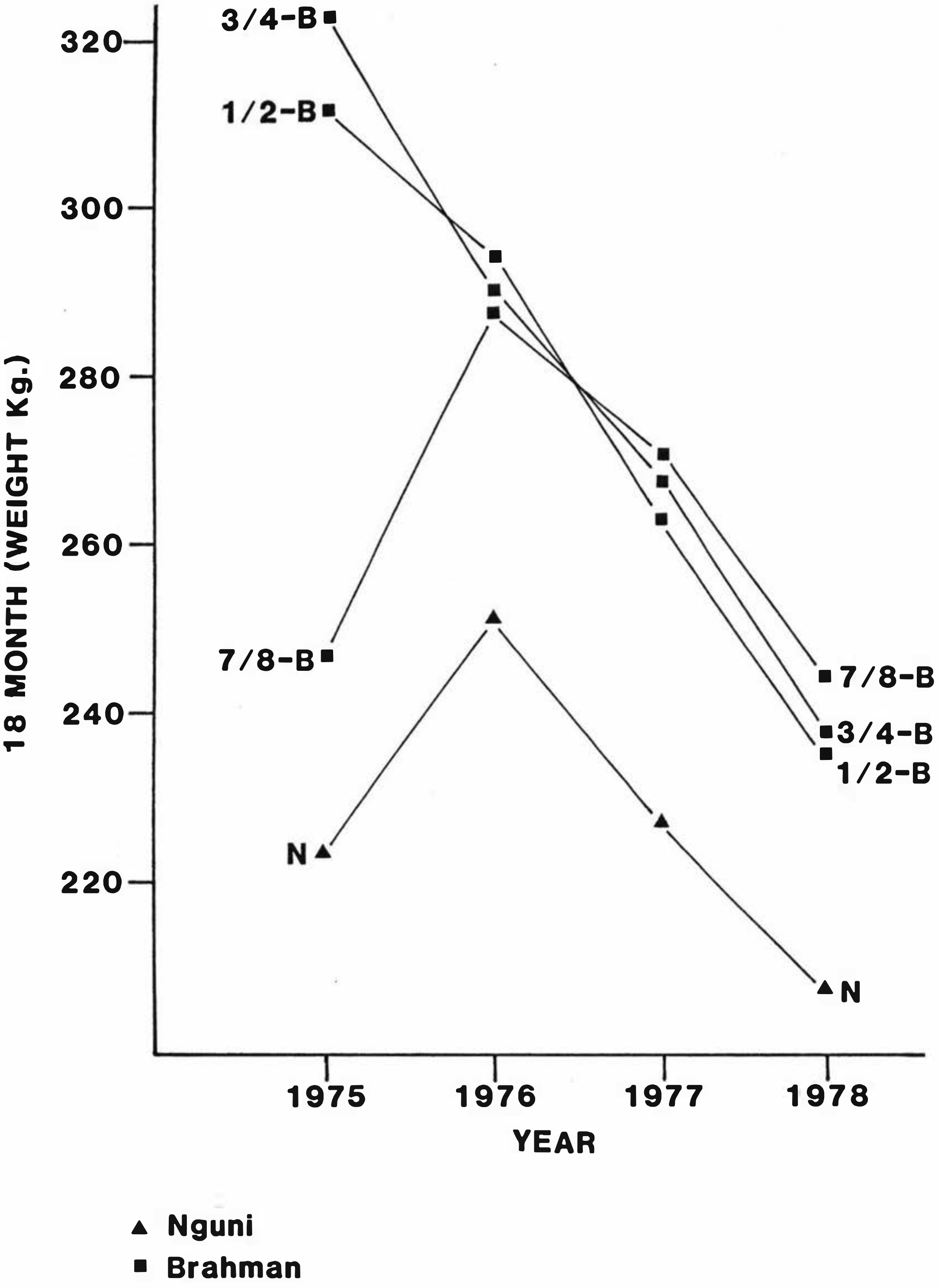

Fig. 1c : Interaction between breed and year for 18-month weight - station 2.

TABLE 4.5 Least Squares Means and Standard Errors for the Effect of Breed x Year Interaction on weights at Birth, Weaning, and 18-month – Station 2.

(a) Birth Weight (kg)

General Mean = 29.3 ± 1.7 kg.

Breed	Year 1	2	3	4	Mean
Nguni	30.4 ± 2.8^{b}	24.2 ± 1.0^{a}	23.6 ± 0.9^{a}	26.9 ± 0.8^{a}	26.3 ± 0.8
$\frac{1}{2}$-Brahman	35.3 ± 0.6^{c}	30.4 ± 0.6^{c}	28.4 ± 0.6^{c}	28.4 ± 0.8^{b}	30.6 ± 0.4
$\frac{3}{4}$-Brahman	36.0 ± 0.7^{d}	29.5 ± 0.7^{b}	27.3 ± 0.7^{b}	29.0 ± 0.7^{c}	30.5 ± 0.4
$\frac{7}{8}$-Brahman	29.2 ± 2.6^{a}	31.1 ± 2.9^{d}	30.5 ± 1.6^{d}	30.8 ± 1.1^{d}	30.4 ± 1.1

(b) Weaning Weight (kg)

General Mean = 170.3 ± 1.7 kg.

Breed	Year 1	2	3	4	Mean
Nguni	142.2 ± 13.0^{a}	159.5 ± 4.4^{a}	145.9 ± 4.1^{a}	143.4 ± 3.7^{a}	147.8 ± 3.8
$\frac{1}{2}$-Brahman	183.9 ± 2.9^{c}	175.3 ± 2.8^{b}	172.9 ± 2.7^{b}	168.5 ± 3.7^{b}	175.1 ± 2.0
$\frac{3}{4}$-Brahman	201.1 ± 3.3^{d}	186.6 ± 3.2^{c}	189.6 ± 3.1^{c}	171.4 ± 3.1^{c}	187.2 ± 1.8
$\frac{7}{8}$-Brahman	150.3 ± 11.7^{b}	177.2 ± 13.0^{b}	194.3 ± 7.1^{d}	178.2 ± 5.2^{d}	175.0 ± 4.9

TABLE 4.5 continued

(c) 18-Month Weight (kg)

General Mean = 261.3 ± 1.7 kg.

Breed	Year 1	2	3	4	Mean
Nguni	233.5 ± 15.5^{a}	252.0 ± 5.3^{a}	227.6 ± 5.0^{a}	208.2 ± 4.4^{a}	230.3 ± 4.6
½-Brahman	312.0 ± 3.5^{c}	294.9 ± 3.3^{c}	262.8 ± 3.2^{b}	236.0 ± 4.4^{b}	276.4 ± 2.4
¾-Brahman	323.4 ± 4.0^{d}	291.3 ± 3.8^{b}	267.5 ± 3.7^{c}	238.1 ± 3.8^{b}	280.1 ± 2.2
⅞-Brahman	247.1 ± 14.0^{b}	288.6 ± 15.6^{b}	271.4 ± 8.6^{d}	244.5 ± 6.3^{c}	262.9 ± 5.9

a,b,c,d Means within the same column with different superscripts differ significantly ($P < 0.01$).

between these crossbreds. Within year means for the $\frac{3}{4}$- and $\frac{7}{8}$- Brahman crosses indicate that the $\frac{3}{4}$-Brahmans were significantly heavier in years 1 and 2 and the $\frac{7}{8}$-Brahmans were heavier ($P < 0.01$) in years 3 and 4.

Estimated least squares means for 18-month weight (Table 4.5c) indicate that the Ngunis were the lightest throughout the years ($P < 0.01$). The crossbreds changed in rank from year to year for this post-weaning trait as depicted clearly in Fig. 1c. The half-breds were lighter ($P < 0.01$) than the $\frac{3}{4}$-Brahmans in years 1 and 3; heavier ($P < 0.01$) in year 2 and there were no significant differences in 18-month weight between these crossbreds during year 4. The $\frac{1}{2}$-Brahmans were in turn heavier ($P < 0.01$) than the $\frac{7}{8}$-Brahmans in years 1 and 2, but lighter than these crosses during years 3 and 4. Three-quarter-Brahmans were significantly heavier than the $\frac{7}{8}$-Brahmans in one year only (Year 1), there were no significant differences in 18-month weight between these crosses in year 2 and during year 3 and 4, the $\frac{7}{8}$-Brahmans were 3.9 kg and 6.4 kg heavier ($P < 0.01$), respectively.

Table 4.7b indicates highly significant sire effects on birth weight, weaning weight and 18-month weight. The interactions of breed of dam x year and breed of dam x sire were all non-significant. The least squares constants in Table 4.8b show that effects associated with sires ranged from -2.5 to 3.1 kg for birth weight,

-10.9 to 9.8 kg for weaning weight and -7.7 to 15.9 kg for 18-month weight. Breed of dam was non-significant on birth and 18-month weights and highly significant for weaning weight at this station (Table 4.7b). Table 4.8b indicate that calves by Nguni dams were about 6 kg below the population mean at weaning, while those by ½-Brahman dams were about 6 kg above average.

4.2.4 Discussion

The significant breed x year interaction indicates that year of birth was an important influence on the magnitude of the crossbred differences for birth weight, weaning weight, and 18-month weight. This interaction suggests that breed comparisons for liveweight should be conducted over a number of years at this station. Significant genotype x year interactions for liveweights have also been reported by Trail et al (1971b) in Uganda, Mentz et al (1979 a,b) and Paterson et al (1980) in South Africa and Thorpe et al (1979, 1980b) in Zambia.

The results have indicated that the Nguni calves were consistently lighter ($P < 0.01$) than any of the Brahman crosses in weight at birth, weaning, and 18-months of age during the four years (with the exception of birth weight in year 1). It is most striking that increases of 10 to 29 percent in weaning weight and 13 to 34 percent in 18-month weight were obtained by crossing the Nguni cows with the Brahman sires. The advantage of the Brahman crosses when compared with the Ngunis agrees with reports from Botswana (Trail et al, 1977, APRU, 1978) which indicated that Brahman crossbreds were generally superior to the local breeds in growth performance. In South Africa, Mentz et al (1979 a,b) also found that under extensive conditions, Brahman crosses out-weighed the indigenous Africanders in pre- and post-weaning growth.

The interaction between breed and year as illustrated in Fig. 1 have indicated a striking variation in the relative position of the various crosses, especially the $\frac{7}{8}$-Brahman in 1975 and 1976. This was probably due to the relatively small number of observations for this class in year 1 and 2 (see Appendix I). Despite the interaction, however, birth weight tended to favour the $\frac{7}{8}$-Brahmans and the $\frac{3}{4}$-Brahmans were obviously superior to the half-breds in weaning weight.

The crossbreds changed in rank from year to year with respect to 18-month weight. The breed means (disregarding the interaction) in Table 4.5c, however, suggest that the $\frac{3}{4}$-Brahmans were the heaviest at this age, followed by the half-breds, and the $\frac{7}{8}$-Brahmans appeared to have the lowest weight. The results of station 1 indicated that the $\frac{3}{4}$-Brahmans were heavier than the $\frac{7}{8}$-Brahmans at 18-months; unfortunately that station did not have half-bred Brahmans for comparison with the high grade Brahmans.

Sire effects were highly significant on birth weight, weaning weight, and 18-month weight, indicating the importance of additive genetic variation on these traits. The weight differences between the best and worst sires increased from 6 kg at birth to 21 kg at weaning. This may be compared with the report of Bosman and Harwin (1966) which noted highly significant sire effects on birth and weaning weight and indicated that weaning weight differences among sires of the same breed were even more marked than birth weight differences. Osman and Rizgalla (1968) reported significant differences of up to 5 kg between sires for birth weight. The 24 kg difference in 18-month weight between progeny of the best and those of the worst sire at this station is almost half that indicated for sires in station 1 (44 kg), suggesting twice as much variation among station 1 sires with respect to the 18-month weight of their progeny. As in station 1, the sire x breed of dam interaction was non-significant here. This has important practical implications in progeny testing where the breeding herd consist of straightbred and crossbred cows.

4.2.5 Station 3

The interactions between breed and year were significant for all the traits at this station (Table 4.1c). These interactions are illustrated in Fig. 2 and Table 4.6 presents the estimated least squares means within years. The means for birth weight in Table 4.6a indicate significant differences between the breeds / crossbreds throughout the years. Nguni calves were the lightest ($P < 0.01$) in years 1 and 3 and in year 2 they were only 1.1 kg heavier ($P < 0.01$) than the $\frac{1}{2}$-Brahmans. The heaviest calves at birth were the Simmentals and $\frac{7}{8}$-Simmentals which ranked highest throughout the three years (Fig. 2a). The $\frac{3}{4}$-Simmentals were heavier ($P < 0.01$) than the half-bred Simmentals in years 1 and 2, and there were no significant differences between these crosses in year 3. Half-bred Simmentals were, in turn, heavier ($P < 0.01$) than half-bred Brahmans during the first two years and the differences in birth weight were non-significant during the last year.

Least squares means for weaning weight presented in Table 4.6b indicate that the Nguni calves had the lowest weights in all the years. The $\frac{1}{2}$-Brahmans were also not very different from the Nguni in weaning weight during the first two years, but were up to 17kg heavier ($P < 0.01$) than the Nguni in year 3 (Fig. 2b). The heaviest calves at weaning were the $\frac{3}{4}$- and $\frac{7}{8}$-Simmentals which were significantly superior to all calves throughout the years (except Simmentals in year 3). This is depicted clearly in Fig. 2b. The straightbred Simmentals were significantly heavier than the $\frac{1}{2}$-Simmentals (7.2 - 15.5 kg) in years 1 and 3, but the half-breds were, in turn, 8.3 kg heavier than these straightbreds in year 2. Half-bred Simmentals were heavier ($P < 0.01$) than half-bred Brahmans in years 1 and 2; in year 3, half-bred Brahmans were heavier

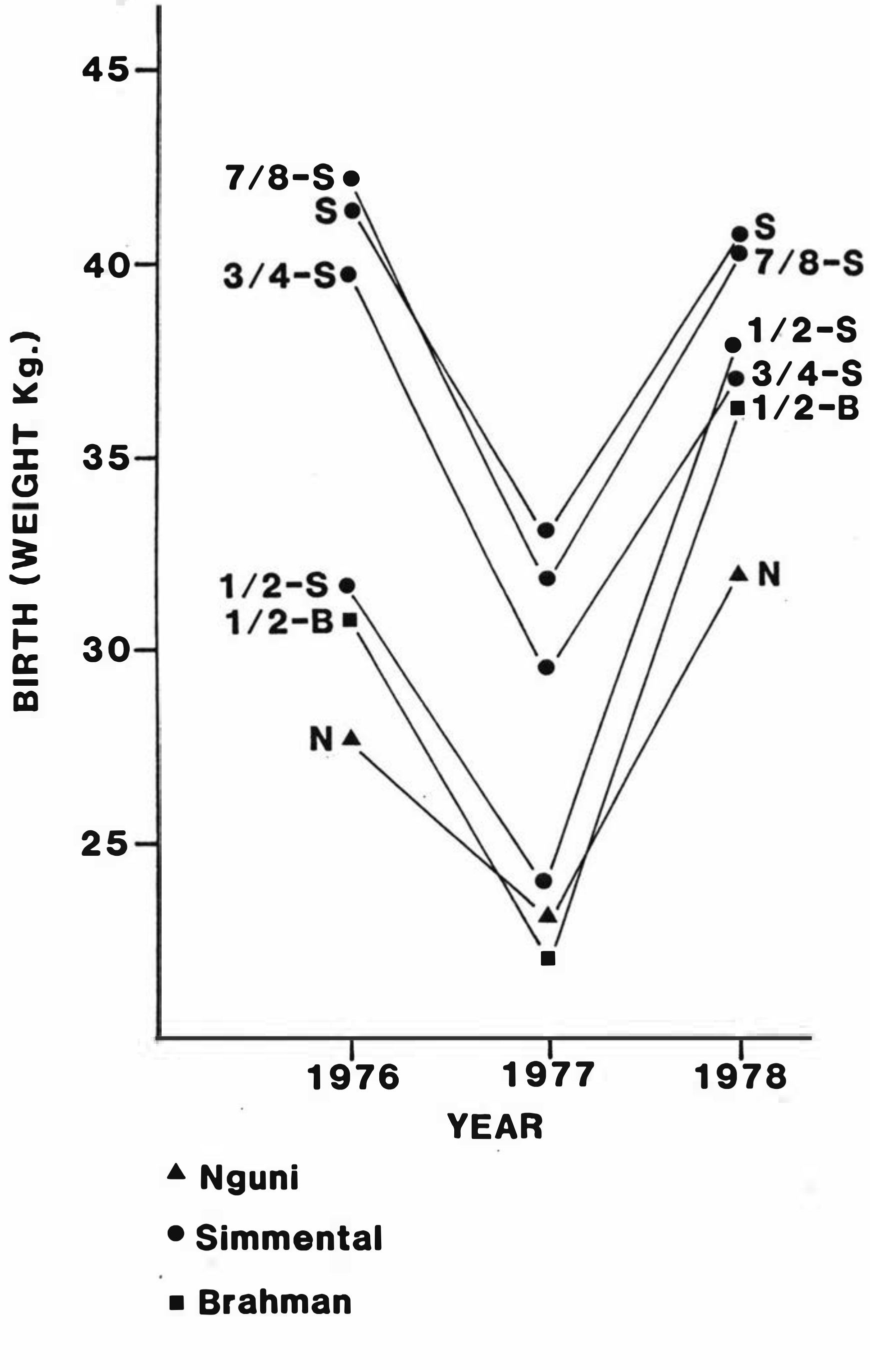

Fig. 2a : Interaction between breed and year for birth weight - station 3.

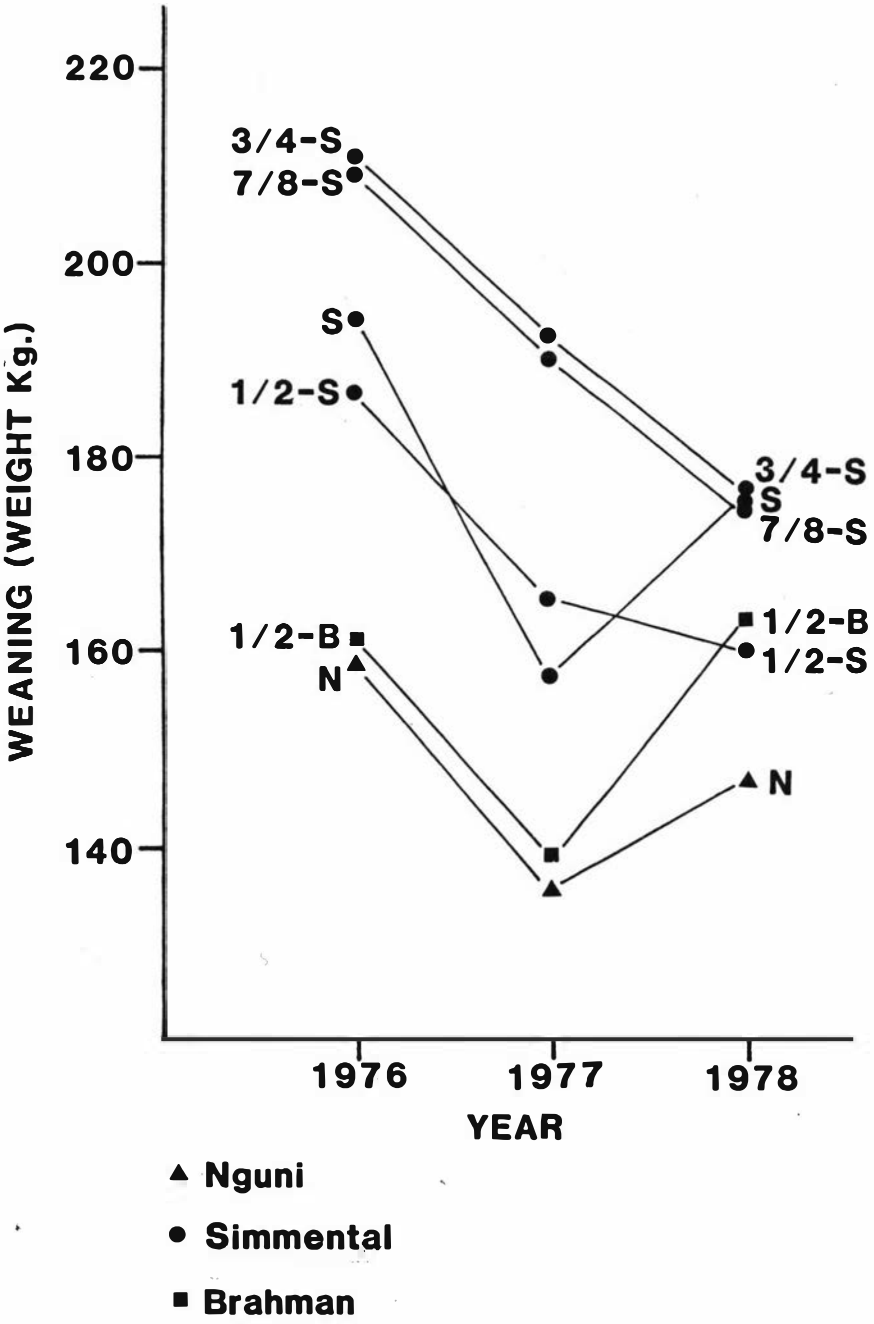

Fig. 2b : Interaction between breed and year for weaning weight - station 3.

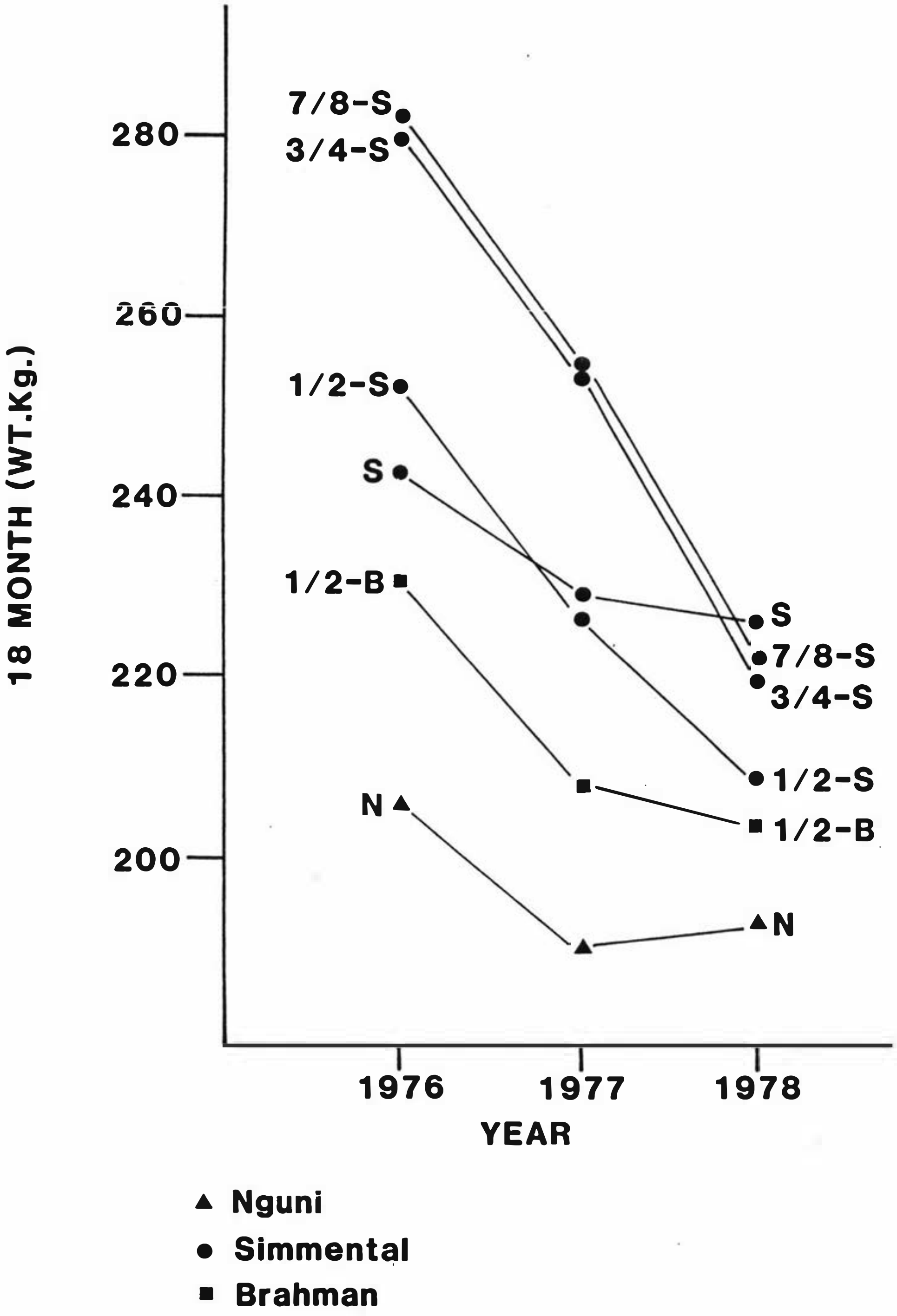

Fig. 2c : Interaction between breed and year for 18-month weight - station 3.

TABLE 4.6 Least Squares Means and Standard Errors for the Effect of Breed x Year Interaction on Birth weight, Weaning weight and 18-month weight — Station 3.

(a) Birth Weight (kg)

General Mean = 32.0 ± 1.7 kg.

Breed	Year 1	 2	 3	 Mean
Nguni	28.0±0.9^{a}	23.2±1.0^{b}	32.4±0.9^{a}	27.9±0.6
Simmental	41.4±1.0^{e}	33.3±0.8^{f}	40.8±0.6^{c}	38.5±0.5
½-Simmental	32.0±1.6^{c}	24.1±1.3^{c}	38.3±1.9^{b}	31.5±1.0
¾-Simmental	39.9±3.4^{d}	29.5±1.8^{d}	37.9±2.0^{b}	35.8±1.6
⅞-Simmental	42.3±4.0^{f}	32.0±1.5^{e}	40.4±1.5^{c}	38.2±1.7
½-Brahman	30.9±1.6^{b}	22.1±1.2^{a}	37.8±3.5^{b}	30.3±1.4

Table 4.6 continued

(b) Weaning Weight (kg)

General Mean = 161.5 ± 1.7 kg.

Breed	Year			
	1	2	3	Mean
Nguni	159.0 ± 4.3^{a}	134.8 ± 4.6^{a}	145.6 ± 4.4^{a}	146.5 ± 2.8
Simmental	194.4 ± 4.6^{c}	156.9 ± 3.8^{b}	175.5 ± 3.0^{d}	175.6 ± 2.3
$\frac{1}{2}$-Simmental	187.3 ± 7.8^{b}	165.2 ± 6.4^{c}	160.0 ± 8.9^{b}	170.8 ± 4.6
$\frac{3}{4}$-Simmental	211.0 ± 16.2^{d}	192.4 ± 8.6^{d}	177.3 ± 9.2^{e}	193.6 ± 7.5
$\frac{7}{8}$-Simmental	208.7 ± 18.7^{d}	190.1 ± 7.1^{d}	175.1 ± 7.3^{d}	191.3 ± 8.1
$\frac{1}{2}$-Brahman	160.9 ± 7.5^{a}	138.2 ± 5.6^{a}	162.6 ± 16.3^{c}	153.9 ± 6.4

(c) 18-Month Weight (kg)

General Mean = 215.6 ± 1.7 kg.

Breed	Year			
	1	2	3	Mean
Nguni	206.2 ± 4.5^{a}	190.2 ± 4.7^{a}	193.3 ± 4.6^{a}	196.5 ± 2.9
Simmental	243.4 ± 4.8^{c}	228.7 ± 3.9^{c}	255.6 ± 3.2^{e}	232.6 ± 2.3
$\frac{1}{2}$-Simmental	252.4 ± 8.0^{d}	227.2 ± 6.6^{c}	208.8 ± 9.3^{c}	229.5 ± 4.8
$\frac{3}{4}$-Simmental	280.0 ± 16.8^{e}	252.8 ± 8.9^{d}	220.3 ± 9.5^{d}	251.1 ± 7.8
$\frac{7}{8}$-Simmental	281.4 ± 19.4^{e}	254.1 ± 7.4^{d}	221.6 ± 7.5^{d}	252.4 ± 8.4
$\frac{1}{2}$-Brahman	229.5 ± 7.7^{b}	208.4 ± 5.8^{b}	203.9 ± 16.9^{b}	213.9 ± 6.6

a,b,c,d,e,f Means within the same column with different superscripts differ significantly ($P < 0.01$).

(2.3 kg) than the ½-Simmentals.

The Ngunis had the lowest weight at 18-months of age in all years (Table 4.6c) and half-bred Brahmans ranked second from the bottom (Fig. 2c). The ¾- and ⅞-Simmentals were the heaviest in all but one year (year 3) during which only the straightbred Simmentals were significantly heavier than these grades. The similarity in weight at 18-months between the ¾- and ⅞-Simmentals is depicted clearly in Fig. 2c. The Simmentals were significantly lighter (9 kg) than the half-bred Simmentals in year 1 and there were no significant differences between these breeds in year 2. Half-bred Simmentals were 22.9 kg, 18.8 kg and 4.9 kg heavier ($P < 0.01$) than the half-bred Brahmans during years 1, 2 and 3 respectively.

4.2.6 Discussion

The significant breed x year interaction at this station might be associated with changes in the composition of the breeding herd since the number of the foundation cows (especially Simmentals) were increased from year to year through additional purchases. The interaction can also be explained by the fact that a new set of Simmental sires was used each year. Similar interactions have been reported by Vorster (1954) and Mentz et al (1979 a,b).

It is apparent from the results that the straightbred Simmentals performed significantly better than the Nguni in growth rate throughout the years of study. At birth, the Simmentals outweighed the Ngunis by 8.3 to 13.4 kg and the weight differences in favour of the Simmentals at weaning and at 18-months of age, respectively were 22.1 to 35.4 kg and 36.0 to 38.5 kg. The advantage of the Simmental breed, in growth performance, compared with other Sanga type breeds have been reported by Maule (1973) and Joubert _et al_ (1977). One of the reports reviewed by Maule (1973) indicated that under intensive conditions the Simmentals were on average 57 kg and 200 kg heavier than the Nguni at weaning (205 days) and 479 days, respectively. However, the differences obtained here are much lower in magnitude, suggesting that the growth rate differences between these breeds are relatively smaller under extensive conditions.

The superiority of the Simmental x Nguni (½-Simmentals) crosses over the straightbred Nguni in weight at birth, weaning and 18-months indicate the advantage of crossbreeding on the growth performance of the indigenous cattle. An increase of 10 to 23 percent (14 to 30 kg) in weaning weight and 8 to 22 percent (16 to 46 kg) in 18-month weight was obtained by crossing the Nguni with the Simmental at this station. Most of the increase in weight among the crossbreds may be attributed to heterosis since the Nguni and the Simmental are widely dissimilar breeds

(Sanga and B. taurus). The performance of the half-bred Brahmans compared to the purebred Nguni at birth and weaning was not as distinct as in station 2. However, the Brahman half-breds were obviously better than the Nguni and 18-months of age (see Fig. 2c) throughout the years of study. The advantage to the Brahman and Simmental crosses when compared with Sanga type cattle agrees with reports from neighbouring countries (Joubert et al, 1977, Trail et al, 1977, APRU, 1978, Mentz et al, 1979 a,b). Similar findings were also obtained in Uganda (Trail et al 1971b) and Zambia (Thorpe et al, 1979, 1980b) when local breeds of cattle were compared with crosses between such breeds and European breeds.

Half-bred Simmentals were generally heavier than Brahman half-breds at all stages (Table 4.6 and Fig. 2). At 18-months, the ½-Simmentals were, on average, 16 kg (7%) heavier than the half-bred Brahmans. The APRU (1978) also found that Simmental-sired calves performed significantly better in growth to 18-months than Brahman-sired calves when these sire breeds were mated to Tswana cows. Mentz et al (1979 a,b) obtained similar results when using Africander cows as a basis for comparisons.

Table 4.6a have indicated that the straightbred Simmentals were 8.3 to 13.4 kg (26 to 48%) heavier at birth than the Ngunis. The relatively high birth weight of the Simmentals has important practical implications with respect to crossbreeding (especially with the small

Nguni) in view of the association between high birth weight and dystocia (Laster et al, 1973, Smith et al, 1976). The $\frac{7}{8}$-Simmentals were also, on average, 7 kg (21%) and 2.4 kg (7%) heavier than the $\frac{1}{2}$- and $\frac{3}{4}$-Simmentals, respectively, indicating an increase in birth weight with upgrading.

The fact that $\frac{3}{4}$- and $\frac{7}{8}$-Simmentals were significantly heavier than the half-bred Simmentals at weaning indicate the superiority of the crossbred Simmental cows in mothering ability (especially milk production) compared to the purebred Nguni cows. Unfortunately, it was not possible to evaluate the influence of breed of dam on growth at this station. The better performance of the $\frac{3}{4}$- and $\frac{7}{8}$-Simmentals at 18-months compared to the $\frac{1}{2}$-Simmentals may be largely attributed to additive gene effects since the influence of heterotic effects on growth is expected to decrease with upgrading (Dickerson, 1973). These high grade Simmentals were also generally heavier at 18-months of age than the purebred Simmentals, probably because of improved adaptability associated with genes derived from the indigenous Nguni.

TABLE 4.7 Analysis of variance for Birth weight, Weaning weight and 18-month weight from Model 2.

(a) Station 1

Source of variation	Degrees of freedom		Mean Square	
		Birth weight	Weaning weight	18-Month weight
Year	3	72.9 *	4600.8 ***	15853.4***
Breed of dam	2	86.1 *	2837.4 **	2377.3 NS
Month of birth	3	82.1 **	4482.2 ***	3963.5**
Age of dam	2	29.0 NS	342.6 NS	1722.7NS
Sex	1	461.2 ***	24435.5 ***	11297.9***
Sire	5	31.2 NS	1034.6 NS	6254.8***
Residual	247	19.5	540.0	919.8
Breed of dam x year	6	8.4 NS	431.1 NS	921.8NS
Breed of dam x sire	10	19.5 NS	769.5 NS	1261.2NS
Residual	231	19.8	532.9	905.0

TABLE 4.7 Continued

(b) Station 2

Source of variation	Degrees of freedom	Mean Square		
		Birth weight	Weaning weight	18-Month weight
Year	3	1841.3***	10176.8***	160019.5***
Breed of dam	1	7.7 NS	18970.5***	1518.2 NS
Month of birth	3	498.2***	21911.4***	27754.9***
Age of dam	2	63.8 NS	9466.8***	3509.4 *
Sex	1	1200.6***	47405.3***	173293.3***
Sire	9	161.5***	1756.6**	3463.2***
Residual	597	29.0	628.5	936.1
Breed of dam x year	3	16.8 NS	997.0 NS	607.6 NS
Breed of dam x sire	9	35.6 NS	371.1 NS	728.4 NS
Residual	584	28.9	628.7	942.1

* = $P < 0.05$

** = $P < 0.01$

*** = $P < 0.001$

NS = Non-significant.

TABLE 4.8 Effects of Sire and Breed of Dam on Birth weight, Weaning weight and 18-month weight (deviation from Station means in kg)*

(a) Station 1

	n	Birth weight	Weaning weight	18-month weight
General Mean	264	28.7±1.9	175.6±1.9	267.6±1.9
Sire				
1	65	0.11	-0.78	-3.60
2	54	-1.18	1.16	3.69
3	26	-1.16	-11.62	-27.14
4	29	0.94	6.22	7.54
5	43	0.61	-0.39	2.16
6	47	0.69	5.41	17.35
Breed of dam				
Brahman	96	-0.78	-4.19	-2.35
½-Brahman	102	-0.02	3.18	3.42
¾-Brahman	66	0.80	1.01	-1.07

TABLE 4.8 continued

(b) Station 2

	n	Birth weight	Weaning weight	18-Month weight
General Mean	617	30.5±2.0	181.8±2.0	278.1±2.0
Sire				
1	61	-0.59	-0.56	-0.73
2	61	-0.54	-1.02	1.00
3	60	1.24	-1.94	-0.23
4	52	-1.32	-3.15	-6.87
5	44	-2.50	-10.88	-7.73
6	64	0.21	3.23	2.78
7	61	-1.39	-0.31	-3.02
8	63	0.42	-0.63	-7.04
9	68	1.32	5.45	5.96
10	83	3.14	9.80	15.87
Breed of dam				
Nguni	360	0.21	-5.57	-0.60
½-Brahman	257	-0.21	5.57	0.60

* Based on Least squares constants derived from Model 2 (see section 3.2.1(ii)).

n =Number of records.

4.3 Maternal Performance of Nguni, Brahman and Crossbred Cows.

4.3.1 Station 1

The mean squares presented in Table 4.9a indicate that sex, year of birth of calf, cow age, and breed of cow all had a highly significant effect on the weight of calf weaned. Preliminary analyses showed that the interactions of year x breed, year x age, breed x age and year x age x breed were all non-significant.

Table 4.10 presents the estimated least squares means for the effect of breed of cow on weight of calf weaned. This table indicates significant ($P < 0.01$) differences between the purebred and crossbred cows in this trait. The weight of calf weaned by the half-bred cows was 26.5 kg and 12.0 kg heavier ($P < 0.01$) than that of the Nguni and Brahman cows, respectively indicating advantages for F_1 cows of 17 and 7 percent in weight of calf weaned. The $\frac{3}{4}$-bred cows were 15 and 6 percent superior to the Nguni and Brahman cows respectively, in weight of calf weaned. There were no significant differences between the $\frac{1}{2}$-Brahman (183.1 kg) and the $\frac{3}{4}$-Brahman (180.5 kg) cows. Among the straightbreds, the weight of calf weaned by the Nguni (156.58 kg) was significantly lighter than that of the Brahman (171.1 kg) cows.

Milk yield is the main component of the maternal ability of the breeding cow (Preston and Willis, 1974, Bishop *et al*, 1975). The differences in maternal performance between the straightbred and crossbred cows indicated by these results are expected to be largely due to milk yield differences. These differences have been found to be associated with maternal heterosis (Mason, 1966, Preston and Willis, 1974). Bishop et al (1975) stated that an increase in weaning weight of 3 to 6 percent due to heterosis can be expected from the time F_1 females enter a breeding herd, and that increases of 20 to 30 percent can be expected if the crossing breed is a dairy or dual-purpose type with higher milk production. The results obtained here also show marked increases in weaning weight due to using crossbred cows.

The results indicated that the straightbred Brahmans had a 9 percent advantage over the pure Ngunis in weight of calf weaned, suggesting that Brahmans are superior to Ngunis in mothering ability. Less encouraging though are the indications that the Brahman breed has a lower calving rate than most indigenous breeds of Southern Africa (APRU, 1978). The review by Preston and Willis (1974) also indicated that Brahmans have a poorer reproductive performance than most breeds. Unfortunately there is no published information on the reproductive performance of the Brahman compared to the Nguni in Swaziland, but, reports by Mahadevan (1964) and Butterworth and Presswood (1978) have indicated that the calving rate of the Nguni is high, especially under good management.

TABLE 4.9 Analysis of Variance for Weight of Calf Weaned.

(a) Station 1

Source of variation	Degrees of freedom	Mean Squares
Sex	1	33974.6 ***
Year	3	6203.1 ***
Cow-age	2	2671.5 ***
Cow-breed	3	15403.9 ***
Residual	448	699.3

Note: Year x breed, year x age, breed x age and year x age x breed interactions were all non-significant.

(b) Station 2

Source of variation	Degrees of freedom	Mean Square
Sex	1	48854.5 ***
Year	3	23129.7 ***
Cow-age	2	11787.3 ***
Cow-breed	2	60196.3 ***
Year x age	6	1597.6 ***
Year x breed	6	2621.2 ***
Residual	861	758.3

Note: Breed x age and year x age x breed interactions were non-significant.

*** = $P < 0.001$.

TABLE 4.10 Least Squares Means and Standard Errors for the Effect of Breed of Cow on Weight of Calf Weaned – Station 1

	Weight of Calf Weaned (kg)
General Mean	172.8 ± 1.4
Breed	
Nguni	156.6 ± 2.5 ^{a}
Brahman	171.1 ± 2.4 ^{b}
½-Brahman	183.1 ± 2.7 ^{c}
¾-Brahman	180.5 ± 3.0 ^{c}

a,b,c,d Means within the same column with different superscripts differ significantly ($P < 0.01$).

4.3.2 Station 2.

The analysis of variance results (Table 4.9b) indicate that sex, year, cow-age, breed of cow, and the interactions of year x age and year x breed all had a highly significant effect on weight of calf weaned. Preliminary analyses showed that breed x age and year x age x breed interactions were non-significant. The estimated least squares means for the effect of breed x year interaction on weight of calf weaned are presented in Table 4.11.

It is apparent from Table 4.11 that the differences in weight of calf weaned between the Nguni and ½-Brahman cows were significant ($P < 0.01$) in all but one year (year 4), during which the weight of calf weaned by the Nguni cows mated to Brahman sires (178.11kg) was not significantly different from that of the ½-Brahman cows (176.10kg). Otherwise, the half-breds performed significantly better than the Nguni cows and the weight of calf weaned by the Nguni cows nursing straightbred calves was lower ($P < 0.01$) than that of the Nguni cows nursing crossbred calves in all years.

The weight of calf weaned by the ½-Brahman cows was, on average, 13.8 kg higher than that of the Nguni cows bred to the same breed of sire (Brahman), indicating an average advantage of 8 percent for the crossbred cows. An average advantage of 25 percent (39.9 kg) for the

TABLE 4.11 **Least Squares Means and Standard Errors for the Effect of Breed x Year Interaction on Weight of Calf Weaned - Station 2**

Weight of Calf Weaned (kg)

General Mean = 179.1 ± 1.5

Breed	Year 1	2	3	4	Mean
Nguni [1]	148.7 ± 14.1^{a}	166.6 ± 4.6^{a}	157.7 ± 4.2^{a}	155.6 ± 3.7^{a}	157.1 ± 4.0
Nguni [2]	192.9 ± 3.2^{b}	180.7 ± 2.7^{b}	181.3 ± 2.6^{b}	178.1 ± 4.0^{b}	183.2 ± 1.6
½-Brahman	210.5 ± 4.2^{c}	200.0 ± 3.3^{c}	201.5 ± 3.1^{c}	176.1 ± 3.8^{b}	197.0 ± 1.7

[1] Nguni cows mated to Nguni sires.

[2] Nguni cows mated to Brahman sires.

[a,b,c] Means within the same column with different superscripts differ significantly ($P < 0.01$).

crossbred cows compared to the Nguni cows bred to Nguni bulls is indicated by the results of this study. Mason (1966) noted that the full benefit of crossbreeding was not reached until the F_1 cow was used for breeding, when she appeared superior to a straightbred by 10 to 15 percent in weaning weight of calf. Cundiff (1970) indicated advantages for crossbred cows of 5.6% in calf weaning weight.

It is important to note that the weight of calf weaned by the Nguni cows bred to produce crossbred calves was significantly higher than that of the Nguni cows bred to produce straightbred calves in all years. The differences in weight of calf weaned between these Nguni cows are reflections of breed of sire effects rather than maternal genetic effects. These results indicate that crossing Nguni cows to Brahman sires increased the weaning weight of calves by about 17 percent.

4.4 Heritability, Genetic and Phenotypic Correlations and Repeatability Estimates.

4.4.1 Heritability estimates.

Estimates of the heritability of birth, weaning, and 18-month weight for each station are presented in Table 4.12. Estimates of each trait, pooled across stations, are also indicated in the same table. These estimates lie generally towards the lower end of the range of values reported by many workers in the literature (see Table 2.4 to 2.7).

The heritability estimates of birth weight have varied from 0.09 (Willis *et al*, 1972) to 0.75 (Mehta *et al*, 1972) in the reports of cattle raised under tropical and sub-tropical conditions. The estimate of 0.06 obtained in station 1 falls outside this range. However, the value of 0.29 obtained in station 2 is approximately in line with other estimates reported by Lombard (1963), Trail *et al* (1971b), Baharin and Beilharz (1975), Harricharan *et al* (1976) and Ghosh *et al* (1978) in other Zebu and crossbred cattle. It is also comparable to the median value of 0.34 obtained by Preston and Willis (1974). This estimate (0.29) suggests that birth weight has a medium heritability, indicating the scope of genetic change for this trait. However, selection for high birth weight is not desirable because of its close association with dystocia

TABLE 4.12 Estimates and Standard Errors for Heritability of Birth Weight, Weaning Weight, and 18-Month Weight.

Trait	Heritability Estimate		
	Station 1	Station 2	Pooled
Birth weight	0.06±0.10	0.29±0.15	0.13±0.08
Weaning weight	0.09±0.12	0.12±0.08	0.11±0.07
18-month weight	0.53±0.34	0.18±0.11	0.21±0.10

(Preston and Willis, 1974).

Estimates of the heritability of weaning weight were very low in both stations (0.09 and 0.12). Comparable estimates were obtained by Osman and Rizgalla (1968) in Sudan and Trail _et al_ (1971b) in Western Uganda. Otherwise, most of the reported heritability estimates of weaning weight are medium in magnitude (Table 2.6).

In station 1, the heritability estimate of 18-month weight was high (0.53), indicating that selection for this trait would be moderately effective in improving it. The estimate of 0.53 for the heritability of 18-month weight is comparable with most values in the literature. For instance, Dunn _et al_ (1970) found a value of 0.56 for the heritability of 550-day weight in crossbred cattle and Hinojosa and Segura (1980) obtained an estimate of 0.51 for the heritability of 414-day weight in Brahman cattle raised only on natural pastures. Mahadevan and Marples (1961) and Stobbs (1966) also found relatively high estimates for the heritability of post-weaning weights in Zebu cattle. A relatively low estimate of the heritability of 18-month weight was obtained in station 2 (0.18). In Western Uganda, Trail _et al_ (1971b) found a value of 0.11 for the heritability of this trait in crossbred cattle.

The generally low heritability estimates obtained in this study may be attributed to various factors. According to Robertson (1959), the accuracy of the paternal half-sib method is dependent on:

(a) The number of degrees of freedom for sires,

(b) the absence of environmental correlations between half-sibs relative to non-related individuals,

(c) the absence of selection between sires and

(d) the number of progeny per sire (the least important).

The degrees of freedom for sires were very small at both stations (5 and 9) and the sires used represented a rather select group. The use of uncorrected data might have also contributed to the lower estimates since it has been found that unadjusted data give lower estimates than data which have been corrected for the major non-genetic factors (Pattie et al, 1970, Seifert, 1975b, Barlow, 1978). Furthermore, heritability estimates based upon half-sib correlations are subject to considerable error because an error in the coefficient is multiplied four-fold in the estimates (Carter and Kincaid, 1959). The relatively large standard errors of the heritability estimates obtained in this exercise are also due to large sampling errors because of the small number of animals involved.

Heritability estimates of birth and weaning weight obtained in station 1 were lower than those calculated from station 2 data. Lower heritability estimates at early ages suggest that the expression of genes might be masked by maternal environment coupled with other non-genetic factors. It will be noted that in station 2, where the effect of breed of dam on birth weight was non-significant (Table 4.7b), a reasonable estimate of 0.29 was obtained for this trait. In station 1, the effects of breed of dam on birth and weaning weight were highly significant and sires had a non-significant effect on these pre-weaning traits. Trail et al (1971b) noted that growth to weaning, especially under fairly harsh range conditions, is very subject to maternal influences, and that calf genotype effects may be masked to a great degree.

The magnitude of the heritability estimate of 18-month weight was lower in station 2 (0.18) than in station 1 (0.53), suggesting that the general enviromental conditions may have been more severe in the former station. However, since half-sib estimates are greatly influenced by the genetic differences among the sires involved, the vast difference between these values may be due to the fact that variation in 18-month weight due to sires was larger in station 1 than in station 2 (see Table 4.8). The variance components (see Appendix III) also indicated relatively larger components for sires in station 1 (140.39) than station 2 (43.33) for 18-month weight.

4.4.2 Genetic and phenotypic correlations.

Estimates of the genetic and phenotypic correlation coefficients between the traits are presented in Table 4.13. It was not possible to estimate genetic correlations from station 3 data.

In station 1, the genetic correlations between birth weight and weaning weight, birth weight and 18-month weight, and weaning and 18-month weight, were 0.69 ± 0.59, 0.75 ± 0.51 and 1.21 ± 0.25, respectively. Estimates for the genetic correlation between the respective traits were 1.11 ± 0.12, 1.05 ± 0.10 and 1.02 ± 0.08 in station 2. These values indicate a very high positive association between the weights, suggesting that genes which are responsible for early body weight are also responsible for body weight at subsequent ages. However, most of the estimates were greater than 1 and have large standard errors, making them of little value. For instance, the standard error values of 0.25 to 0.59 associated with the estimates from station 1 would indicate caution in putting complete trust in these estimates. It has been observed that estimates of genetic correlations are subject to larger sampling error than are heritability estimates based on the same number of animals (Barlow, 1978, Warwick et al, 1979).

TABLE 4.13 Estimates of the Genetic and Phenotypic Correlation between Weights at Birth, Weaning, and 18-month.

(a) Station 1

Trait	Correlation	Weaning weight	18-month weight
Birth weight	Genetic:	0.69±0.59	0.75±0.51
	Phenotypic:	0.49	0.37
Weaning weight	Genetic:	-	1.21±0.25
	Phenotypic:	-	0.68

(b) Station 2

Birth weight	Genetic:	1.11±0.12	1.05±0.10
	Phenotypic:	0.22	0.21
Weaning weight	Genetic:	-	1.02±0.08
	Phenotypic:	-	0.65

(c) Station 3

Birth weight	Phenotypic:	0.08	0.00
Weaning weight	Phenotypic:	-	0.74

(d) Pooled Estimates

Birth weight	Genetic:	1.08±0.12	1.03±0.10
	Phenotypic:	0.27±0.02	0.21±0.02
Weaning weight	Genetic:	-	0.92±0.07
	Phenotypic:	-	0.67±0.02

Otherwise, the fact that the genetic correlation coefficients obtained in both stations were all positive should suffice in indicating that selection for any of these traits should result in correlated improvement in the others. High positive genetic correlations between body weights in cattle have been reported by various authors (Preston and Willis, 1974, Barlow, 1978). Genetic correlation values ranging from 0.82 to 1.04 between birth and weaning weight have been reported by Berruecos and Robison (1968), Trail et al (1971b), Heyns (1977) and Govindaiah and Singh (1980). Trail et al (1971b) and Seifert (1975b) obtained high values of the genetic correlation between birth and 18-month weight (0.81 and 0.59, respectively). The results of these latter authors and those of Francoise et al (1973) also indicated a very high genetic correlation between weaning weight and 18-month weight (0.61 to 0.95).

The phenotypic correlation between birth and weaning weight were 0.49 and 0.22 in stations 1 and 2, respectively and estimates of 0.37 and 0.21 between birth and 18-month weight were obtained for the respective stations. These correlations indicate that variation in birth weight accounted for 24 and 14 percent of the variation in weaning and 18-month weight, respectively in station 1. In station 2, the variation in birth weight accounted for only 5 and 4 percent respectively, of the variation in weaning and 18-month weight.

The correlation coefficients obtained in these two stations are more or less similar to those reported in the literature. Naude (1965) found a phenotypic correlation coefficient of 0.42 between birth and weaning weight in Nguni cattle. Values of 0.34 (Trail et al, 1971b), 0.27 (Seifert, 1975b), 0.21 (Heyns, 1977) and 0.25 (Govindaiah and Singh, 1980) for the phenotypic correlation between birth and weaning weight have been obtained in studies involving other tropical and subtropical cattle. The correlation coefficient for birth and 18-month weight appear to be generally lower than those for birth and weaning weight, indicating a closer association between the pre-weaning growth traits due to common environmental influences (mainly maternal). Govindaiah and Singh (1980) noted that the magnitude of the phenotypic association between birth weight and post-weaning weights were not significantly different from zero. They found a phenotypic correlation coefficient of 0.05 between birth and 18-month weight.

In station 3, the phenotypic correlations between birth weight and weaning weight (0.08) and birth weight and 18-month weight (0.00) were essentially zero, indicating that there was no association between birth weight and later weights. Since genes responsible for pre-natal growth are also responsible for post-natal growth (Chapter 2), the low coefficients obtained here might be reflections of a strong negative environmental correlation between pre- and post-natal growth at this station. Most of the cows transferred from the other ranches to station 3 and those purchased from various sources were in calf when they joined the breeding herd. Thus, the dams of the majority of calves born in station 3 were in the main exposed to different environmental conditions during the gestation period and afterwards. This may have contributed to a strong negative environmental correlation between birth weight, which is a measure of pre-natal growth, and later weight.

The phenotypic correlation coefficients between weaning and 18-month weight were fairly high and positive, suggesting a close association between the weaning (210 days) weight and 18-month weight of calves. The values of 0.68, 0.65 and 0.74 obtained for the phenotypic correlation between weaning and 18-month weight in stations 1, 2 and 3, respectively, indicate that variation in weaning weight accounted for 46, 42 and 55 percent of the variation in 18-month weight at the respective stations.

4.4.3 Repeatability estimates.

The intra-class correlation repeatability estimates of weaning weight of calf as a trait of the dam are presented in Table 4.14 for each breed of dam. Repeatability estimates were 0.24±0.12, 0.27±0.13, 0.25±0.11 and 0.39±0.13 for the Nguni, Brahman, $\frac{1}{2}$-Brahman and $\frac{3}{4}$-Brahman dams, respectively. These estimates fall

TABLE 4.14 Intra-class Correlation Repeatability Estimates of Weight of Calf Weaned - Station 1

Breed	No. of Cows	Repeatability estimate
Nguni	50	0.24 ± 0.12 (114)*
Brahman	68	0.27 ± 0.13 (124)
½-Brahman	42	0.25 ± 0.11 (115)
¾-Brahman	57	0.39 ± 0.13 (102)

* Figures in parentheses indicate total number of records.

within the range of values reported in the literature (Table 2.13). They are, however, lower than the estimates obtained in Uganda (0.39 - 0.47) by Trail et al (1971b) and Zambia (0.46 - 0.62) by Thorpe et al (1980a), using the same method of estimation. Nevertheless, they do indicate that the weight of calf weaned is a moderately repeatable character, suggesting that a cow weaning a heavy calf is likely to do so throughout its lifetime.

In station 2 the repeatability estimates were computed by the regression technique. Table 4.15 presents these estimates for each breed of dam. The regression coefficients on the diagonal refer to records which are separated by one year. The off diagonal estimates are separated by two or more years.

It is apparent from Table 4.15 that there were no consistent differences between the estimates obtained at the different degrees of adjacencies. The trend for repeatability estimates to decrease as the degree of adjacency increased noted by Cunningham and Henderson (1965), Boston et al (1970) and Vanmiddlesworth et al (1977) was not indicated by these results, possibly because of the small number of pairs involved. Also some of the estimates were negative, presumably because of the relatively small number of pairs involved.

TABLE 4.15 **Regression Repeatability Estimates of Weight of Calf Weaned computed from Pairs of Records of Different Degrees of Adjacency and from Cows of Different Ages.**

(a) Nguni cows.

Age of dam (first record)		Age of dam (second record) 3	4	5	6	7	8	9	10+
2	Repeatability	0.31	-0.18	-	-	-	-	-	-
	Pairs of records	18	14						
3	Repeatability		0.12	0.12	0.07	-	-	-	-
	Pairs of records		20	13	12				
4	Repeatability			0.21	0.46	-0.01	-	-	-
	Pairs of records			31	34	12			
5	Repeatability				0.30	0.23	-	-	-
	Pairs of records				34	15			
6	Repeatability					0.52	0.38	-0.20	-
	Pairs of records					30	10	5	
7	Repeatability						0.78	-0.12	-
	Pairs of records						14	9	
8	Repeatability							0.38	0.40
	Pairs of records							15	9
9	Repeatability								0.33
	Pairs of records								9

TABLE 4.15 Continued

(b) $\frac{1}{2}$ - Brahman cows.

Age of dam (first record)		Age of dam (second record)						
		3	4	5	6	7	8	9
2	Repeatability	0.24	0.08	1.36	-	-	-	-
	Pairs of records	9	8	5				
3	Repeatability		0.40	0.19	-0.05	-	-	-
	Pairs of records		38	40	15			
4	Repeatability			0.09	-0.13	0.51	-	-
	Pairs of records			34	18	5		
5	Repeatability				0.10	-0.20	-	-
	Pairs of records				22	4		
6	Repeatability					-0.22	-0.12	0.56
	Pairs of records					9	5	4
7	Repeatability						0.49	0.44
	Pairs of records						4	3
8	Repeatability							0.18
	Pairs of records							4

TABLE 4.16 Pooled Regression Repeatability Estimates of Weight of Calf Weaned - Station 2

Breed	No. Pairs	Repeatability
Nguni	304	0.29 ± 0.17
½-Brahman	227	0.19 ± 0.28
Both breeds	531	0.24 ± 0.15

Because there were no differences in estimates among the levels of separation (see Table 4.15), all estimates were then pooled within and across breeds. The resulting pooled estimates (Table 4.16) show values of 0.29 and 0.19 for the repeatability of weight of calf weaned for the Nguni and $\frac{1}{2}$-Brahman dams, respectively. The pooled estimate for the two breeds was 0.24. These estimates are in close agreement with those obtained in station 1 using the intra-class correlation technique and they also fall within the range of values reported in the literature. The regression estimates of repeatability are said to be unbiased and not affected by selection based on earlier records (Curnow, 1961). However, bias due to selection of dams for superior mothering ability should be minimal even in the intra-class correlation estimates because virtually all culling carried out at each station was for poor fertility, disease, or old age. The magnitude of the repeatability estimates obtained in this study is medium, indicating that selection for high-producing cows can be practiced early in their productive life.

4.5 The Association Between 14- and 18-month weight.

Investigation of the feasibility of changing the performance test age of breeding stock from 18-months to 14-months warranted the estimation of the heritability of these post-weaning weights and the genetic and phenotypic correlations between them. The results are presented in Table 4.17. It is important to note that these estimates are based on fewer observations than those obtained in the previous sections. However, the degrees of freedom for sires were the same in all analyses.

The heritability of 14- and 18-month weight, respectively, were 0.19 ± 0.17 and 0.56 ± 0.30 in station 1. Estimates of 0.07 ± 0.09 and 0.19 ± 0.15 were obtained for the respective traits in station 2. These values indicate that 18-month weight is more heritable than 14-month weight.

Estimates of the genetic correlations were above unity and had large standard errors at both stations, due to large sampling error because of the small number of observations. However, the positive estimates are indications that, despite large sampling errors, growth at both ages was controlled by many of the same genes. High positive genetic correlations between various post-weaning weights have been reported in the literature (see Table 2.12).

The phenotypic correlation coefficients between 14- and 18-month weight were 0.59 and 0.51 in stations 1 and 2, respectively, indicating that 14-month weight accounted for 35 and 26 percent of the variation in 18-month weight at the respective stations. These correlations suggest that animals ranking high in 14-month weight are likely to rank high in 18-month weight.

TABLE 4.17 Estimates of the Heritability and the Genetic and Phenotypic Correlations between 14- and 18-month weights.

	Heritability		Correlation	
	14-month weight	18-month weight	Genetic	Phenotypic
Station 1	0.19±0.17	0.56±0.30	1.15±0.74	0.59
Station 2	0.07±0.09	0.19±0.15	1.30±0.43	0.51
Pooled	0.10±0.08	0.27±0.13	1.19±0.37	0.55±0.05

The feasibility of using 14-month weight as an alternative selection criterion for 18-month weight (indirect selection) in this study may be assessed by considering the genetic correlation between 14- and 18-month weights and the heritabilities of these traits (Falconer, 1960, Searle, 1965, Pirchner, 1969). A high genetic correlation indicates that, on average, an animal selected as having high genetic merit for the alternative trait will be high in genetic merit for the basic trait. The relative efficiency of the direct and indirect method of selection in terms of genetic gain, can be compared by calculating the ratio of the gains:

$$\frac{\Delta GI}{\Delta GD} = r_g \frac{h_{440\text{-day}}}{h_{540\text{-day}}}$$

where,

ΔGI and ΔGD is the gain by indirect and direct selection, respectively,

r_g is the genetic correlation between 14- and 18-month weights, and

$h_{440\text{-day}}$ and $h_{540\text{-day}}$ is the square root of the heritability of the alternative (14-month weight) and basic (18-month weight) trait, respectively.

Indirect selection (disregarding husbandry and economic considerations), will only be more effective than direct selection if r_g is high and $h_{440\text{-day}} > h_{540\text{-day}}$ (Searle, 1965, Turner and Young, 1969). It is apparent from

Table 4.17 that the ratio of (gain in 18-month weight under indirect selection for 14-month weight) to (gain in 18-month weight under direct selection) would be subject to considerable uncertainty since each of the parameter estimates has rather large sampling error and the genetic correlation estimate is greater than 1. The heritability of 18-month weight (0.27) appears to be much greater than that of 14-month weight (0.10), indicating that selection for the latter trait might not be as effective as when 18-month weight was used as a selection criterion. However, it is important to note that selection for 14-month weight would be desirable because it would enable animals to be disposed of earlier without costly maintenance. Indirect selection on 14-month weight would also lower the generation interval, thus increasing the annual rate of genetic gain (Falconer, 1960, Turner and Young, 1969, Dalton, 1980).

CHAPTER FIVE

CONCLUDING DISCUSSION

This study was undertaken primarily to compare the growth and maternal performance of the Nguni and crossbred cattle in the Swaziland Government breeding stations. According to reviews of research on growth of cattle in Southern Africa (Naude, 1965, Maule, 1973), it is well established that the growth ability of the straightbred Nguni is relatively low. It is thus reasonable to expect an increased growth potential in the progeny of Nguni crossed to other breeds with high growth rates. The present work has shown remarkable improvement in growth performance due to crossbreeding the Ngunis with the exotic Brahmans and Simmentals. The superiority of the Brahman crossbreds over the Ngunis ranged from 10 to 29 percent at weaning and 10 to 34 percent at 18-months. Increases of 10 to 23 percent in weaning weight and 8 to 22 percent in 18-month weight were obtained by crossing the Nguni cows with the Simmental sires. It was also found that the straightbred Brahmans and Simmentals are superior in liveweight to the straightbred Ngunis. The advantage of the crossbreds may be due to additive gene effects as well as heterotic effects.

There is no evidence from Swaziland on the value of crossbreeding for increasing the productivity of beef cattle, but several experiments carried out in some other Southern African States have shown substantial improvement in a number of productive traits (Trail et al 1977, APRU, 1978, Thorpe et al, 1979, 1980 a,b). Since early sexual maturity, which in turn depends to a large extent on body weight, is useful in female progeny retained as herd replacements, crossbreeding should help to improve reproductive efficiency by reducing the time for the females to reach puberty. In the case of males, the advantage of superior growth to 18-months means that the animals will reach acceptable weight for slaughter at a younger age when the carcass has a greater proportion of the desired lean meat relative to fat (Preston and Willis, 1974). The liveweight advantages for Brahman and Simmental crosses with the Nguni also suggest that carcass weight advantages will occur with crosses sired by these exotic breeds. In Zambia, Thorpe et al (1979) found that the use of exotic breeds for crossbreeding was clearly advantageous in growth and carcass production. The crossbred progeny were superior to the Angoni, Barotse, and Boran straightbreds in their study, giving on average +19, +16, and +14 percent more carcass, respectively.

It has been established that crossbreeding offers a rapid means of improving maternal ability and that this will apply even to breeds which differ little in this trait (Cundiff, 1970, Preston and Willis, 1974, Bishop, 1975). The present study has found that crossbred cows have a superior maternal performance to straightbreds. Half-bred cows were 8 to 25 percent better than straightbred Nguni cows in weight of calf weaned in the present study. Studies in Botswana (APRU, 1978), Uganda (Sacker *et al*, 1971b,c) and Zambia (Thorpe *et al*, 1980 a,b) have all clearly indicated the superiority of crossbred dams to straightbreds in reproductive performance and maternal ability.

Investigations on the potential role of the currently recommended breeds and the resultant crossbreds in beef cattle production improvement in Swaziland are still continuing, and findings presented here are definitely provisional. Further comparisons are needed to substantiate the results of the present study. There are indications that a criss-cross system involving Brahman and Nguni cattle might be valuable. Investigations on a three-way cross system whereby Simmental bulls are mated to Brahman x Nguni F_1 cows are underway in station 2 and it is hoped that preliminary results on the growth performance of the three-breed progeny will soon be available. The use of first-cross, small-sized dams mated to large sire breeds could increase cow slaughter productivity and efficiency, through heterosis for dam reproductive and maternal abilities, and for calf survival and growth (Dickerson, 1973, Cundiff, 1980).

It may be pointed out, however, that growth performance of animals is by no means the only criterion by which the potential of various breeds for crossbreeding with the Nguni, as well as their ultimate usage in crossbreeding systems, can be evaluated. While the results of this study have shown large advantages in growth performance resulting from crossbreeding, final recommendations on inter-breed selection and crossbreeding must consider all phases of the production cycle. Rennie _et al_ (1977) have shown that low reproductive performance and maternal ability are the main factors that depress productivity of cattle in Botswana. The relatively superior maternal performance of the crossbred cows to the straightbred Nguni, Brahman, and Simmental, indicated by the present findings should be verified in subsequent studies. Comparative mortality rates, relative reproductive efficiencies, and lifetime productivities of straightbred and crossbred progeny must all be considered.

There are indications that Simmental-sired progeny are better than Brahman-sired progeny in growth to

18-months of age. Similar findings were reported by the APRU (1978) in Botswana. Less encouraging though is the fact that large sire breeds tend to cause more calving difficulties than smaller breeds, mainly because the calves are heavier at birth (Preston and Willis, 1974, Smith *et al*, 1976). In the present study, Simmental-sired calves were on average 27 and 38 percent heavier at birth than those sired by the Brahman and Nguni, respectively. It may thus be necessary to investigate the incidence of dystocia especially in station 3 where the relatively small Nguni cows are mated to the large Simmental sires. The fertility of cows is detrimentally affected by dystocia and the production of heavy calves (Laster *et al*, 1973, Smith *et al*, 1976, Barlow, 1978). In South Africa, however, Joubert *et al* (1977) observed that the incidence of dystocia was not very high when Simmentals were mated to the indigenous Africander mainly because Africander cows are easy calvers.

It has been found in the present study that the interaction between breed and year was important in stations 2 and 3, suggesting that comparison of the breeds and crosses for growth would be more dependable if based on data collected over many years. Some reasons for the differential responses of the breeds and crosses to year effects in station 3 were discussed in Chapter 4. However, there is a need for more detailed investigations as to the cause of the interactions at both stations.

The present investigation has also revealed that sire x breed of dam interactions were non-significant, suggesting that progeny testing of sires within crossbred populations would be as effective as evaluating sires on the basis of straightbred progeny. These findings have important practical implications in progeny testing of sires where the breeding herd involves straightbred and crossbred cows.

The results on the influence of environmental factors on the growth traits showed that weight records need to be corrected for effects due to year, sex, month of birth, and age of dam, to ensure an accurate comparison between and within breeds. The most important factor which emerged and may be controlled to a certain extent by management was the influence of month of birth on calf growth from birth to 18 months of age. Calves born during the last month of the 4-month calving season were 12 to 18 percent and 8 to 12 percent lighter than earlier-born calves at weaning and 18-months, respectively. The heaviest animals at 18-months of age were those born in October and November in stations 1 and 2, and September and October in station 3. A need to have a more compact calving season is indicated by these results, and, regulation of the breeding season to prevent cows from calving after November would avoid the unfavourable consequencies of seasonal variation on calves born after that time.

An important objective of beef cattle breeding research is the estimation of genetic interrelationships of important traits in order that selection indices permitting maximum progress may be constructed. Heritability, in addition to being an important factor in the prediction of genetic progress, determines the reliability of the phenotypic value as an indicator of the individual's breeding value (Falconer, 1960). Since mass selection in beef cattle has recently been launched on a national basis in Swaziland, a definite need exists for estimates of genetic parameters applicable to local populations. In the present work most of the genetic correlation estimates exceeded unity and had relatively high standard errors. The pooled heritability estimates of 0.13, 0.11 and 0.21 for birth, weaning, and 18-month weight, respectively, are lower than most values reported in the literature, partly because there were few sires involved and possibly because they are based on a relatively small set of data. The heritability estimate of 0.53 for 18-month weight obtained in station 1 is, however, comparable with most reported values and it suggests that considerable progress can be made for this economically important trait through mass selection. There are indications that the heritability of weaning weight is much lower than that of 18-month weight, suggesting that in order to achieve a reasonable amount of genetic progress, the selection programme should give more emphasis on 18-month weight. Furthermore, desired improvement in weaning weight is to be expected when selecting for 18-month weight because of the high genetic correlations between these traits. The phenotypic correlation estimates between weaning and 18-month weight obtained in this study indicate that weaning weight accounted for 42 to 55 percent of the variation in 18-month weight. More work is required to determine whether weaning weight may be a useful criterion for preliminary culling during severe years.

It is well known that the economic worth of a beef cow is determined by her ability to consistently wean heavy calves. Several important practical questions are involved in considering the repeatability of cow performance with respect to growth rate of calves to weaning. Among these are the extent to which the growth rate of the first calf is a permanent characteristic of the cow, and the amount of culling that can safely be done on the basis of the first calf produced. The present study indicates that cows weaning heavy calves are likely to do so in future crops and vice versa, suggesting that selection for high-producing cows can be practiced early in their productive life. The repeatability estimates of weight of calf weaned obtained in this investigation are medium in magnitude (0.24 to 0.39).

The present study also investigated the feasibility of changing the current age at which animals are performance tested for growth in the Government breeding stations (540 days) to 14 months of age (440 days). Selecting bulls and heifers on their adjusted 540-day weight has presented some managerial problems in that it has not been feasible for the DIU to generate and distribute the selection listings (see Section 3.1.1) to the breeding stations early enough to enable the ranch managers to cull undesirable animals before the dry winter season. Selection for 14-month weight, on the other hand, would make it possible for selection decisions to be made before the beginning of autumn each year instead of in July or August and below average animals would, therefore, be disposed of before the winter feed shortage. The findings presented here, indicate that animals superior for 14-month weight are likely to be superior for 18-month weight and *vice versa*, suggesting that there would be negligible differences in the rating of animals at those two ages. Selection for 14-month weight would also be expected to result in correlated improvement in 18-month weight because of the positive genetic correlation between these weights. The heritability of 14-month weight (0.10) appears to be much lower than that of 18-month weight (0.27). However, it was not possible to assess the relative efficiency of indirect selection for 14-month weight to direct selection for 18-month weight because the genetic parameter estimates were unreliable.

Additional investigations are needed to substantiate the results obtained before any decisions may be made.

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APPENDIX I

Monthly and annual rainfall data (mm) for the three breeding stations during the period 1974 - 1978.

Year	Month	Mpisi	Lowveld	Highveld
1974/75	October	34.4	24.3	53.5
	Nov.	122.9	53.5	153.5
	Dec.	251.5	139.0	179.0
	Jan.	181.0	116.0	94.0
	Feb.	231.0	62.4	215.5
	Mar.	167.5	37.6	94.5
	Apr.	66.5	27.2	87.5
	May	55.5	12.8	45.5
	June	2.0	Nil	Nil
	July	Nil	Nil	5.5
	Aug.	5.0	3.0	Nil
	Sept.	Nil	2.4	Nil
	Total	1117.3	478.2	928.5
1975/76	Oct.	62.5	89.0	100.0
	Nov.	163.5	121.5	83.5
	Dec.	93.5	75.5	58.5
	Jan.	52.5	82.9	72.0
	Feb.	155.0	170.3	161.5
	Mar.	75.5	78.1	98.0
	Apr.	9.0	13.6	30.5
	May	2.0	15.5	4.0
	June	Nil	4.5	Nil
	July	Nil	Nil	Nil
	Aug.	12.0	6.5	Nil
	Sept.	34.0	56.9	107.5
	Total	659.5	714.3	715.5

Appendix I (continued)

Year	Month	Mpisi	Lowveld	Highveld
1976/77	Oct.	40.5	Nil	11.0
	Nov.	75.5	38.0	168.5
	Dec.	159.5	26.4	41.5
	Jan.	79.4	99.9	273.5
	Feb.	39.2	60.0	124.5
	Mar.	115.0	173.7	96.5
	April	31.0	42.5	84.0
	May	54.9	26.7	17.5
	June	Nil	1.5	Nil
	July	21.0	20.6	22.5
	Aug.	6.5	Nil	14.0
	Sept.	24.5	22.5	60.5
	Total	646.5	511.8	914.0
1977/78	Oct.	116.0	68.0	107.5
	Nov.	49.5	144.3	185.5
	Dec.	49.1	86.1	56.0
	Jan.	2.0	74.3	124.0
	Feb.	2.0	2.7	78.0
	Mar.	76.0	–	103.0
	Apr.	–	–	–
	May	–	–	16.0
	June	–	–	–
	July	–	–	–
	Aug.	65.0	–	16.0
	Sept.	34.0	36.0	47.0
	Total	393.6	411.4	733.0

APPENDIX II

Table 1: The distribution of numbers of observations in each subclass for Station 1.

	Years				
Breed	1	2	3	4	Total
Nguni	16	31	26	35	108
Brahman	18	35	18	50	121
¾ Brahman	24	31	29	30	114
⅞+ Brahman	13	28	10	50	101
Total	71	125	83	165	444
Month born					
Up to Sept.	9	58	29	4	100
October	24	46	21	64	155
November	29	13	26	67	135
December +	9	8	7	30	54
Dam Age					
2-3 year-olds	27	34	23	58	142
4-6 year-olds	27	66	42	67	202
7+ years	17	25	18	40	100
Sex					
Female	32	64	38	88	222
Male	39	61	45	77	222
Total	71	125	83	165	444

Table 2: The distribution of numbers of observations in each subclass for Station 2.

Breed	Years				
	1	2	3	4	Total
Nguni	4	36	42	56	138
$\frac{1}{2}$ Brahman	131	114	119	59	423
$\frac{3}{4}$ Brahman	68	77	85	78	308
$\frac{7}{8}$+ Brahman	5	4	13	25	47
Total	208	231	259	218	916
Month Born					
Up to Sept.	5	24	68	18	115
October	46	88	64	64	262
November	107	55	79	76	317
December +	50	64	48	60	222
Total	208	231	259	218	916
Dam Age					
2 year-olds	13	22	37	42	114
3 year-olds	38	55	51	30	174
4-6 years	106	77	99	85	367
7+ years	51	77	72	61	261
Total	208	231	259	218	916
Sex					
Female	109	118	127	104	458
Male	99	113	132	114	458
Total	208	231	259	218	916

Table 3: The distribution of numbers of observations in each subclass for Station 3.

Breed	Years			
	1	2	3	Total
Nguni	58	50	47	155
Simmental	38	55	89	182
$\frac{1}{2}$ Simmental	14	21	10	45
$\frac{3}{4}$ Simmental	3	8	6	17
$\frac{7}{8}$+ Simmental	0	14	13	27
$\frac{1}{2}$ Brahman	15	28	3	46
Total	128	176	168	472
Month Born				
Up to August	70	57	16	143
September	25	46	35	106
October	12	48	62	122
November +	21	25	55	101
Total	128	176	168	472
Dam Age				
2 & 3 year-olds	30	26	40	96
4 - 6 years	68	113	106	287
7 + years	30	37	22	89
Total	128	176	168	472
Sex				
Female	64	85	84	233
Male	64	91	84	239
Total	128	176	168	472

APPENDIX III

Estimates of variance and covariance components for birth weight (BWT), weaning weight (WWT) and 18-month weight (18-MTH)

(a) Station 1.

Trait	σ^2_s	σ^2_e	σ_{12s}	σ_{12e}	σ_{13s}	σ_{13e}	σ_{23s}	σ_{23e}
BWT(1)	0.31	19.53						
			1.38	54.51				
WWT(2)	13.02	540.02						
					4.90	52.01		
18-MTH (3)	140.39	919.82					51.61	488.01

(b) Station 2.

Trait	σ^2_s	σ^2_e	σ_{12s}	σ_{12e}	σ_{13s}	σ_{13e}	σ_{23s}	σ_{23e}
BWT(1)	2.27	29.03						
			7.39	27.60				
WWT(2)	19.34	628.54						
					10.42	30.63		
18-MTH (3)	43.33	936.08						
							29.41	488.04