TITLE

GROWTH AND SURVIVAL TO WEANING OF CROSSES OF AYRSHIRE, BROWN SWISS AND SAHIWAL CATTLE

BY

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DECLARATION

This thesis is my original work and has not been presented for a degree in any other University.

Signed ....

This thesis has been submitted with our approval as University supervisors:

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ABSTRACT

A total of 1443 records from a private ranch in the coastal lowland tropics of Kenya were used to estimate the comparative calf performance to weaning of the different crosses of Ayrshire (A), Brown Swiss (B) and Sahiwal (S). Individual and maternal additive and heterotic effects for, and heritabilities of, and correlations among, the preweaning traits were also estimated.

A fixed effects least squares model was used for analysis of growth traits while a logistic model was employed in the analysis of survival rate (SRATE). Linear coefficients for breed and heterosis effects were substituted for genetic group effects to estimate individual and maternal additive genetic and heterotic effects. Heritabilities were estimated by derivative-free restricted maximum likelihood procedure in a univariate analyses fitting an animal model. Genetic and phenotypic correlations were estimated by paternal half-sib procedures.

Mean birth weight (BWT) was 30.9 ± 0.18 kg, 93% of calves survived to weaning, and mean preweaning average daily gain (PADG) was 488 ± 2.10 g/day. Calves took an average of 126 days to reach the mean weaning weight of 92 kg.

The effect of breed of sire was not statistically significant ($P>0.05$) for any of the preweaning traits. The effect of dam genotype was only statistically significant ($P<0.001$) for BWT with calves from three-breed cross dams having heavier BWT than those from two-breed rotational dams. Calf genotype had a significant effect ($P<0.001$) on BWT. BWT tended to increase as the percentage of *Bos taurus* genes increased. Mating system significantly ($P<0.01$) affected BWT and PADG with the two-breed rotational crosses having lower BWT and higher PADG than the three-breed rotational crosses, although the scale of the post-natal differences were small. The individual and maternal additive genetic effects for A and S were not significant ($P>0.05$) for any of the traits. Similarly, the individual heterotic effect of *B. taurus* - *B. indicus* heterozygosity was not significant ($P>0.05$) for calf performance. A small effect of AS individual heterosis on PADG was found. It was estimated that F_1 AS calves gained 26 g/day faster ($P<0.1$) than the mean of the purebred A and S calves. The maternal heterotic effect of *B. taurus* - *B. indicus* heterozygosity for BWT was -3.19 ± 1.25 kg and of opposite sign to estimates reported in the literature.

Heritability estimates were 0.14 ± 0.08 for BWT, 0.21 ± 0.08 for PADG, 0.24 ± 0.09 for WAGE and 0.01 ± 0.07 for SRATE. The genetic and phenotypic correlations between PADG and WAGE were high and negative (-0.87 ± 0.49 and -0.74, respectively), indicating that a high PADG

resulted in a desirable younger WAGE.

In this production environment, selection on PADG is likely to yield genetic progress. Both additive genetic breed differences and heterosis effects were small in the *B. taurus* - *B. indicus* heterozygosity, possibly due to the favourable feeding and management conditions. The absence of any major variation among calf genotypes showed that the individual and maternal breed and heterotic effects of the sire breeds and dam genotypes summed to give very similar aggregate preweaning performance for all traits except BWT. Therefore, in this herd, no emphasis should be given to preweaning performance when selecting among these sire breeds and mating systems. These decisions will be determined by relative lactation and reproduction performances. It is concluded that while crossbreeding results in improvement in the performance of the current generation, continued improvement of performance will require an efficient within-breed selection programme for the economically important production traits.

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DEDICATION

This thesis is dedicated to my parents, brothers and sister.

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1. INTRODUCTION

The indigenous African cattle breeds do not have high genetic merit for milk production (Mahadevan et al., 1962). Natural and artificial selection have emphasized survival under the climatic, disease, and nutritional conditions that prevail in the region. Under these circumstances most breeds of cattle in Africa are classified as beef or dual-purpose. In pursuit of commercial profits and increased milk availability on the continent, there has been considerable importation of exotic (*Bos taurus*) breeds of dairy cattle to Africa. The results have been partially successful in tropical highland and sub-tropical regions (Mahadevan and Hutchinson, 1964; Kiwuwa, 1974). Where *B. taurus* dairy breeds have performed poorly, their failures has been attributed to seasonal fluctuations in quality and quantity of pasture feeds, disease incidence and lack of adequate technology for modern dairy cattle management. Hence, it has been suggested that crossbreeding between exotic (*B. taurus*) and indigenous (*Bos indicus*) breeds should be pursued for the genetic improvement of dairy production under most tropical conditions (Cunningham and Syrstad, 1987). Crossbreeding permits the introduction of imported germplasm within the constraints of slowly changing local farming conditions.

B. taurus dairy cattle were introduced into East Africa in the 1900's. Since then the dairy industry has developed using them as purebreds and as crosses with indigenous Zebu breeds (e.g., Small East African Zebu (EAZ) and Boran (BN)). The dominant exotic cattle breed is the European Friesian (F). Other breeds include:- Ayrshire (A), Jersey, Guernsey and Brown Swiss (B). *B. indicus* breeds in the region, e.g., Sahiwal (S) and Small East African Zebu (EAZ) have lactation milk yields ranging from 500 to 1500 kg; it appears from studies that the EAZ has only about half the genetic potential of the S for milk production (Mahadevan et al., 1962). These *B. indicus* breeds are generally well adapted to the climatic, nutritive and disease environments of the major ecological zones of Africa (Kiwuwa, 1987).

Many breeds of *B. taurus* cattle have the additive genetic merit to produce large amounts of both milk and meat (Gregory and Trail, 1981). For this potential to be realized, they need an environment similar to that found in the temperate zones. In the tropical lowlands of Africa this will entail the modification of the harsh environment. This is not economically and technically feasible in many situations. Thus, the challenge is to combine specific breeds of *B. taurus* and *B. indicus* cattle to achieve the optimum genetic composition for production in the current environment. Crossbreeding, although a threat to indigenous animal genetic resources (Rege, 1992), has become increasingly accepted and recommended for commercial beef and milk production. In addition to potential additive and heterotic benefits from crossbreeding, the wide variety of cattle types currently available allows considerable flexibility in matching complementary breed types to local environmental resources and constraints (Gregory and Cundiff, 1980).

Crossbreeding involves the mating of two or more breeds. Methods of systematic crossbreeding include terminal sire crossing, of which there are several variations including recreation of the F_1 in each generation, and three way crossing, rotational crossing and combinations of terminal crossing and rotational crossing (FAO, 1982). Willham (1970) has documented the consequences of crossbreeding in domestic livestock. The basic objective of crossbreeding systems in cattle is to make optimal use of both nonadditive (heterosis) and additive (breed difference) effects of genes (Gregory and Cundiff, 1980; Plasse, 1983; Swan and Kinghorn, 1992).

The S breed is adapted to several ecological zones and was introduced into Kenya from Pakistan in the early 1930's. It has been utilized in crossbreeding (Mahadevan et al., 1962; Kimenye and Russell, 1975) to improve genetically milk and meat production and to supply stock for A.I and natural mating in pure and crossbreeding systems in coastal, semi-arid and arid inland areas (Meyn and Wilkins, 1974). Among the *B. indicus* breeds, S is considered unequalled in additive effects for milk production. Preweaning performance of crosses having different proportions of the breed in several ecological zones in the tropics and sub-tropics is well documented :- with F (Mwandotto, 1978; Kang'ethe, 1990), A (Kimenye and Russell, 1975;

Mwandotto, 1978; Gregory and Trail, 1981; Trail and Gregory, 1981b, 1982; Kang'ethe, 1990), BN (Trail and Gregory, 198la, 1981b), EAZ (Mwandotto, 1978; Trail and Gregory, 1981b); but there are no reports of the comparative preweaning performance of crossbreds with various proportions of A, B and S genes and few estimates of the individual and maternal additive genetic and heterotic components of performance. These estimates are needed together with their interaction with different environment and management systems (levels).

At Kilifi Plantations, the source of the data for this study, some use has been made of the B breed in a crossbreeding programme with S and A for dairy production (**Figure 3.1**) which is the major breeding and production goal. However, since the inception of this crossbreeding programme, there has been no comprehensive analyses of the calf growth and mortality data to obtain estimates of genetic and phenotypic parameters (heritabilities and correlations). Thus, estimates for these breed crosses under the specific production environments (rearing system) are needed. Kilifi Plantations lies in the coastal lowland cashewnut-cassava agro-ecological zone (Jaetzold and Schmidt, 1983), with a relatively favourable nutritive environment but a rather stressful climate (Trail and Gregory, 1981b).

The overall objective of this study is to evaluate the comparative preweaning performance of dairy crosses in coastal lowland Kenya. The specific objectives are:-

(i). To estimate the comparative calf performance to weaning of different crosses of the A, B and S breeds. The influence of environmental factors will be estimated concurrently. The traits will be:- birth weight (BWT), preweaning average daily gain (PADG), weaning age (WAGE) and survival rate to weaning (SRATE).

(ii). To estimate the individual and maternal additive genetic and heterotic effects for these preweaning traits.

(iii). To estimate heritabilities of, and correlations among, the calf preweaning traits.

2. LITERATURE REVIEW

The productivity of and profit from any milk or beef production enterprise will be influenced by the preweaning performance of the calves. Thus, accurate estimates of this performance for different sources of germplasm and mating systems are necessary for designing effective breeding programmes to improve the efficiency of these enterprises for preweaning performance in tropical dairy production. Information is needed on the expected performance of the available breeds and their crosses for the economically important characters at specific levels of resource availabilities and management and in discrete geographic areas and climatic conditions. The economically important characters for preweaning performance are birth weight (BWT), preweaning average daily gain (PADG), weaning weight (WWT) or weaning age (WAGE) and survival rate to weaning (SRATE).

2.1. Birth Weight.

BWT has been shown to be influenced by genetic and environmental (non-genetic) factors.

2.1.1. Genetic factors

BWT is influenced by the genes received from the sire and dam (direct effects), by the maternal environment provided by the dam (maternal effects) and by interactions among direct and maternal effects. Calves sired by bulls of large mature size tend to be heavier at birth than the calves sired by bulls of smaller size (Pahnish et al., 1969; Crockett et al., 1978a; Dhuyvetter et al., 1985; Nadarajah et al., 1985). Breed of sire differences reflect differences in additive direct effects between breeds. Some of these heavy sire breeds include :- Charolais, Santa Gertrudis, Simmental, South Devon and F. Heavy BWT are associated with increased mortality due to dystocia. In their survey of dystocia rates, Laster et al. (1973) reported that calves sired by the Simmental, South Devon, Charolais and Limousin bulls caused significantly more dystocia, 32.7, 32.3, 30.9 and 30.8%, respectively, than calves sired by Hereford, Angus and Jersey bulls, 15.8, 9.9 and 6.5%, respectively. Of the factors influencing dystocia rate, calf BWT had the greatest effect, with a 2.3 % increase in rate of dystocia rate for every kilogram increase in BWT. Thus, we should be careful to select parental breeds that minimize dystocia, which can lead to both calf and dam losses.

In their study to characterize maternal productivity of first and second generation cows from a diallel of Angus, Brahman, Hereford, Holstein and Jersey when mated to sires of a third breed (Charolais and Red Poll), Sacco et al. (1989) reported that Charolais-sired calves were 3.6 kg heavier ($P<0.01$) at birth than Red Poll-sired calves. Montana et al. (1990) reported that Charolais- and Chianina-sired calves were on average 4% heavier at birth than B-, Indu-Brazil- and Limousin-sired calves. Estrado-Arteage et al. (1990) found that Charolais sires had a superior additive genetic breed effect for BWT over Brangus and Hereford (4.7 kg and 6.5 kg, respectively). In another study using Angus, Polled Hereford and Santa Gertrudis bulls on crossbred females, Chapman et al. (1970) reported heavier BWT for Santa Gertrudis-sired calves. This indicates that the Santa Gertrudis, Chianina and Charolais sires with their relatively large mature size compared to the Red Poll, Angus and Polled Hereford sires of the same age, impart relatively good growth potential to their calves.

At Kilifi Plantations, Gregory and Trail (1981) working with two-breed rotational crosses of A and S, reported that S-sired calves were 2.9 kg heavier ($P<0.01$) at birth than A-sired calves. In the two-breed rotation, A sires were mated to 67% S 33% A (Sr) dams while S sires were mated to 67% A 33% S (Ar) dams (**Figure 3.1**). The heavier BWT of the S-sired progeny were attributed to the fact that the Ar dams had a maternal additive genetic superiority over the Sr dams. In the study reported in this thesis, it will be interesting to compare the B breed with A and S. Breed of sire effects are expected to be important sources of variation in rotational crossbreeding.

In some studies, breed of sire has failed to significantly affect BWT. Kang'ethe (1990) found no significant difference in BWT between the S, F and A sire breeds. However, calves sired by A bulls tended to have the heaviest BWT (a mean of 26.7 kg). Lack of significant effect of sire breed on BWT has also been reported by Trail and Gregory (1982) at Deloraine Estates where A, S and Simmental were the sire breeds.

Significant breed of dam effects on BWT have been reported by many authors including Willis and Wilson (1974), Andersen et al. (1975), Smith et al. (1976a) and Gregory et al. (1978b). At Deloraine Estates, Trail and Gregory (1981b), reported that calves produced by straightbred A cows were significantly heavier than calves produced by F_1 AS cross cows (first breed in cross indicates the breed of sire), pedigree S cows and foundation S cows (32.0 vs. 29.5, 24.7 and 23.2 kg, respectively), but not SA cross cows (30.3 kg). These results indicate that apart from the pure A having a higher merit for maternal additive effects than the pure S the crossbred cows displayed maternal heterosis for calf BWT. By contrast, heavier BWT have been reported in calves born to crossbred dams than those born to purebred dams by Marshall et al. (1984) working with B x Hereford, Simmental x Angus, B x Angus and Hereford x Angus crossbred dams. Kang'ethe (1990) compared the performance of S and its crosses with A and F and reported a significant effect ($P<0.01$) of the dam genotype on BWT. The F_1 FS dams gave birth to the heaviest calves, while the BWT of calves from high-grade ($\geq$87.5%) S and Exotic dams (either F or A) were the lightest. Ar dams gave birth to calves that were 2.8 kg heavier than the Sr dams. This could be attributed to the higher proportion of *B. taurus* genes in the Ar dams, that is, due to maternal additive breed effects.

A calf could have a high BWT due to its superior individual additive genetic composition and, in the case of crossbreds, any advantage resulting from individual heterosis. Several reports indicate that crossbred calves are born heavier than straightbred calves. In a study of crosses of Hereford, Angus, Shorthorn, Charolais, Simmental, Holstein and B, Nadarajah et al. (1985) reported that Shorthorn x Hereford crosses were heavier at birth (32.4 kg) than straightbred Hereford calves (30.0 kg). McElhenney et al. (1985) reported a 1.3 kg heavier BWT ($P<0.01$) for crossbred calves than straightbred calves. These results were attributed to the individual additive and heterosis effects. At Mariakani, Thorpe et al. (1993) reported a 2.5 kg heavier ($P<0.01$) BWT in 67% S 33% Exotic (either F or A) calves than in the 67% Exotic 33% S calves. This result was attributed to the difference in maternal additive genetic effects. The 67% S 33% Exotic calves were born to 67% Exotic 33% S dams, while the 67% Exotic 33% S calves were born to 67% S 33% Exotic dams. Thus, the 67% S 33% Exotic calves were born to dams with a higher proportion of exotic genes and these had a superior additive maternal effect.

In contrast, heavier BWT have been reported in straightbred Hereford calves by Pahnish et al. (1969) when working with Hereford and its crosses. Amongst the crossbreds, Simmental x Hereford and Charolais x Hereford calves weighed the most at birth and Angus x Hereford calves weighed the least. B x Hereford, Holstein x Hereford and Shorthorn x Hereford crosses were similar in BWT and intermediate to other crossbred types. Similar results had been reported by Smith et al. (1976b). The results indicate that the Charolais and Simmental breeds were superior for additive genetic effects as their crosses weighed the heaviest.

2.1.2. Environmental effects

Environmental effects known to affect calf BWT include:- year and season of birth, sex, parity of dam, type of birth (single or multiple) and their interactions. These environmental effects are considered in the analyses of studies comparing breeds and crosses because of the need to adjust (correct) the performance of the genotypes for these effects when the genotypes are compared in unbalanced designs. Environmental factors are considered by including them as factors in the statistical models. This allows one to separate genetic and environmental effects to obtain more accurate estimates of the magnitude of differences between genotypes that arise from differences in genetic composition.

Gregory and Trail (1981), Agyemang et al. (1991) and Tawah et al. (1993) reported that calves born during and immediately after a dry season when nutrition is poor are usually lighter than those born during the rest of the year when nutrition is better. This can be explained in terms of the effect the dry season nutrition has on the dam and the foetus during gestation. In cattle, fetal growth during the final third of gestation accounts for about two-thirds of the BWT. It follows that sub-optimal maternal nutrition will exert its maximal influence during the last trimester. These results are consistent with those reported by Singh et al. (1970), Taneja and Bhat (1972), Thorpe et al. (1981), Trail and Gregory (1981b), Wagenaar et al. (1986) and Tawah et al. (1992) who found that calves born in the dry season had lighter BWT.

The year of birth effect follows the same pattern as the season of birth effect. Its effect is attributed in the tropics to fluctuations in forage quality and quantity and milk production and any confounding effects due to management changes. Those calves born in drier years will have lighter BWT, unless their dams are given additional feed, than those born in years with good rainfall (Gregory and Trail, 1981). Similar trends were also shown by Thorpe et al. (1993). Trail and Gregory (1982) reported that year of birth did not significantly influence calf BWT in their analyses of performance records from Deloraine Estates in Kenya. This was attributed to supplemental feeding of dams during periods of feed scarcity.

Male calves are generally heavier at birth than female calves (Koch et al., 1959, 1973; Lowell, 1973; Trail and Gregory, 1982; Nelsen et al., 1984, 1986; Mwandotto, 1986b; Sacco et al., 1989; Gregory et al., 1991; Tawah et al., 1992, 1993). At Kilifi Plantations, Trail and Gregory (1981b) reported that male calves were about 2.1 kg ($P<0.01$) heavier at birth than female calves. Boston et al. (1980), Estrado-Arteage et al. (1990) and Thorpe et al. (1993) reported that the difference in BWT between males and females was 5.6%, 3% and 6.3%, respectively. Thorpe et al. (1981), Ahunu and Makarehian (1986) and Agyemang et al. (1991) observed, respectively, a 5%, 6.4% and 8% lower BWT in females than in males. This superior performance of males is due to hormonal differences between males and females which result in differential abilities to grow prenatally.

Calves born to early parity cows are generally significantly lighter than those from later parity cows (Massey and Benyshek, 1981b; DeNise et al., 1988; Agyemang et al., 1991). At Deloraine Estates, Trail and Gregory (1982), working with A, S and their crosses, reported that calves born to the first parity cows were 1.2 kg lighter ($P<0.05$) than the mean BWT (28.0 kg) of calves born from the fourth parity cows. This was attributed to the fact that heifers were undergoing two major physiological processes, maintenance of pregnancy and growth. Thus, some of the energy needed for maintenance of pregnancy was used for growth purposes. The foetus therefore gets less nutrients for its growth and is limited by the smaller body size of the heifer, hence, the low BWT. Results contrary to the general parity effect have been reported by Kang'ethe (1990) who found no effect of parity on BWT. In their studies with Santa Gertrudis calves, Willis and Wilson (1974) attributed the non-significant effect of parity to a rather high age at first parity, 40.4 months. This could not, however, be the cause of lack of significance in Kang'ethe's study. In the tropics with reasonable management heifers will calve at around the age of 27 - 28 months, depending on the environment. Thus, the age at first calving in Kang'ethe's study was not very advanced relatively (about 36 months), and might not fully account for the lack of significance for parity of dam on BWT. Possibly the dams were able to achieve a high proportion of their mature size by first calving. The analysis of live weight records would be required to test these relationships between puberty, conception, age at first calving and progeny BWT.

Type of birth (single or multiple) has been reported to affect the BWT of calves. Anderson et al. (1979) reported a higher BWT for singles than for twins (33.9 ± 1.4 vs. 26.4 ± 0.5) in the Hereford breed. This lower BWT in twins is attributed to the fact that they share the uterine space and nutrients during prenatal development.

Other environmental factors which are specific to each farm include management related factors like nutrition, disease affliction and control. These factors need to be studied and the extent to which they are affecting production estimated in order to judge how best to develop management systems to optimize productivity and profitability. Usually it is not possible to adjust for these factors in a statistical model because quantitative data describing these effects are not available.

2.2. Preweaning average daily gain.

Preweaning average daily gain (PADG) is a function of BWT and WWT (and factors affecting them) and thus a compound growth trait. Rapid growth is important because animals produce more live weight at the end of a fixed feeding period and reach maturity at a younger age thus improving feed efficiency and the length of the production cycle.

2.2.1. Genetic factors

Breed of sire has been reported to have a significant effect on the preweaning rate of gain (Gregory et al., 1978a, 1978b; Charles, 1980; Marlowe et al., 1983; Adeneye, 1985; Nadarajah et al., 1985; Reynolds et al., 1991). Lack of significance however, has been reported by Smith and Cundiff (1976). Due to the positive association between mature size and growth rate, the progeny of sires of temperate country breeds (*B. taurus*) generally show a higher growth rate than *B. indicus* sire breeds (individual additive genetic effect). For example, Thorpe et al. (1993) reported that the progeny of F sires grew faster preweaning (486 g/day), than those sired by S (409 g/day). A-sired calves had intermediate PADG (440 g/day). These differences in PADG show that F had the highest merit for direct additive genetic effects while the A was intermediate and the S was lowest. At Kilifi Plantations, Gregory and Trail (1981) reported a 45 g/day greater PADG from birth to 90 kg for the A- than for the S-sired calves. This difference was attributed in part to the greater difficulty in training S-sired calves to drink milk from the pail during the first few days after birth. Thus, low intake of colostrum resulted in low intake of antibodies which had a long term effect on subsequent development of the progeny.

Among the *B. taurus* breeds, the progeny of those with heavier mature weights have higher preweaning rate of gain than those sired by breeds with lighter mature weight. In their studies with Charolais and Limousin as terminal sire breeds, Dhuyvetter et al. (1985) reported a 31 g/day higher PADG in Charolais- than Limousin-sired calves with the Charolais having a larger mature weight than the Limousin. Hence the Charolais breed has a higher merit for direct additive genetic effects for PADG than the Limousin breed.

In suckled calves, PADG is also an indicator of the dam's milk production. Immediately after birth and during the next few weeks a calf depends solely on its dam's milk. The calf's rate of live weight gain therefore will be determined partly by the dam's potential for milk production and partly by the calf's genetic potential for weight gain. This calf genetic potential will not be realized if it does not get optimal quantities of milk from the dam. *B. indicus* mothers have poor potential for milk production (Mahadevan et al., 1962). When they produce F_1 calves, these calves are unable to express fully heterotic effects for growth due to lack of adequate nutrition (maternal environment). With age, however the calves depend less and less on the dam's milk and instead satisfy their nutritional requirements by increasing their intake of forage and other feedstuffs.

Highly significant effects of dam genotype on PADG have been reported. In their studies with Red Poll, B, Hereford and Angus crossbred dams, Gregory et al. (1978a) reported that calves with Red Poll and B dams had a 162 g faster ($P<0.01$) PADG than their reciprocal crosses with Hereford and Angus sires. In a similar experiment, Gregory et al. (1978b) reported a PADG of 80 g more in the F_1 calves reared by Angus dams than in those calves reared by Hereford dams. These results were consistent with those reported earlier by Long and Gregory (1974). Calves from Angus dams gained faster from birth to weaning than calves from Hereford dams. This indicates that the Angus dams have a superior maternal ability, a reflection of their milk production potential. Variation in calves' growth rate normally associated with dam genotype is largely from differences in milk production ability. Thus, given the situation (ranches where calves run freely with their mothers, and thus suckled) under which the studies were conducted by Long and Gregory (1974) and Gregory et al. (1978b), the superiority of the Angus dams is attributable to the fact that they produced more milk than the Hereford dams and were superior in maternal additive breed effects (Boston et al., 1975).

Non-significant effects of dam genotype on PADG have also been reported, especially in situations where calves are bucket fed. Kang'ethe (1990), at Mariakani reported a non-significant effect, although calves born of high-grade exotic dams (mainly A), numerically had the highest rate of gain with a least squares mean of 461 g/day, while those born to high grade S dams had the lowest PADG (428 g/day). This suggests that the exotic dams were superior to the S in terms of transmitted effects (additive maternal breed effects) for PADG.

The direct effect of calf genotype is expressed less in BWT than in rate of gain. At birth, the effect of calf genotype is obscured by the expression of the maternal effects. Pahnish et al. (1969) working with Hereford, Angus and Charolais sires mated to Hereford, Angus and B dams, reported a superiority in PADG in calves having 50% B genes (from the dam) compared to those having 50% Hereford and 50% Angus genes. This superiority was attributed to a favourable maternal environment provided by the B dams which had a relatively high level of milk production. This indicates that calves with a higher proportion of B genes have a superior additive genetic potential to Hereford and Angus for PADG. It would be of interest to see if calves at Kilifi Plantations, especially those having about 50% B genes, will perform as above. Gregory and Trail (1981) reported that Sr calves gained 45 g/day less ($P<0.05$) than the Ar calves. Due to the Sr dams having an inferior additive genetic effect, the latter group of calves had been born lighter. At Mariakani, Thorpe et al. (1993) similarly reported that 75% Exotic 25% S calves had a significantly higher rate of gain than the 75% S 25% Exotic backcross calves (451 vs. 404 g/day). These observations were attributed to the superior additive genetic composition of the calves with a higher proportion of exotic genes (either A or F).

2.2.2. Environmental effects

PADG tends to be slower for calves whose preweaning growth occurs during the dry season. Calf growth is affected by inadequate nutritional level and reduced intake due to high ambient temperature (Gregory and Trail, 1981; Urick et al., 1981; DeNise et al., 1988; Tawah et al., 1992, 1993).

The effect of year of birth on PADG follows the same pattern as that for season. Calves born in dry years have poorer daily gain than those born in wet years (Gregory et al., 1978b; Gregory and Trail, 1981; Trail and Gregory, 1981b). Thorpe et al. (1993) reported a significant effect of year of birth on PADG. This was attributed to annual fluctuations in weather conditions, disease incidence, sires used or changes in management. Changes in management will be important with respect to feeding of the dams in late gestation and of the calves preweaning.

The relative daily gains of male and female calves vary from report to report. Gregory et al. (1978b) and Urick et al. (1981) have reported a significant effect of sex on PADG with the males gaining more than females. Koch et al. (1959, 1973) and Estrado-Arteage et al. (1990) reported that the daily gain of bull calves from birth to weaning was, respectively, 7.0%, 8.1% and 7.0% greater than that of heifers. Non-significant effects of sex on PADG have been reported by Gregory and Trail (1981) and Kang'ethe (1990). They attributed this lack of significance to the calf feeding regimes. Generally it is recommended that a calf is fed according to its body weight. Since males in both studies had higher BWT, on average, than females calves, then it follows that they should receive more milk than the females. This was not the case at Kilifi Plantations and Mariakani where the quantity of milk fed daily was dictated by a time scale. This may have deprived the males of the ability to express their potential in PADG.

Parity of dam has also been reported to affect PADG. The effect is attributable to the fact that first calvers give birth to lighter calves and also have poor mothering ability because they have less milk. Thus, calves of these first calvers end up having a poorer maternal environment than those of later parities (Francoise et al., 1973; DeNise et al., 1988). Gregory et al. (1978b) reported that calves born to third parity (5 years old) cows gained 48 g/day faster than calves from second parity (4 years) cows. Others have reported a non-significant effect (Kang'ethe, 1990)(**section 2.1.2**).

2.3. Weaning Weight.

Because of the weaning criterion (a fixed weight) at Kilifi Plantations, weaning age (WAGE) will be used as a proxy for WWT. Literature on the analyses of WAGE as a preweaning trait are few. WWT is an economically important trait in beef/milk cow-calf production. Cows that produce heavier calves at weaning are more valuable to the producer than those that wean calves of a lighter weight. WWT reflects not only the growth ability of the calf but also the maternal environment created for the calf by its dam.

2.3.1. Genetic factors

Through its influence on BWT and PADG, breed of sire has been observed to affect WWT. Sacco et al. (1989) reported that calves sired by bulls of larger mature weight were heavier at weaning. Charolais-sired calves were 14.8 kg heavier ($P<0.01$) at weaning than the Red Poll-sired calves. Dhuyvetter et al. (1985) reported a 9.0 kg heavier WWT ($P<0.01$) for Charolais-sired calves than for Limousin-sired calves, as a result of the Charolais breed having a superior additive direct effect for PADG and WWT to the Limousin and Red Poll breeds. Due to the close relationship between mature weight of sire breed and WWT, some *B. taurus* sire breeds have been shown to have superior PADG to *B. indicus* sire breeds. Kang'ethe (1990) reported that calves sired by F and A (both *B. taurus*) were respectively, 7.5 kg and 4.3 kg heavier at weaning than those sired by S (*B. indicus*). This is attributable to a high merit for transmitted effects for PADG in the *B. taurus* breeds. A non-significant effect of sire breed has been reported by Trail and Gregory (1982) in a restricted suckling system using A and S sires. They attributed this observation to the management practice which may have allowed the calf in poor condition to extract more milk from its dam. This practice may have limited the opportunity for differences in transmitted effects between sire breeds to be expressed.

The effect of dam genotype on WWT arises from both maternal additive genetic and heterotic effects. Maternal additive effects are a general concept while maternal heterosis is only relevant in crossbreeding, that is, where crossbred dams are used. Crossbred cows have been shown to wean heavier calves than straightbreds. Ellis et al. (1979) in a comparison of WWT of calves from crossbred cows (crosses of Hereford, Charolais and Angus) with calves from straightbred cows reported an advantage for crossbred cows. In every case, the mean WWT of the reciprocal crossbred dams were heavier than the mean of the straightbred dams. This indicated that maternal heterotic effects were important. Thorpe et al. (1981) reported otherwise, in that, calf WWT of the Angoni-Barotse and Angoni-BN reciprocal crossbred dams were less than 2% above the mean of the parental purebreds and in neither case were the progeny of the crossbred dams superior to those of the better parental breed. Crossbred cows have also been shown by Turner (1969) to perform better for calf WWT than straightbreds. Identical WWT (8 months) have been reported in BN and S breeds (170 ± 2.6 kg) by Trail and Gregory (1981a). These identical WWT of calves result from the superior additive maternal effect of the S breed which compensates for inferior additive genetic merit for growth rate relative to the BN breed. These studies indicate that in any crossbreeding programme proper choice of dam breeds (or combination of breeds) must be done to maximize weaner production.

Long and Gregory (1974) and Mwandotto (1978), have reported a significant effect of calf genotype on WWT. A calf could perform better due to its superior additive genetic composition and, in the case of crossbreds, any advantage resulting from heterosis. In their studies with F, S, BN and EAZ and their crosses, Mwandotto et al. (1988) reported that F-sired crosses with EAZ and the EAZ purebreds were lighter in WWT than the F-sired crosses with S and BN. The S and BN breeds were on average 6.2% lighter than the FBN and FS crossbred calves. These results indicate a high genetic merit for transmitted effects for rate of gain and WWT for the F. In a similar study, Kang'ethe (1990) reported a higher WWT (at 5 months) in the F_1 FS calves (93.9 kg) than in the high-grade S calves (78.8 kg). The F_1 FS and AS calves differed significantly for WWT indicating that F had superior additive genetic effects for PADG to A. In another study, Nadarajah et al. (1985) working with crossbred calves from Hereford dams and Angus, Shorthorn, Charolais, Simmental, B and Holstein sires, also observed that breed of calf had a significant influence on WWT of calves. The difference in WWT among crossbreds were not significant but the ranking (high to low) for sire breed was Holstein, Angus, Charolais, Shorthorn, Simmental and B. All crossbred calves were somewhat heavier than straightbred Hereford. This superior WWT in the crossbred calves is due to the aggregate individual and maternal additive and heterotic effects. Higher WWT (relative to the latter study) had been reported by Laster et al. (1976) using crossbred calves from Hereford dams and Angus, Shorthorn, Simmental, Charolais, B and Holstein sires. These differences were attributed to the preweaning plane of nutrition. Calves studied by Laster et al. (1976) were creep fed whereas those in the other study were not. Thus, Holstein has a higher merit for individual additive genetic effects for PADG and WWT than the other breeds.

2.3.2. Environmental effects

WWT has been shown to be influenced by WAGE with late weaned calves having higher WWT than early weaned calves. This relationship has been estimated as the regression coefficient of WWT on WAGE. Boston et al. (1980) reported that the partial regression of WWT on WAGE was 1.3 kg/day in their studies with range beef and dairy beef calves. This result indicated that a 1- day increase in WAGE was associated with a significant 1.3 ± 0.1 kg increase ($P<0.01$) in WWT. Ahunu and Makarechian (1986) reported that the linear and quadratic components of WAGE effect were highly significant for WWT in a beef crossbred population (1.0 ± 0.06 kg and -0.01 ± 0.002 kg, respectively), but only the linear component was significant in Hereford and Beef synthetic populations (0.77 ± 0.05 kg and 1.0 ± 0.04 kg, respectively). The average WAGE for the Hereford, Beef synthetic and Beef crossbred were, respectively, 157.4, 160.8 and 162.9 days. Negative significant quadratic components have been reported by Pell and Thayne (1978) in Hereford and Angus breeds. This negativity indicates that the change in weight for additional increments of age is not constant but rather decreases in magnitude with increasing age.

Optimal calving and weaning dates, and hence WAGE, will be determined by grazing conditions, availability of supplementary feeds and cow condition, and their effect on subsequent reproductive and productive performance. Bailey et al. (1975) reported that calves weaned at 10 months of age were heavier than those weaned at 8 months ($P<0.05$), but that live weight gains would be largely affected by grazing conditions and stocking rates.

WWT tends to be lower for calves whose preweaning growth occurs during the dry season than those whose growth occurs during the wet season (Gregory and Trail, 1981). Tawah et al. (1992) reported that Gudali and Wakwa calves born late in the dry season weighed on average 16.5% and 10.3% more ($P<0.01$), respectively, at weaning than those born in the wet season. This was attributed to the fact that these calves had their preweaning growth when feed was readily available, i.e., in the wet season. Sellers et al. (1970) reported that calves born in the spring weaned 2 kg heavier than winter-born calves, 6.6 kg heavier than summer-born calves and 3.6 kg heavier than fall-born calves. This was attributed to the better management made necessary by the cold winter received by winter- and spring-born calves. Similar results had been reported by Pherigo et al. (1969).

Significant effects of year of birth on WWT have been reported by Crockett et al. (1978a), Mwandotto (1978), and Tawah et al. (1992). SA calves born in various ranches in Kenya showed important effects of year of birth on WWT (Trail and Gregory, 1981b). Those calves born in drier years had lower WWT (Gregory and Trail, 1981b). It would be of interest to see what effect year of birth has on the performance of calves at Kilifi Plantations calf performance since these calves were bucket fed until weaning.

Generally male calves are heavier at weaning than females (Long and Gregory, 1974; Gregory and Trail, 1981; Tawah et al., 1993). Trail and Gregory (1982) reported that males were 18 kg (10.5%) heavier ($P<0.01$) at weaning than females. Singh et al. (1970) reported a 10.7 kg higher WWT in males than in females. In the N'Dama cattle, male calves were weaned at a heavier weight than females (88.7 vs. 84.7 kg) (Agyemang et al., 1991). In Mexico, Estrado-Arteage et al. (1990) reported a 6% superior WWT in males than in females. In contrast, Thorpe et al. (1993) reported a non-significant effect of sex on WWT, although males still weaned heavier by 2.2 kg. This lack of significant effect was attributed to the fact that calves at Mariakani were fed on a fixed milk (time scale) ration; thus, some calves, especially the bigger ones at birth, were probably not able to express their growth potential.

As one would expect from its effect on BWT and PADG, parity of dam has been reported to affect the WWT of the calf (Hohenboken and Brinks, 1969; Mwandotto, 1978; Urick et al., 1981). First calvers, give birth to lighter calves and also have a poor mothering ability because generally they produce less milk. Consequently calves of these first calvers end up having a poorer maternal environment than those of later parity, and they are weaned at lower weights. Massey and Benyshek (1981a) in their studies with the Limousin breed reported that 2 year old dams produced calves with the lowest WWT. WWT increased with the largest calves produced by the 5 and 6 year old cows.

2.4. Survival rate to weaning (Viability).

The survival of a calf to weaning is an important trait that influences overall reproductive efficiency and therefore the profitability of a herd. Dam effects will be more important in the range areas where cows are allowed to run with their calves up to weaning as opposed to cases where the calves are reared indoors and are thus protected from the extremes of weather. Dystocia (difficult parturition), disease, parasites, predators and environmental factors such as heat, cold, rain, droughts etc. have been implicated as causes of preweaning calf mortality. Therefore, survival (viability) is influenced by genetic and environmental factors.

2.4.1. Genetic factors

High BWT are directly associated with difficult births and thus with preweaning mortality due to dystocia (Laster et al., 1973; Laster and Gregory, 1973). Because of its effect on BWT, the sire genotype has been reported to significantly influence SRATE, with the progeny of sire breeds representing biological types of large size, e.g., Charolais, having a lower SRATE (Crockett et al., 1978b). In a study using Charolais and Limousin sires, Dhuyvetter et al. (1985) observed that Charolais-sired calves had a 9.9% higher incidence of calving difficulty score than did Limousin-sired calves. The Charolais-sired calves had a 4.6% greater preweaning mortality than did Limousin-sired calves. This higher mortality of Charolais-sired calves was associated with their increased calving difficulty. This indicates that sire breed influences calf mortality through its influence on the calf's BWT because the Charolais-sired calves had been born 2.7 kg heavier than the Limousin-sired calves. Similar results have been reported by Smith et al. (1976a) using the same sire breeds. Gregory et al. (1978a, 1978b) reported a 96.1 ± 2.4 and 91.1 ± 1.4% SRATE, respectively for progeny sired by B relative to the mean of progeny sired by Hereford, Angus and Red Poll. In various reports, non-significant effects of sire breed have been reported (Gregory and Trail, 1981; Trail and Gregory, 1982; Kang'ethe, 1990). However, Marlowe et al. (1983) in their work with Angus, Charolais and Holstein sires reported higher (numerically) SRATE in the Holstein-sired calves than in the others (83.9% vs. 81.8: Angus-sired and 80.5: Charolais-sired).

In many production systems perinatal and early postnatal calf mortalities are the major sources of calf losses. Laster and Gregory (1973) in a study with *B. taurus* crosses, reported that the breeding group of dam influenced ($P<0.01$) calf mortality in parturitions involving dystocia but did not significantly influence calf mortality in unassisted parturitions. In this study, calf losses in dystotic parturitions ranged from 6.6% for Jersey x Angus to 28.8% for straightbred Hereford. They reported more dystotic parturitions in Hereford than in Angus cows bred to the same Jersey, South Devon, Limousin, Simmental and Charolais bulls (the last four breeds have heavy mature weights) ($P<0.01$). This was attributed to higher BWT of calves ($P<0.05$) from Hereford dams. Using the same sire breeds, Smith et al. (1976a) reported that death losses were 2% higher ($P<0.05$) for Hereford than for Angus dams in late preweaning stages. Thus, in crossbreeding, the compatibility of breeds with regard to the relative size of dam and sire is an important factor to consider if high rates of early mortality are to be avoided. In the tropics, there is little evidence that dystocia is an important cause of mortality in *B. taurus* x *B. indicus* mating systems.

Gregory et al. (1978b) and Frahm and Marshall (1985) have reported significant effects of the genotype of dam on the mortality rate of their progeny. Ellis et al. (1979) reported that the reciprocally crossed Angus and Hereford cows had a higher SRATE than the average of the straightbred cows, evidence therefore of heterosis for preweaning survival. Trail and Gregory (1981a) reported a 2% higher (numerically) SRATE in the S than in the BN breed (96 ± 1.3 vs. 94 ± 1.2%). This was also attributed to the higher milk production of the S breed. Among the Angoni, BN (both *B. indicus*) and Barotse (a Sanga breed), Thorpe et al. (1981) reported a non-significant effect of dam genotype on SRATE. Calves born to crossbred dams (96%) had marginally higher SRATE than the rate (95.3%) of the calves born to the purebred dams, indicating that in some cases crossbred dams do not show any significant advantage over the purebred dams especially when preweaning mortality rates are low.

Calf genotype has been reported to affect early mortality in situations where dystocia is important (Smith et al., 1976a). Crossbred calves tend to have higher SRATE than their contemporary straightbreds. Laster and Gregory (1973) reported that calf mortality was 11.6% higher ($P<0.01$) in straightbred Hereford and Angus calves than the average of the Hereford x Angus and reciprocal calves. Death losses for all types of parturitions (including calving assistance) were 3.8% higher ($P<0.01$) in straightbred than in crossbred calves. These results suggest that crossbred calves tolerate the higher levels of stress associated with difficult birth better than straightbreds, and that the higher mortality rates in calves experiencing dystocia are related to calf stress as a result of delayed and difficult parturition. Gregory et al. (1978a) similarly, in a study with Red Poll, B, Hereford and Angus breeds and their crosses, reported that purebred B calves had a high preweaning calf mortality (20.1%), but this was reduced substantially in crosses with the other breeds. This indicates that the B breed (purebreed) had a poor additive effect which however may have resulted in high level of heterosis (although not estimated) in its crosses. It will be of interest to estimate heterosis effects on SRATE at Kilifi Plantations. Other reports indicate that crosses generally have SRATE that are intermediate to purebred values, demonstrating therefore no individual heterosis advantage. Thorpe et al. (1993) reported that the high grade exotic calves had the highest SRATE (97.2%), crosses were intermediate with the backcross and rotational cross calves having a higher proportion of S, i.e., 75% S 25% Exotic and 67% S 33% Exotic, having higher SRATE than their reciprocals. The high-grade S calves had the lowest SRATE (77.5%). The high exit rate in the S was not attributed wholly to mortality. It was a management practice to cull calves that had a BWT below 18 kg, the majority of which were calves in the high-grade S group. Perhaps because of this management practice, individual additive genetic breed effects were not important in accounting for survival differences.

2.4.2. Environmental effects

Generally year and season of birth effects on SRATE result in part from their influence on the dam's nutrition (and hence the quantity and quality of milk available to the calf). They also affect pasture quality and quantity on which the calf is subsequently weaned and the stress related to seasonal and annual variations in weather conditions and concomitant effects on disease incidences (pneumonia, parasite etc.). Significant effects of year of birth on SRATE have been reported by Trail and Gregory (1982) and Morris et al. (1993a). Wagenaar et al. (1986) reported a significant effect of season of birth on calf mortality and thus survival. Non-significant effects of year of birth on SRATE have been reported by Gregory and Trail (1981). This was attributed to the type of management. Calves were bucket fed in a calf house and this could have reduced the variation between the years of birth.

Sex of calf has also been reported to influence preweaning mortality especially when calves experienced dystocia. Gregory et al. (1978a) reported a 3.2% level of perinatal mortality. This was 1.1% greater ($P<0.05$) in males than in females. This was because more than twice (11.6% vs. 5.0%) as many male as female calves required major assistance ($P<0.01$) at birth. Similar results were reported by Laster and Gregory (1973) who reported higher losses due to dystocia ($P<0.05$) in males than in females (22.4% vs. 16.3%). In cases where calves do not experience dystocia, the same tendency is generally observed. Sacco et al. (1989), Kang'ethe (1990) and Gregory et al. (1991) reported a 3, 4.8 and 2% significantly higher ($P<0.05$) SRATE in females than in males, respectively. These results were attributed to higher BWT for male calves than female calves. A non-significant effect of calf sex on SRATE has been reported by Gregory and Trail (1981), although males still had a lower SRATE than females.

In various reports, dam parity has been shown to influence SRATE (Crockett et al., 1978b; Sacco et al., 1989). However, Trail and Gregory (1982) has reported a non-significant effect of dam parity on SRATE. There was a tendency towards a higher level of SRATE in the later parturitions (Trail and Gregory, 1981a). This is because later parity cows were fully mature and produced larger amounts of milk and thus had better mothering ability than first parity cows. Laster and Gregory (1973) reported that cow age had no significant influence on calf mortality in parturitions involving dystocia. Mortality in all parturitions was higher ($P<0.01$) for progeny of 2 year old dams (15.6%) than for 3 year olds (7.5%) and cows 4 years and older (5.6%). Similar results were reported by Laster et al. (1973). Thus, in general, the effect of parity on calf mortality seems to be related to the occurrence of dystocia.

2.5. Partitioning of genetic effects.

The genetic basis of crossbreeding effects can be divided into two major components: additive and nonadditive (heterotic). These effects have been determined by fitting coefficients indicating the proportions of genes in the calf and dam contributed by each of the parental breeds and the proportion of loci in the calf and dam with alleles originating from different parental breeds. The coefficients for both the direct and maternal heterosis effects are based on the assumption that a linear relationship exists between dominance and degree of heterozygosity (Koger et al., 1975).

This procedure is advantageous over the conventional analyses of crossbreeding data in that it is a less complex statistical procedure, provides a clearer understanding of the genetic component and allows prediction of breed crosses that are not included in the data set (Robison et al., 1981). This procedure can also be used in designing programmes to utilize efficiently variation among breeds in crossbreeding systems and in computer simulations (modelling) studies.

2.5.1. Additive genetic effects

The additive component of merit for the trait of interest is that which is due to the averaging of merit in the parental lines or breeds, with simple weighting according to level of representation of each parental breed in crossbred genotype (Swan and Kinghorn, 1992). This additive component can be divided into the individual and maternal additive genetic effects. The Individual additive genetic effect (G_I) is the contribution to offspring phenotype attributable to its own (the individual's) set of genes. Maternal additive genetic effects (G_M) are defined as any contribution or influence on offspring phenotype attributable to its own dam, exceeding the inherited sample half of the dam's nuclear genes (Gregory and Maurer, 1993). Maternal effects can be classified into prenatal (e.g., cytoplasm of the egg and uterine environment) and postnatal (e.g., milk production, method of rearing and/or mothering ability) (Baker, 1980).

Both non-significant as well as significant G_I have been reported by various scholars in different dairy and beef breeds and for different production systems. In their analyses of crossbreeding data from the Southern region of the USA, Wyatt and Franke (1986) reported significant values as deviations from Angus for G_I of Brahman of 7.4 kg for BWT and 2.5 kg for WWT. The direct additive effect of Charolais on BWT was large, 12.7 kg ($P<0.001$). These results were comparable to those observed by Olson et al. (1993) who reported that G_I of the Brahman relative to Angus were 6.1 ($P<0.001$) and 8.0 kg ($P<0.05$) for BWT and WWT, respectively. The G_I of Charolais on BWT was 13.0 kg ($P<0.001$). The Brahman G_I on WAGE was large and negative, -10.0 days ($P<0.01$).

In a study with breeds of British, European and Zebu origin, Peacock et al. (1981) reported that Brahman calves had significant ($P<0.01$) negative coefficients for WAGE and WWT, while the coefficient for Charolais were significant ($P<0.05$) and positive. The negative value for Brahman calves reflects the slow growth rate of purebred Brahman calves and is associated with large heterosis estimates for Brahman crosses. In the tropics of Kenya, non-significant G_I for BWT and SRATE have been reported by Thorpe et al. (1993) in their studies with *B. taurus* (A and F) and S crosses. However, G_I for PADG and WWT were highly significant ($P<0.001$). S were 70 g/day inferior to *B. taurus* calves for PADG and 9.8 kg lighter at weaning. These results are consistent with those reported by Trail and Gregory (1982) for partially suckled calves of the A and S breeds and their crosses. The breed of sire, breed group of dam, and their interaction had no significant effect on SRATE at 9 months. Significant G_I on BWT have been reported by Trail et al. (1982) in their studies with Red Poll and BN breeds of cattle.

Maternal additive genetic breed effects are well documented in beef cattle (Baker, 1980). In dairy cattle the importance of G_M is controversial: both negligible (Cunningham and Syrstad, 1987) and significant G_M estimates have been reported (Robison et al., 1981; Ahlborn-Breier and Hohenboken, 1991) for lactational and reproductive traits. For preweaning traits of progeny, significant G_M has been reported more frequently in beef calves than for dairy calves. Beef calves are suckled (i.e., run freely with the dam), and thus, preweaning growth is an indicator of the dam's milk production. The calf's rate of live weight gain will therefore be partly determined by the dam's potential for milk production.

In their studies with beef cattle, Olson et al. (1993) reported that the G_M of Brahman on BWT as a deviation from Angus was -4.2 kg ($P<0.001$). This was comparable to the -6.1 kg reported by Wyatt and Franke (1986). Significant G_M has been observed for BWT (6.0 kg) for calves with Red Poll dams by Trail et al. (1982) compared to BN dams. This was consistent with results reported by Trail and Gregory (1981) and Thorpe et al. (1993) for crosses of breeds of *B. taurus* and *B. indicus* cattle. Thorpe et al. (1993) observed that calves born to *B. taurus* dams had BWT nearly 2 kg heavier than those born to S dams. Trail and Gregory (1981) reported that the S breed had an inferior maternal effect for BWT than A, but that the S breed showed superior additive direct effects for growth rate.

The G_M for WWT and WAGE as a deviation from Brahman were non-significant for Angus but significant ($P<0.05$) (and in favour of) for Charolais (Peacock et al., 1981). This was computed as deviation from Brahman. Trail et al. (1982) reported non-significant G_M for WWT and SRATE. However G_M for WWT approached significance and favoured calves with BN dams compared to calves with Red Poll dams. They concluded that there was a reversal of the additive maternal effect between prenatal and postnatal gains reflecting superior mothering ability of the Boran dams in that environment. Non-significant G_M for PADG, WWT and SRATE have been reported by Thorpe et al. (1993) in *B. taurus* x *B. indicus* crosses. They attributed this absence of G_M in part to the bucket rearing of calves.

2.5.2. Nonadditive (heterotic) genetic effects

Heterosis is the nonadditive effect of crossbreeding. It is the amount by which merit in crossbreds deviates from the additive component (Swan and Kinghorn, 1992). Heterosis is usually attributed to genetic interactions within loci (dominance) and interactions between loci (epistasis) (Sheridan, 1981). Heterotic effects can be classified into individual and maternal heterosis. Individual heterosis (H_I) is the improvement (or superiority) in performance in an individual relative to the average of the parental breeds, with maternal, parental or sex-linkage effects playing no role. Maternal heterosis (H_M) refers to heterosis in the population attributed to using crossbred instead of purebred dams and occurs due to the dam itself possessing heterosis. Results from *B. taurus* breed crosses indicate substantial heterosis for reproductive traits (10 to 15%), moderate heterosis for growth (4 to 7%) and relatively little heterosis for feed efficiency, carcass composition, or meat quality traits (1 to 2%) (Baker, 1982). Although the same relative order of expression of heterosis is maintained, more heterosis is expressed in *B. indicus* x *B. taurus* breed crosses as a result of heterozygosity. Therefore, the differences in gene frequencies are much wider between *B. taurus* and *B. indicus* breeds, and this leads to high levels of heterosis in crosses between them. In the following review, estimates for heterosis represent the difference between the average of the reciprocal F_1 crosses and the average of the calves of the purebred parental breeds, for H_I and the difference between the average of the reciprocal F_1 crosses and the average of the purebred dams for H_M.

In his review, Barlow (1981) reported that heterosis for growth among ruminants appeared to be favoured by a benign nutritional environment. Such sentiments have also been expressed by Sheridan (1981) and Cunningham and Syrstad (1987) when environmental conditions were less than optimal. In the study reported in this thesis, it will be interesting to see if there will be an inverse relationship between heterosis and the nutritional environment bearing in mind that these calves were reared in a relatively good production system.

Non-significant H_I effects for BWT and WWT in Angus and Charolais crosses have been reported by Wyatt and Franke (1986) and Olson et al. (1993). Previous studies by Pahnish et al. (1969) in temperate regions, have also indicated similar non-significant H_I effect on BWT and WWT in Angus and Charolais crosses. In the tropics of Kenya, Thorpe et al. (1993) reported that H_I effects were large and significant ($P<0.05$) for all preweaning traits of crosses between *B. taurus* (i.e., A and F) and S breeds. The F_1 *B. taurus* x S calves were 1.1 kg heavier at birth, 32 g/day faster growing, 5.4 kg heavier at weaning and had a 5% higher SRATE than the mean of the purebred *B. taurus* and S calves. Peacock et al. (1981) reported significant ($P<0.01$) H_I effect for WWT for Angus and Brahman and Brahman and Charolais crosses, but not for Angus and Charolais crosses. Non-significant H_I effect on SRATE in F_1 populations has been reported by Trail et al. (1982) in Africa and Gregory et al. (1991, 1993) in the US. In the US studies, effects of heterosis on SRATE were not consistent, either among composite populations or among generations within composite populations. Heterosis was significant ($P<0.01$) for SRATE for the F_2 generation and approached significance ($P = 0.06$) for the combined F_3 and F_4 generations. These results suggested that heterosis for SRATE in advanced generations of *inter se* mated composite populations was not less than expected from retained heterozygosity. Thus, this heterosis seems to be due to dominance effects of genes and can be attributed to recovery of accumulated inbreeding depression that has accrued in breeds since their formation.

Maternal heterosis effects have been reported by Olson et al. (1993) to significantly ($P<0.05$) increase BWT, WAGE and WWT in Angus and Brahman crosses. Similar results have been reported by Koger et al. (1975) in Brahman and Shorthorn crosses. Using crosses of Angus, Brahman and

Charolais breeds, Williams et al. (1991) failed to find significant H_M effect on SRATE. Sacco et al. (1989) observed a significant H_M effect for BWT of crosses of Angus and Hereford but the average H_M estimate for crosses among these breeds and those of Brahman, Holstein and Jersey breeds was small and non-significant. Peacock et al. (1981) reported a significant ($P<0.01$) H_M effect for WWT in F_1 crosses of Angus, Charolais and Brahman breeds. These results from beef cattle, emphasize the advantage to be gained from the use of crossbreeding in commercial beef cattle production. In a Kenyan study, Thorpe et al. (1993) reported a significant H_M effects for BWT and not for other traits (i.e., PADG, WWT and SRATE) using *B. taurus* and S dams. Calves born to F_1 dams were, on average nearly 1.9 kg heavier than the mean weight of calves born to purebred *B. taurus* and S dams.

2.6. Heritabilities and correlations.

Unbiased heritability estimates and accurate correlations (genetic and phenotypic) among performance traits are required in order to design selection programmes for livestock. Reliable genetic parameter estimates and economic weights would allow for development of optimal linear selection indices that are directly applicable to programmes selecting for improved performance.

2.6.1. Heritabilities

Heritability refers to that portion of the phenotypic variance of a population that is due to heredity. Heritability may be used in either a narrow or a broad sense. In the narrow sense, heritability includes additive gene actions or the average effects which the individual genes have in that population. Heritability in the broad sense includes all of the effects of the entire heredity of each individual. Heritability in the broad sense includes, in addition to variation due to additive gene action, that which is due to dominance and epistasis (Lasley, 1978).

Heritability estimates normally apply directly to the specific population and environment from which the data were collected, thus, estimates may vary from one herd to another depending on gene frequency, previous selection, environment and past history of the population. A wide range of heritability estimates have been reported for preweaning growth traits. Differences arise mainly from method/model of estimation, breed, species, sex and amount of data (Thrift et al., 1973; Thorpe et al., 1981; Nelsen et al., 1984; Kiriro, 1986; Inyangala, 1989; Kegode, 1990; Odenya et al., 1992; Meyer, 1992b). Thus it is not recommended to take estimates made in one population for application in another. Characters can be classified as having high (>0.50), medium (0.25 to 0.50), or low (<0.25) heritability (Preston and Willis, 1974).

An illustration of the differences in heritability estimated for preweaning traits calculated by different methods/models and in several populations is given in **Table 2.1**. With a few exceptions, the estimate from the parent-offspring regression (i.e., RDD and RSS) are similar to or larger than the estimates from PHS (ANOVA). The estimate from RDD by Thorpe et al. (1981) are larger because of the important common maternal and environmental effects between the offspring-dam pairs. The offspring-sire regression (RSS) is not likely to be biased by common environmental effects between generations, but contains twice the proportion of the interaction variance contained in the estimate from PHS. The PHS estimate is the least biased because common environmental effects within half sib families are rather less likely than for the other relationships (RDD and RSS). Thus where possible, it is advisable to use the half sib estimate, because it approximates most closely to the value of heritability in the narrow sense.

Table 2.1 presents estimates of heritability partitioned into direct, maternal and the total heritability. Direct and maternal heritabilities are those attributed to the direct (individual) genetic effects and genetic maternal effects originating from the dam, respectively. These estimates are useful to a breeder to allow him to decide how best to utilize these groups (individuals and dams) in a breeding programme. The total heritability has been defined by Willham (1972) as the regression of an animal's total genotype (direct and maternal) on

Table 2.1. Published estimates of heritability of preweaning traits of cattle.

Authors[a]	Breed[b]	Analyses[c]	Parameters[d]			
			h^2	m^2	h^2_T	r_{AM}
		Birth weight				
Thorpe et al., 1981	AN	RDD	0.86			
	BR	RDD	0.58			
	BN	RDD	0.79			
Reynolds et al., 1991	HEF	RSS	0.21			
Baker et al., 1992	ANGX, HEFX	PHS	0.31			
Mwandotto, 1986a.	S	PHS	0.17			
Lubout and Swanepoel, 1992	P	PHS	0.35			
Tawah et al., 1992	W	PHS	0.79			
	G	PHS	0.36			
DeNise et al., 1988	HEF, ANG	PHS	0.19			
Rege et al., 1991	S	PHS	0.40			
Trail et al., 1971	ANG, BN, RP P, AK, Z	PHS	0.21			
Bertrand & Benyshek, 1987	L	S-D-MGS	0.22	0.05	0.22	0.16
	BRAN	S-D-MGS	0.22	0.13	0.28	-0.12
Hetzel et al., 1990	AX	S-D-MGS	0.47	0.05	0.49	
	HS	S-D-MGS	0.23	0.03	0.24	
	BX	S-D-MGS	0.45	0.14	0.52	
Quaas et al., 1985	SIM	S-MGS	0.16	0.06	0.13	-0.44
Trus & Wilton, 1988	SIM	S-MGS	0.34	0.20	0.36	-0.22
Garrick et al., 1989	SIM	S-MGS	0.44	0.12	0.37	-0.38
Meyer, 1992b	HEF	AM	0.56		0.56	
Tawah et al., 1993	G	AMM	0.39	0.06	0.22	-0.86
	W	AMM	0.65	0.22	0.23	-0.93
Mackinnon et al., 1991	ZX	AMM	0.61	0.11	0.68	0.01

Table 2.1. Continued.

Authors[a]	Breed[b]	Analyses[c]	Parameters[d]			
			h^2	m^2	h^2_T	r_{AM}
Koch, 1989	HEF	AMM	0.43	0.12	0.51	0.07
O'Rourke, 1989	BX	AMM	0.45	0.10		
Meyer, 1992b	HEF	AMM	0.38	0.14	0.47	0.05
		AMP	0.41	0.08	0.46	0.04
Meyer, 1993b	HEF	AMP	0.58	0.19	0.39	-0.57
Nelsen et al., 1984	HEF		0.36	0.82	0.35	-0.51
Baker, 1980			0.40	0.19	0.34	-0.42
Preweaning average daily gain						
Reynolds et al., 1991	HEF	RSS	0.29			
Nelson et al., 1986	HEF	RSS	0.35			
DeNise et al., 1988	HEF, ANG	PHS	0.18			
Tawah et al., 1992	W	PHS	0.25			
	G	PHS	0.24			
Pani et al., 1977	HEF, ANG	PHS	0.14			
Baker et al., 1992	ANGX, HEFX	PHS	0.12			
Massey & Benysheks, 1981a	L	PHS	0.10			
Nelsen & Kress, 1979	HEF, ANG	PHS	0.38			
Brown et al., 1990	HEF	S-D-MGS	0.58	0.39	0.74	-0.05
	ANG	S-D-MGS	0.57	0.15	0.50	-0.32
Hetzel et al., 1990	AX	S-D-MGS	0.11	0.33	0.27	
	HS	S-D-MGS	0.21	0.15	0.29	
	BX	S-D-MGS	0.11	0.09	0.15	
Trus & Wilton, 1988	SHH	S-MGS	0.39	0.26	0.46	-0.14
	CHA	S-MGS	0.27	0.16	0.27	-0.26
Mackinnon et al., 1991	ZX	AMM	0.16	0.31	0.32	0.00

Table 2.1. Continued.

Authors[a]	Breed[b]	Analyses[c]	Parameters[d]			
			h^2	m^2	h^2_T	r_{AM}
Baker, 1980			0.26	0.24	0.17	-0.45
		Weaning weight				
Thorpe et al., 1981	AN	RDD	0.80			
	BR	RDD	0.91			
	BN	RDD	0.50			
Nelsen et al., 1986	HEF	RSS	0.34			
Susan et al., 1984	ANG	PHS	0.46			
Koch et al., 1973	HEF	PHS	0.25			
Baker et al., 1992	ANGX, HEFX	PHS	0.13			
Lubout & Swanepoel, 1992	P	PHS	0.12			
Tawah et al., 1992	G	PHS	0.25			
	W	PHS	0.27			
Odenya et al., 1992	ANG, BRAH	PHS	0.35			
Bertrand & Benyshek, 1987	L	S-D-MGS	0.16	0.15	0.17	-0.30
	BRAN	S-D-MGS	0.28	0.20	0.28	-0.29
Hetzel et al., 1990	AX	S-D-MGS	0.14	0.29	0.29	
	HS	S-D-MGS	0.20	0.12	0.26	
Meyer, 1992b	HEF	AM	0.26		0.26	
	ANG	AM	0.44		0.44	
	ZX	AM	0.34		0.34	
Robinson, 1990	BX	AMM	0.34	0.16	0.42	
Mackinnon et al., 1991	ZX	AMM	0.20	0.32	0.36	0.00
Koch, 1989	HEF	AMM	0.16	0.19	0.20	-0.20
Meyer, 1992b	HEF	AMM	0.14	0.46	0.14	-0.60
	ANG	AMM	0.19	0.18	0.33	0.20
	ZX	AMM	0.60	0.49	0.24	-0.74

Table 2.1. Continued.

Authors[a]	Breed[b]	Analyses[c]	Parameters[d]			
			h^2	m^2	h^2_T	r_{AM}
Tawah et al., 1993	G	AMM	0.27	0.20	0.13	-0.68
	W	AMM	0.29	0.27	0.26	-0.39
Meyer, 1992b	HEF	AMP	0.14	0.13	0.09	-0.59
	ANG	AMP	0.20	0.14	0.32	0.22
	ZX	AMP	0.59	0.36	0.23	-0.78
Meyer, 1993a	HEF	AMP	0.22	0.07	0.09	0.16
Baker, 1980			0.30	0.52	0.25	-0.72
		Survival rate to weaning				
Baker et al., 1990	ANGX, HEFX	PHS	0.01			
Cundiff et al., 1982			0.04			
Morris et al., 1993a[e]	ANG, HEF	PHS	0.03			
Morris et al., 1987[e]	ANG, HEF	PHS	0.02			
Morris et al., 1993b[e]	ANGX, HEFX	PHS	0.01			

[a] Part of this table has been modified from Meyer (1992b) and Davis (1993).

[b] AK, Ankole; AN, Angoni; ANG, Angus; ANGX, Angus cross; AX, Africander cross; BN, Boran; BR, Barotse; BRAH, Brahman; BRAN, Brangus; BX, Brahman cross; CHA, Charolais; G, Gudali; HEF, Hereford; HEFX, Hereford cross; HS, Hereford-Shorthorn cross; L, Limousin; P, Pedi; RP, Red Poll; S, Sahiwal; SHH, Shorthorn; SIM, Simmental; W, Wakwa and ZX, Zebu cross.

[c] AM, Simple animal model; AMM, Animal model with maternal genetic effect; AMP, Animal model with a permanent environment dam effect; PHS, Paternal half sib; RDD, Dam-Daughter Regression; RSS, Son-Sire Regression; S-D-MGS, Combination of S-MGS and sire-dam model; S-MGS, Sire-maternal grandsire model;

[d] h^2, direct heritability; m^2, maternal heritability; h^2_T, total heritability; r_{AM}, direct-maternal genetic correlation.

[e] Estimated as trait of the dam.

its phenotype. It measures the fraction of the selection differential that would be realized if selection were based on the phenotypic value of the offspring (Tawah et al., 1993). During the last decade most estimates of direct and maternal heritabilities and direct-maternal genetic correlations have been obtained by equating variance component estimates from a sire-maternal grandsire and sire-dam models analyses to their expectations, while more recently estimates have been obtained using an animal model incorporating maternal effects. This has been estimated by restricted maximum likelihood procedure (REML) using a derivative-free algorithm and fitting an animal model. Maximum likelihood estimators are often considerably less biased by selection than their ANOVA counterparts (Meyer, 1991). Thus, estimates are normally slightly higher than those from the other methods. Tawah et al. (1992, 1993), using nearly the same data set, estimated slightly higher heritability estimates using REML than when using PHS. Because of its statistical properties, REML is now considered the optimal procedure for a wide range of analyses and has become the standard method for estimating genetic parameters. This method will be applied to the Kilifi Plantations calf data to estimate heritabilities using different animal models to reduce any bias resulting from selection.

Apart from the method and model of calculation, it must be stressed that heritability estimates are specific to the generation and population (breed) providing the data from which they were derived. In part, this point is illustrated in **Table 2.1**. Within the estimation methods/models, estimates from *B. taurus* cattle are generally lower than those from *B. indicus* and Sanga breeds. This difference can be attributed at least in part to variation in selection intensities. Most *B. taurus* cattle populations have been subjected to more selection than either *B. indicus* or Sanga breeds. Selection of parents reduces the genetic variance in the progeny by generating gametic phase disequilibrium (Falconer, 1981). The reduced additive variance therefore results in a reduced heritability among the progeny. As an estimate of heritability is needed in order to plan breeding programmes effectively it is advisable, in the absence of a reliable estimate from the specific population on which the breeding programme is to be carried out, to take an estimate which has been calculated on data on the same breed and if possible the same geographical area. Thus, the estimates generated in this study will assist Kilifi Plantations and units in the region keeping similar cattle to plan their breeding programmes.

The following general conclusions can be drawn from **Table 2.1**:

1. The heritability estimates (direct, maternal and total) for BWT, PADG and WWT are all of reasonable magnitude indicating that opportunity exists to improve these traits through selection. However, response to selection will not be as effective as it would be if the genetic

correlation (r_{AM}) between these effects were zero (Baker, 1980).

2. Heritability estimates (direct and maternal) are of a similar magnitude for PADG and WWT.
3. For BWT, h^2 is greater than m^2 in all cases.
4. For SRATE h^2 is very low (<0.05) indicating that it is more under environmental influences. Within breeds, h^2 is low and tends to be high when SRATE is considered as a trait of dam than as a trait of the offspring.

Therefore, both the direct and maternal component should be taken into account to achieve optimum progress in a selection programme, especially if an antagonistic relationship between them exists. An excellent review on the influence of maternal effects on the efficiency of selection has been given by Baker (1980). Most of these estimates of maternal effects are from beef cattle systems in which the calf ran freely with its dam (suckled system); estimates from dairy systems in which calves are bucket-reared are few.

2.6.2. Correlations.

A correlated response is any automatic response in the unselected traits occurring simultaneously with the response in the trait under selection (Shelby et al., 1963). A correlated response can be either positive or negative. Higher genetic correlations among growth traits have been reported than the corresponding phenotypic correlations (Nelsen and Kress, 1979; Massey and Benyshek, 1982; Susan et al., 1984).

Phenotypic correlations among traits are the gross correlations that include both the environmental and the genetic portions of the covariances. They are important because they directly affect the size of the selection differentials when several traits are used in the selection index, especially when the correlations are high (Lasley, 1978).

Genetic correlations among traits indicate how two traits are affected by the same genes, that is the correlation between the additive genetic values of two traits. The genetic correlation can be partitioned into the direct genetic correlation attributed to the individual's set of genes and the maternal genetic correlation attributed to maternal effects (**section 2.5.1**).

Estimates of genetic and phenotypic correlations among the preweaning traits have varied considerably. **Table 2.2** presents estimates from the literature. The estimates of the phenotypic correlation between BWT and PADG indicate that selection for PADG will have some influence on the BWT. The corresponding genetic correlation is moderate and influenced by the same set of genes. Thus, BWT would be increased directly by selection for PADG. BWT has been shown to be a major factor in calving difficulty, thus unrestricted selection for preweaning growth might eventually lead to an

Table 2.2. Estimates of genetic and phenotypic correlations among the preweaning traits in different breeds[a].

Traits		Authors	Breeds	r_A	r_M	r_P
BWT	PADG	DeNise et al., 1988	HEF, ANG	0.16		-0.03
		Koch et al., 1973	HEF	0.20		0.24
		Massey and Benyshek, 1982	L	0.45		0.08
		Massey and Benyshek, 1981a	L	0.78		
		Nelsen and Kress, 1979	HEF, ANG	0.42		
		Smith and Cundiff, 1976	HEF, ANG	-1.04		
		Pahnish et al., 1964	HEF	0.30		0.20
		Pani et al., 1977	HEF	0.14		
BWT	WWT	DeNise et al., 1988	HEF, ANG	0.34		0.25
		Koch et al., 1973	HEF	0.53		
		Koots et al., 1991		0.46	0.33	
		Mackinnon et al., 1991	ZX	0.57		0.43
		Meyer, 1994	ANG	0.81	0.59	0.52
			ZX	0.82	0.99	0.81
		Nelsen and Kress, 1979	HEF, ANG	0.53		0.53
		Pahnish et al., 1964	HEF	0.42		0.42
		Susan et al., 1984	ANG	0.59		0.35
BWT	SRATE	Baker et al., 1990	ANGX, HEFX	-0.90		-0.05
		Cundiff et al., 1982		-0.61		0.01
PADG	WWT	DeNise et al., 1988	HEF, ANG	0.98		0.97
		Koch et al., 1973	HEF	0.96		0.98
		Massey and Benyshek, 1981b	L	1.00		
		Pahnish et al., 1964	HEF	0.90		1.08
		Reynolds et al., 1991	HEF	1.00		
		Tawah et al., 1992	W	0.99		

[a] See footnote in Table 2.1; r_A, direct-genetic correlation; r_M, maternal-genetic correlation; r_P, phenotypic correlation.

increased calving difficulty.

The estimates of phenotypic and genetic correlations between WWT and BWT or PADG are large and positive implying that significant change can be made in BWT and PADG by selecting for heavier WWT. Selection can either be based on the individual or the dam depending on the breed and system of rearing. In the study by Meyer (1994) using Zebu crosses, it was concluded that selection would be more successful if based on the dam because the maternal genetic correlation was higher than the direct genetic correlation. Thus, there could be a concomitant improvement in both traits from selection on WWT.

The correlations between BWT and SRATE reported by Cundiff et al. (1982) and Baker et al. (1990) are both negative indicating that high BWT subsequently leads to a reduction in SRATE. Higher levels of SRATE were associated genetically with lower BWT indicating that these traits were under the influence of similar genes. Thus, direct selection for increased growth rate would tend to offset effects of natural selection to increase survival in cattle.

2.7. Conclusions.

It appears from the literature that, as well as the contribution of the sire genetic group (genotype), the maternal environment plays a major role in the genetic expression of performance characters and contributes significantly to phenotypic variation. The genotype of the dam affects the phenotype of the young through a sample of half of her direct additive genes for growth as well as through her genotype for maternal effects on growth. Maternal effects for preweaning traits other than BWT are expressed more in beef calves (because they are allowed to run with the dam) than in dairy calves (which are generally bucket fed). Crossbreeding experiments in which maternal effects are not estimated need to be interpreted with caution because of the possible confounding of maternal and individual effects.

Genetic parameters are characteristic of the population structure and will vary with the environment. They are not only necessary for planning future breeding strategies, but are also relevant for predicting response to selection and for evaluating genetic programmes. The magnitude of the genetic parameters of the preweaning traits indicate whether or not selection will yield significant improvement in performance. But, to achieve optimal progress in a selection programme, both the direct and maternal component should be taken into account, especially if an antagonistic relationship between them exists.

3. MATERIALS AND METHODS

3.1. Data source

The data for this study were extracted from cow and calf records kept at Kilifi Plantations in Kilifi District of Coast Province. Kilifi Plantations is a private dual purpose ranch with high priority on dairy production and sisal estate of approximately 2500 ha situated 60 km north of Mombasa Island along the Mombasa-Malindi road.

The Plantations lies in the coastal lowland cashewnut-cassava agro-ecological zone (Jaetzold and Schmidt, 1983) and is located at approximately 10 m above sea level on the Indian Ocean at 40° longitude east and 3.5° latitude south, with an average annual rainfall of 900-1000 mm. The rainfall is bimodal with the first rains ("Long Rains") generally falling towards the end of March. They are heavy in April and May, and decrease gradually until October. The second rains ("Short Rains") start towards the end of October, last until December or January but with no pronounced end. The highest temperatures occur during January and February, with the lowest temperatures recorded in June-July season. The soils have been described by Jaetzold and Schmidt (1983) as "imperfectly to poorly drained, deep, greyish brown, extremely firm, slightly calcareous, moderately sodic and moderately saline, slightly cracking clay, with a very thin topsoil of sandy clay loam". Sisal is grown for export, while milk is sold locally. The Plantations are divided by the Mombasa-Malindi road into two sections: the one to the east of the Mombasa-Malindi road is larger, having the offices, sisal estates, milk and sisal plants, airstrip, grazing and maternity paddocks and calf bomas; the beef herds are kept to the west of the road, where there are mainly grazing paddocks. Generally the milking/breeding herds are kept on the eastward side of the road because it has a lower trypanosomiasis challenge than the westward side.

The data were available through the KARI/ILCA collaborative programme. Each record consisted of calf identity and breed, date of birth, date of weaning, birth weight, weaning weight, calf sex, sire identity and breed, dam identity and breed, dam parity and date and reason of disposal (for assessment of SRATE). From this information, WAGE and PADG were estimated. Calves that survived to weaning were coded 1 while those not present at weaning were coded 0.

3.2. Breeding programme

The herd, which was established in 1939 from a continuous two-breed rotation crossbreeding system involving the Sahiwal (S) and Ayrshire (A) breeds, was transferred to Kilifi in 1963. A bulls were mated to cows with breed content of 67% S 33% A (Sr) and S bulls were mated to 67% A 33%

S (Ar) cows. These cows were sometimes mated back to bulls of the same breed as their sires to produce genotypes of 83% S 17% A or 83% A 17% S. In the mid 1970s, B was introduced to the rotation and first mated to the Sr and Ar cows to produce genotypes with breed compositions of 50% B 33% S 17% A or 50% B 33% A 17% S. In accordance with the rotation, these were usually mated to A and S bulls, respectively, though sometimes they were mated to B bulls or S or A. That is, the rotation was not followed strictly and several genotypes were generated with a minimum of 8% and maximum of 83% of any one breed. They are shown in **Figure 3.1**. The mating was by A.I and was not influenced by relative body size of the breed. A and S semen was from the Kenyan National A.I service while B semen was imported from the USA. Cows were bred to calve throughout the year.

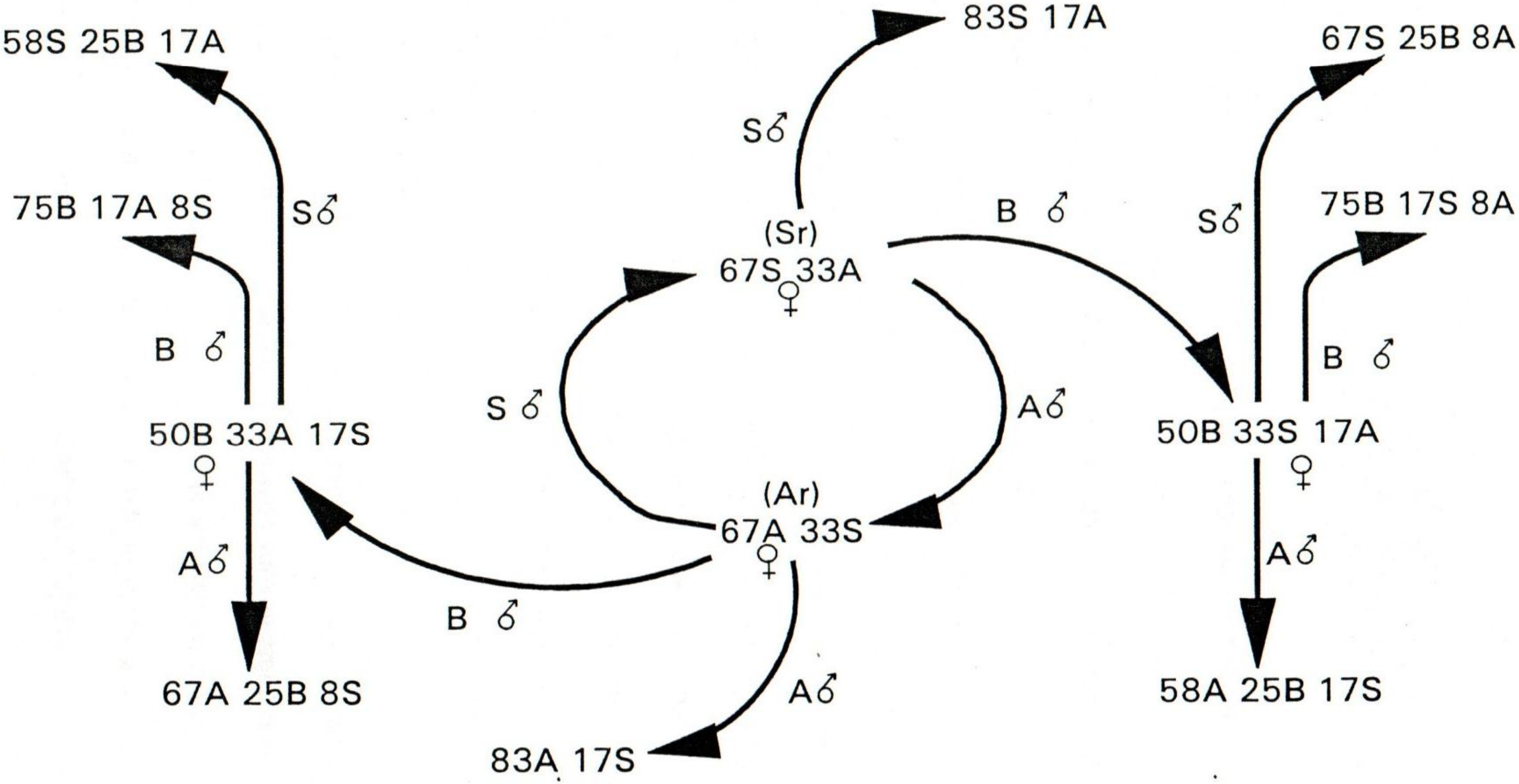
3.3. Calf management

After a calf was born, it was allowed to suckle colostrum from its own dam for about 24 hours after which it was confined in a movable calf pen within the cow paddock and taught to suckle on an artificial teat and then the bucket over the first four days. During these four days, the calves were ear tagged and then ear tattooed.

Subsequently, calves were transferred to the calf rearing area and grouped according to weight, being shifted from one pen to the next as they

Figure 3.1

MATING SYSTEMS



A, Ayrshire; B, Brown Swiss; S, Sahiwal; r, stabilized two-breed rotation. Figure indicates percent contribution of a breed.

got older. Each calf was fed 1.5 kg of whole milk three times a day at 6.00 a.m., 11.00 a.m. and 5.00 p.m. until the calves attained a weight of 55 kg at about 6-8 weeks of age. Thereafter, and up to weaning at about 90 kg, they were fed whole milk at the rate of two rations per day of 1.5 kg each. A concentrate mixture consisting of maize bran, maize germ, wheat germ, copra cake, sisal bole, molasses and mineral lick was always available in feeding troughs inside the calf boma. The material was supplied fresh each day on an *ad libitum* basis. All calf paddocks were supplied with clean fresh water daily.

Within two weeks of birth, calves were vaccinated against viral diseases and sprayed for ticks. If any calf was sickly and or weak it was treated for trypanosomiasis (without necessarily being diagnosed positive) and injected with a wide spectrum antibiotic. The most common disease problem was pneumonia which was prevalent during the wet seasons. Every calf was dewormed at about 6-8 weeks of age and again immediately before weaning. Regardless of age, weaning was done at around 90 kg. Castration of bull calves that were not retained for breeding was done postweaning. Thus, castration does not influence any comparison of males and females during the preweaning period. After weaning, the calves were moved to the young-stock paddocks and were separated by sex.

3.4. Data editing

The data set covered a period of 8 years (1985-1992). Initial analyses were carried out using SAS (SAS, 1987) to clean up the data for subsequent analyses. This comprised the elimination of incomplete records; e.g., those with missing sire genotype, dam genotype, calf genotype or dam parity. Also deleted were those records with improperly recorded and/or miscoded variables, for example, calves whose dates of birth and weaning were inconsistent with their dam's records and known management practices. Calves progeny of matings by crossbred sires were deleted. After this editing, the number of records available for analysis were 1443. **Table 3.1** gives the number of calves born (alive or dead) by sire breed and dam genotype. These calves were progeny of 38 A, 47 B and 31 S sires and 870 crossbred dams. **Table 3.2** shows the numbers of sires by breed and by year of calf births. Numbers of sires repeated across years are also indicated. **Table 3.3** gives the number of calves born (alive or dead) by sire breed and year.

3.5. Classification of effects

The sire breed were A, B and S. The dam genotypes were 67% S 33% A (Sr), 67% A 33% S (Ar), 50% B 33% S 17% A (B x Sr) and 50% B 33% A 17% S (B x Ar). The twelve calf genotypes (i.e., the diallel crossing of the three sire breeds by the four dam genotypes) are shown in **Figure 3.1**.

Table 3.1. **Numbers of progeny records by sire breed and dam genotype.**

	Dam genotype[a].				
Sire breed	Sr	Ar	B x Sr	B x Ar	Sire breed totals
Ayrshire	139	73	114	128	454
Sahiwal	54	228	74	240	596
Brown Swiss	133	143	46	71	393
Dam genotype totals	326	444	234	439	1443

[a] A, Ayrshire; B, Brown Swiss; S, Sahiwal; r, stabilized two-breed rotation; breed of sire shown before breed of dam.

Table 3.2. Numbers of sires used by breed and year.

	Year in which calves were born[a]								
Breed of sire	1985	1986	1987	1988	1989	1990	1991	1992	Total[b]
Ayrshire	9	10(7)	6(2)	13(4)	14(7)	12(8)	6(4)	1(1)	38
Sahiwal	6	2(2)	2(2)	6(2)	4(4)	3(2)	9(1)	15(3)	31
Brown Swiss	25	14(13)	11(4)	15(11)	2(1)	2(1)	1(1)	10(2)	47
Total	40	26(22)	19(8)	34(17)	20(12)	17(11)	16(6)	26(6)	116

[a] Repeat sires (in bracket) are also included in the total of sires for the year.
[b] Total number of unique sires (i.e. repeat sires excluded).

Table 3.3. Numbers of calves born classified by sire breed and year born.

	Year in which calves were born								
Breed of sire	1985	1986	1987	1988	1989	1990	1991	1992	Total
Ayrshire	99	46	18	56	114	72	48	1	454
Sahiwal	116	136	43	111	62	17	38	73	596
Brown Swiss	86	58	21	79	63	23	23	37	393
Total	304	240	82	246	239	112	109	111	1443

Parity of dam classes consisted of the first through fifth lactation numbers which were coded 1 to 5. The sixth and greater lactation numbers were combined and coded as parity class 6. The years were numbered individually from 1985 to 1992. Four seasons were defined: January to March for the first dry season; April to June for the main wet season; July to September and October to December as the secondary dry and wet seasons, respectively. Sex of calf was coded as 1 = female and 2 = male. The reasons of exit for those calves that never reached weaning were coded as: 1 - died from unknown reasons; 2 - died due to weakness; 3 - death from pneumonia; 4 - death from diarrhoea (scouring); 5 - death from other diseases; 6 - died due to accidents; 7 - culled due to weakness; 8 - culling for unknown reasons; 9 - Not seen. A total of 101 calves (7% of those born) either died or were culled before weaning due to these various reasons.

3.6. Data analyses.

Least squares analyses of variance were used to establish appropriate statistical models by first fitting all main effects and their first-order interactions. Non-significant interactions were then removed.

3.6.1. Analyses of preweaning growth traits

Analyses were done using the Model 1 of Harvey's (1990) least squares and maximum likelihood computer programme. The following fixed effects model was used to analyze preweaning growth traits.

$$Y_{ijklmn} = \mu + B_i + R_j + S_k + Y_l + W_m + (RS)_{jk} + e_{ijklmn}$$

where

Y_{ijklmn} is the observation on the n^th^ calf belonging to the i^th^ genetic group, born in the j^th^ year and k^th^ season of the l^th^ sex and born in the m^th^ parity of the dam.

μ is the underlying population constant common to all records.

B_i is the effect of i^th^ genetic group of calf.

R_j is the effect of the j^th^ year of birth.

S_k is the effect of the k^th^ season of birth.

Y_l is the effect of the l^th^ sex of calf.

W_m is the effect of the m^th^ parity of dam.

$(RS)_{jk}$ is the effect of the interaction between j^th^ year and k^th^ season of birth.

e_{ijklmn} is the random residual, assumed to be normally distributed with mean 0, and variance σ^2_e.

In another series of analyses the effect of the genotype of calf (B_i) was substituted by the effects of the genotype of sire and that of dam and their interaction. To determine the significance of specific class differences, linear contrasts of least squares class means were computed.

3.6.2. Analyses of survival rate to weaning

Calf survival was analysed using a logit transformation. The logistic transformation of a success probability p is log {p/(1-p)} which is written as logit (p). The ratio p/(1-p) is the odds of a success and so the logistic transformation of p is the log odds of a success (Collet, 1991). The logistic model used to study the effects of calf genotype (B), year of birth (R), season of birth (S) and sex (Y) was:

$$Z_{ijkl} = m + B_i + R_j + S_k + Y_l + e_{ijkl}$$

where

Z_{ijkl} is the logit of percent mortality for the i^{th} genotype, the j^{th} year, k^{th} season and l^{th} sex.

B_i is the logit for the i^{th} genotype.

P_j is the logit for the j^{th} year.

S_k is the logit for the k^{th} season.

Y_l is the logit for the l^{th} sex.

e_{ijkl} is the residual term.

The logistic models were fitted using an interactive maximum likelihood technique within the CATMOD procedure of SAS (SAS, 1987). This logistic approach gave estimates that were very similar to those from the least squares analyses of the binomial trait.

Because of the large number of subclasses that resulted when using 8 year categories with only 101 deaths or culls, fitting of year was not possible. Therefore, four periods were defined by combining years into groups according to whether a year had high mortality ($\geq$ 10%), medium high mortality (between 7.1 and 9.9%), medium low mortality (between 4.1 and 7%) and low mortality ($\leq$4%). Grouping years according to the response variable mortality creates a bias on the year effect which will obviously be significant. Period 1 (high mortality) included the year 1989; period 2 (medium high mortality) included the years 1988, 1991, and 1992; period 3 (medium low mortality) included the years 1986 and 1990 and period 4 (low mortality) included the years 1985 and 1987. These mortality subclasses according to year periods were rather arbitrary and biased the analysis of the effect of year on SRATE. The other classes were those defined in **section 3.5.**

These series of analyses were repeated fitting the calf mating system instead of the calf genotype. The mating systems were classified as: Sr and Ar, two-breed rotation (TWBR); S x Sr and A x Ar, two-breed backcross (TWBB); B x Sr and B x Ar, three-breed cross (THBC); B x (B x Sr) and B x (B x Ar), three-breed backcross (THBB); A x (B x Sr), S x (B x Sr), A x (B x Ar) and S x (B x Ar), three-breed rotation (THBR).

3.6.3. Estimation of crossbreeding parameters

To estimate genetic effects, each record was assigned coefficients according to maternal breed composition, individual breed composition, and the expected contributions of individual heterosis (H_I) and maternal heterosis (H_M). This procedure is advantageous over the conventional analyses of crossbreeding data in that it is a less complex statistical procedure, provides a clearer understanding of the genetic component and allows prediction of breed crosses that are not included in the data set (Robison et al., 1981). This procedure can also be used in designing programmes to utilize efficiently variation among breeds in crossbreeding systems.

The coefficients were computed as functions of the proportion of genes from each breed contributed to each individual and her dam. Similar procedures have been used by Robison et al. (1981), Ahlborn-Breier and Hohenboken (1991) and Thorpe et al. (1993). These parameters were

Table 3.4. **Coefficients for expected genetic effects of genetic groups (between specific breeds).**

Genetic group[a] Calf	Dam	G_IA[b]	G_IS[b]	G_MA[b]	G_MS[b]	H_IAB[c]	H_IAS[c]	H_MAB[c]	H_MAS[c]
S x Sr	S x Ar	.167	.833	.333	.667	0	.333	0	.667
S x Ar	A x Sr	.333	.667	.667	.333	0	.667	0	.667
S x (B x Sr)	B x Sr	.083	.667	.167	.333	0	.167	.333	0
S x (B x Ar)	B x Ar	.167	.583	.333	.167	0	.333	.667	0
A x Sr	S x Ar	.667	.333	.333	.667	0	.667	0	.667
A x Ar	A x Sr	.833	.167	.667	.333	0	.333	0	.667
A x (B x Sr)	B x Sr	.583	.167	.167	.333	.500	.333	.333	0
A x (B x Ar)	B x Ar	.667	.083	.333	.167	.500	.167	.667	0
B x Sr	S x Ar	.167	.333	.333	.667	.333	0	0	.667
B x Ar	A x Sr	.333	.167	.667	.333	.667	0	0	.667
B x (B x Sr)	B x Sr	.083	.167	.167	.333	.167	0	.333	0
B x (B x Ar)	B x Ar	.167	.083	.667	.167	.333	0	.667	0

[a] See footnote in Table 3.1. Genotypes are shown for calf and dam separately.

[b] Coefficient for the individual additive genetic breed effect (G_I) and maternal additive genetic effect (G_M) were calculated as the expected proportions of Ayrshire (A) and Sahiwal (S) genes in the offspring (I) and the dam (M), respectively.

[c] Coefficient for individual heterosis (H_I) and maternal heterosis (H_M) describes the probability that one gene at a locus was from A ancestry and the other from B ancestry for AB and that one gene at a locus was from A ancestry and the other from S ancestry f AS.

Table 3.5. Coefficients for expected genetic effects of genetic groups (*B. taurus-B. indicus*)[a].

Genetic group[b] Calf	Dam	$G_I TI$[c]	$G_M TI$[c]	$H_I TI$[d]	$H_M TI$[d]
S x Sr	S x Ar	-.667	-.333	.333	.667
S x Ar	A x Sr	-.333	.333	.667	.667
S x (B x Sr)	B x Sr	-.333	.333	.667	.667
S x (B x Ar)	B x Ar	-.167	.667	.833	.333
A x Sr	S x Ar	.333	-.333	.667	.667
A x Ar	A x Sr	.667	.333	.333	.667
A x (B x Sr)	B x Sr	.667	.333	.333	.667
A x (B x Ar)	B x Ar	.833	.667	.167	.333
B x Sr	S x Ar	.333	-.333	.667	.667
B x Ar	A x Sr	.667	.333	.333	.667
B x (B x Sr)	B x Sr	.667	.333	.333	.667
B x (B x Ar)	B x Ar	.833	.667	.167	.333

[a] After: Ahlborn-Breier and Hohenboken (1991).

[b] See footnote in Table 3.1. Genotypes are shown for calf and dam separately.

[c] Coefficient for the individual additive genetic breed effect (G_I) and maternal additive genetic effect (G_M) were calculated as the deviation of the proportion of Sahiwal genes from *B. taurus* genes for offspring (I) and the dam (M), respectively.

[d] Coefficient for individual heterosis (H_I) and maternal heterosis (H_M) describes the probability that one gene at a locus was from *B. taurus* ancestry and the other from Sahiwal (*B. indicus*) ancestry.

estimated in two ways. In the first analysis (**Table 3.4**), the covariables fitted to the breed cross means with all the fixed effects described above except calf genotype were: G_IA, G_IS, G_MA and G_MS, for expected proportions of A and S genes in the breed cross (I) and dam (M); H_IAB, for expected heterozygosity among *B. taurus* (A and B) derived genes in the individual calculated as G_I^mA $(1 - G_I^fA - G_I^fS) + G_I^fA$ $(1 - G_I^mA - G_I^mS)$ where superscripts f and m denote the breed content in the sire and the dam, respectively; H_IAS, for expected heterozygosity between A and S derived genes in the individual, calculated as G_I^mA $G_I^fS + G_I^fA$ G_I^mS; H_MAB for expected heterozygosity among *B. taurus* derived genes in the dam (M) of the individual (to estimate maternal heterosis); and H_MAS, for expected heterozygosity between A and S derived genes in the dam of the individual. Additive breed contents were fitted for two of the three breeds, A and S, because the third breed content is entirely dependent on the first two.

In the second analysis (**Table 3.5**), the A and B breeds were classified as *B. taurus* because performance of A and B crosses did not differ in the genetic group analysis. The covariables fitted were: G_ITI calculated as the deviation of the proportions of S genes (*B. indicus* - I) from *B. taurus* (T) genes for the individual, i.e. G_ITI was calculated as $1 - 2G_IS$; G_MTI, calculated as $1 - 2G_MS$; H_ITI, for expected heterozygosity between S and *B. taurus* derived genes in the individual calculated as G_I^fS $(1 - G_I^mS) + G_I^mS$

(1 - $G_I{}^fS$); and, H_MTI, for the *B. taurus-B. indicus* heterozygosity in the dam of the individual. The coefficients for both the individual and maternal heterosis effects are based on the assumption that a linear relationship exists between dominance and degree of heterozygosity.

3.6.4. Estimation of genetic and phenotypic parameters

Heritabilities were calculated from variance and covariance components estimated using a derivative-free restricted maximum likelihood (DFREML) procedure (Meyer, 1992a). Correlations were estimated using the paternal half sib procedure (Harvey, 1990).

3.6.4.1. Heritabilities

To obtain the starting heritability estimates to be used in DFREML, Model 3 of Harvey's (1990) least squares and maximum likelihood computer programme was used. This gave paternal half sib heritability estimates. The following mixed model was fitted.

$$Y_{jklmnpqr} = \mu + R_j + S_k + Y_l + W_m + (RS)_{jk} + D_n + A_p + (DA)_{np} + N_{qp} + e_{jklmnpqr}$$

where

$Y_{jklmnpqr}$ is the measure on the r^{th} offspring born in year j and season k to a dam of genetic group n of parity m, to a sire q and of genetic group p, and of sex l.

D_n is the effect of the n^{th} genetic group of dam.

A_p is the effect of p^{th} genetic group of sire.

$(DA)_{np}$ is the effect of the interaction between n^{th} genotype of dam and p^{th} genotype of sire.

N_{qp} is the effect of the q^{th} sire nested within p^{th} genotype of sire.

The other factors remain as in the previous models.

For this estimation all sires with fewer than 4 progeny were deleted. Therefore 30 A, 32 B and 17 S sires were used resulting in a reduction in the number of records from 1443 for BWT and SRATE to 1384, and from 1337 for PADG and WAGE to 1282 (**Table 4.9**).

These paternal half sib estimates were then fitted in Models 1, 3 and 4 of DFREML (Meyer, 1992a) as 'starting values' in an univariate analyses (single-trait analyses). The fixed (main) effects fitted were genotype of calf (breed), year-season subclass, sex and dam parity. Preliminary analyses for BWT, PADG and WAGE identified a significant interaction between year and season of birth. Subsequently analyses were carried out fitting year-season of

Table 3.6. **Characteristics of the data structure for univariate REML analyses.**

	Trait[a]			
	BWT and SRATE		PADG and WAGE	
	Model 1	Model 3 & 4	Model 1	Model 3 & 4
No. records	1443	1443	1337	1337
No. animals	1914	2429	1776	2276
No. sires	93	116	93	113
No. dams	378	870	346	826
Progeny per sire	15.5	12.4	14.4	12.8

[a] BWT, birth weight; SRATE, survival rate to weaning; PADG, preweaning average daily gain; WAGE, weaning age.

birth subclasses as a single main effect since DFREML does not accommodate interactions. Characteristics of the data structure for all traits and models are summarized in **Table 3.6.**

The first analyses fitted Model 1, a simple animal model which ignored any maternal influence but which had the animal's additive genetic effect as the only random effect. Model 3 fitted the maternal genetic effect as a second random effect for each animal with the same covariance (relationship) structure as the direct additive genetic effects. It attributed all maternal effects to the genotype of the dam and assumed that direct and maternal effects was uncorrelated, i.e., $\sigma_{AM} = 0$. Model 4 allowed for a covariance between direct and maternal effects, i.e., $\sigma_{AM} \neq 0$. All known pedigree information was included in the analyses in order to minimize bias due to selection and to increase the accuracy of estimation through additional ties between animals (Meyer, 1994).

Statistically, with the fixed effects F_{ijklm} identical for all analyses, the three models were:-

Model 1

$Y_{ijklmn} = F_{ijklm} + a_n + e_n$

Model 3

$Y_{ijklmno} = F_{ijklm} + a_n + m_o + e_n$

with Cov $(a_n, m_o) = 0$

Model 4

$Y_{ijklmno} = F_{ijklm} + a_n + m_o + e_n$

with Cov $(a_n, m_o) \neq 0$

with $F_{ijklmn} = B_i + RS_{jk} + Y_l + W_m$

where

$Y_{ijklmn(o)}$ is the BWT, PADG, WAGE or SRATE record for animal n with dam o and fixed effects combination F_{ijklm}.

B_i is the effect of i^{th} genetic group of the calf.

RS_{jk} is the effect of the j^{th} year and k^{th} season of birth subclass.

Y_l is the effect of the l^{th} sex of calf.

W_m is the effect of the m^{th} parity of dam.

a_n is the direct additive genetic effect of the n^{th} animal.

m_o is the maternal additive genetic effect of the o^{th} dam.

$e_{ijklmn(o)}$ is the random residual error pertaining to $Y_{ijklmn(o)}$.

In matrix notation these models can be written as:-

Model 1

$y = X\beta + Z_1u_1 + e$

with

$E(y) = X\beta,$

and

$Var(y) = Z_1AZ_1'\sigma^2_A + I\sigma^2_e$

Model 3

$y = X\beta + Z_1u_1 + Z_2u_2 + e$

with

$E(y) = X\beta,$

and

$Var(y) = Z_1AZ_1'\sigma^2_A + Z_2AZ_2'\sigma^2_M + I\sigma^2_e$

Model 4

$y = X\beta + Z_1u_1 + Z_2u_2 + e$

with

$E(y) = X\beta$

and

$$\mathrm{Var}(y) = Z_1AZ_1'\sigma^2_A + Z_2AZ_2'\sigma^2_M + (Z_1AZ_2' + Z_2AZ_1')\,\sigma_{AM}$$
$$+ I\sigma^2_e$$

where

y is a vector of phenotypes (BWT, PADG, WAGE and SRATE).

ß is a vector of fixed effects (genetic group of calf, year and season of birth subclass, sex of calf and parity of dam).

u_1 is a vector of random direct additive genetic effects.

u_2 is a vector of random maternal additive genetic effects.

σ^2_A is the additive genetic variance.

σ^2_M is the maternal genetic variance.

σ_{AM} is the direct-maternal genetic covariance.

σ^2_e is the error variance.

X, Z_1 and Z_2 are the design matrices relating elements of y to the fixed and random effects.

With A equal to the numerator relationship matrix between animals and I is the identity matrix, the (co)variance structure for the analyses was described as

$V(u_{1}) = A\sigma^2_A$

$V(u_2) = A\sigma^2_M$

$V(e) = I\sigma^2_E$

$Cov\ (u_1, u_2) = A\sigma_{AM}$

Heritabilities (direct, h^2 and maternal, m^2) and direct-maternal genetic correlation (r_{AM}) were estimated as follows:-

$h^2 = \sigma^2_A/\sigma^2_P$

$m^2 = \sigma^2_M/\sigma^2_P$ and

$r_{AM} = \sigma_{AM}/\sqrt{(\sigma^2_A\ \sigma^2_M)}$

where

σ^2_P is the phenotypic variance and equal to the sum of the direct (σ^2_A), maternal (σ^2_M), and error (σ^2_e) variance and direct-maternal covariance (σ_{AM}) components.

Heritability of total influences (h^2_T) was estimated as follows (Willham, 1972):

$$h^2_T = (\sigma^2_A + 0.5\sigma^2_M + 1.5\sigma_{AM})/\sigma^2_P$$

All calculations were carried out using the DFUNI program of Meyer's (1992a) DFREML package employing the simplex procedure to locate the maximum of the log likelihood as described by Meyer (1989).

3.6.4.2. Correlations

Paternal half-sib estimates of genetic and phenotypic correlations were obtained using the same mixed model as for the paternal half sib heritability estimates. But this time, BWT and SRATE were included in the same model while in another model, BWT, PADG and WAGE were fitted simultaneously as the dependent variables. Sires with fewer than 4 progeny were deleted. Thus 1384 records were used in the model with BWT and SRATE as the dependent variable. In the other model, 1282 observations, were used.

4. RESULTS

4.1. Means and variances

Table 4.1 shows the overall means, residual standard deviations (SD) and coefficients of variation (CV) for the preweaning traits. The CV for PADG and WAGE were the same (11.4%) because of the inherent interdependence of PADG and WAGE. The mean (±SE) BWT was 30.9 ± 0.18 kg and the mean PADG was 488 ± 2.1 g/day. This resulted in the attainment of a mean WWT of 92 kg in 126 ± 0.6 days. The SRATE averaged 93 ± 0.9%.

4.2. Environmental factors

4.2.1. Effect of year and season of birth and their interactions

The trends over the years and season and their interactions are shown in **Figures 4.1, 4.2** and **4.3**. The levels of significance of these fixed effects are presented in **Table 4.1**. The year of birth significantly influenced ($P<0.01$) all the preweaning traits (BWT, PADG, WAGE and SRATE). The significant effect on SRATE was expected because years were grouped into periods according to the level of mortality. BWT was highest in 1985 and lowest in 1987 with a least squares difference of 3.4 kg between them.

Table 4.1. Least squares means (LSM) and standard errors (SE) by parity and sex for BWT, PADG, WAGE and SRATE.

	Traits[a]											
	BWT(kg)			PADG(g/day)			WAGE (days)			SRATE(%)		
Source[a]	n	LSM	SE	n	LSM	SE	n	LSM	SE	n	LSM	SE
Parity												
1	419	29.9	0.28	393	490	3.3	393	128	0.9	419	94	1.4
2	244	30.9	0.34	225	490	4.0	225	126	1.1	244	93	1.7
3	178	31.2	0.40	167	494	4.6	167	124	1.2	178	95	2.0
4	169	31.7	0.40	155	483	4.7	155	126	1.2	169	92	2.0
5	126	31.1	0.46	114	482	5.5	114	127	1.4	126	92	2.3
6+	307	30.4	0.32	283	491	3.7	283	126	1.0	307	95	1.6
Sex												
Female.	673	29.5	0.24	625	486	2.8	625	129	0.7	673	94	1.2
Male.	770	32.2	0.22	712	489	2.5	712	123	0.7	770	92	1.1
Overall	1443	30.9	0.18	1337	488	2.1	1337	126	0.6	1443	93	0.9
Mean(S.D)		31(5.36)			485(55.3)			127(14.5)			93(25.2)	
C.V(%)		15.9			11.4			11.4			26.8	
Anova[b]												
Calf genotype		***			+			ns			ns	
Year of birth(Y)		***			***			***			***	
Season of birth(S)		***			***			**			ns	
Parity		**			ns			ns			ns	
Sex		***			ns			***			ns	
Y x S		***			***			***			-	

[a] See footnote in Table 3.5; S.D., Residual standard deviation; C.V., Coefficient of variation.

[b] ANOVA, Analyses of variance; ns, non-significant (P>0.1); + P<0.1; * P<0.05; ** P<0.01; *** P<0.001.

Figure 4.1 **Relationship between BWT, PADG, WAGE and SRATE by year of birth**

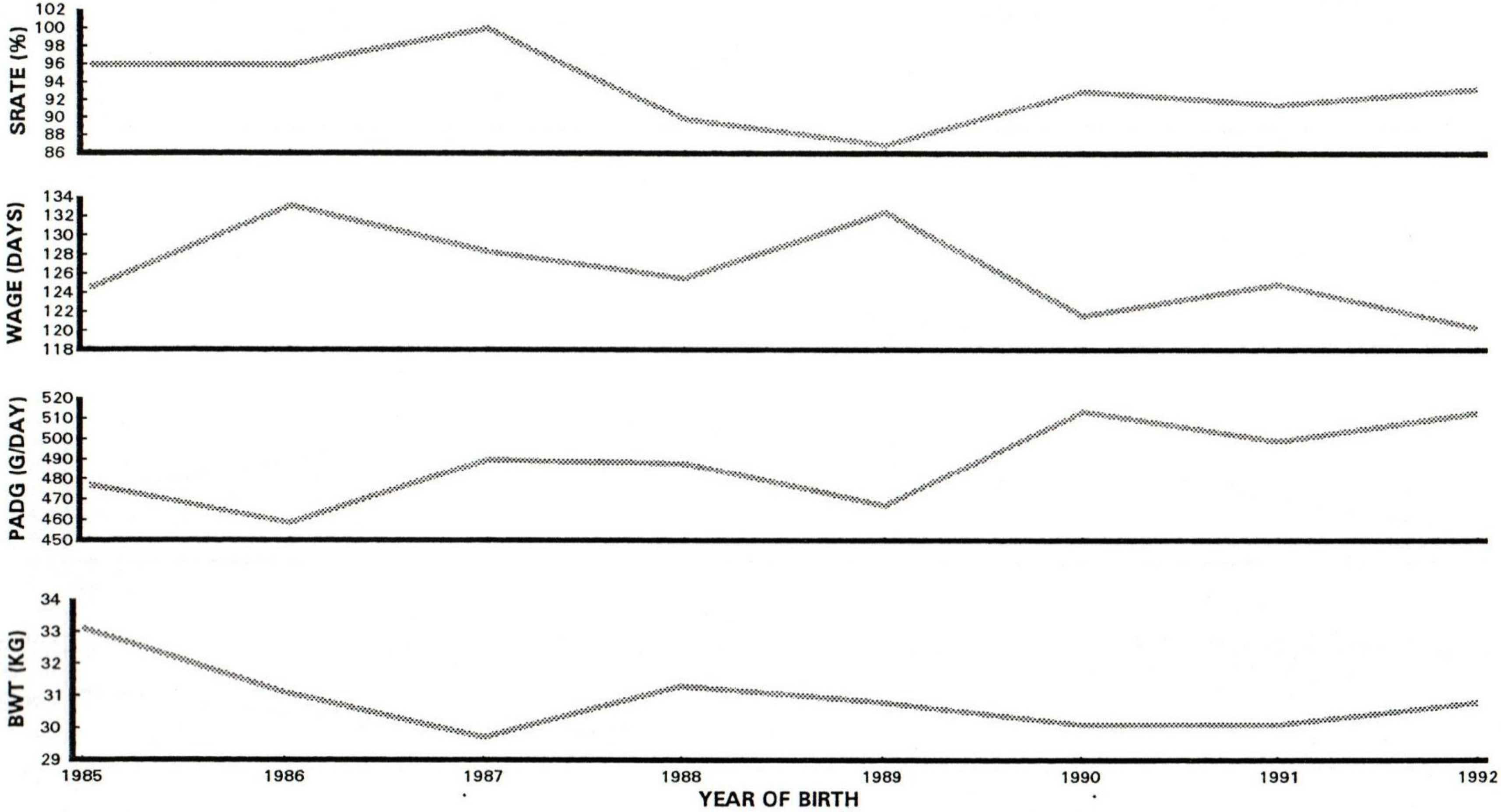


Figure 4.2 Relationship between BWT, PADG, WAGE and SRATE by season of birth

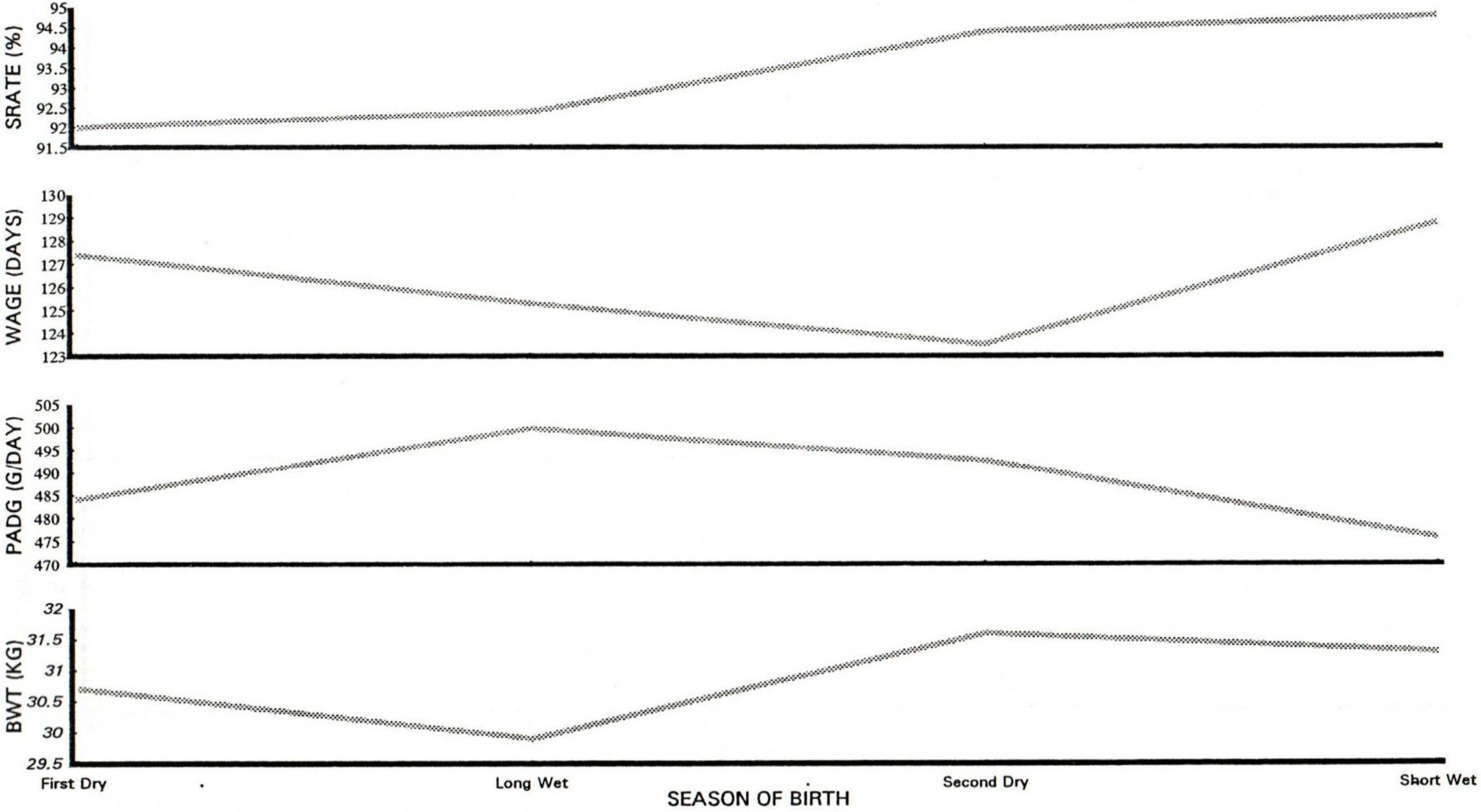
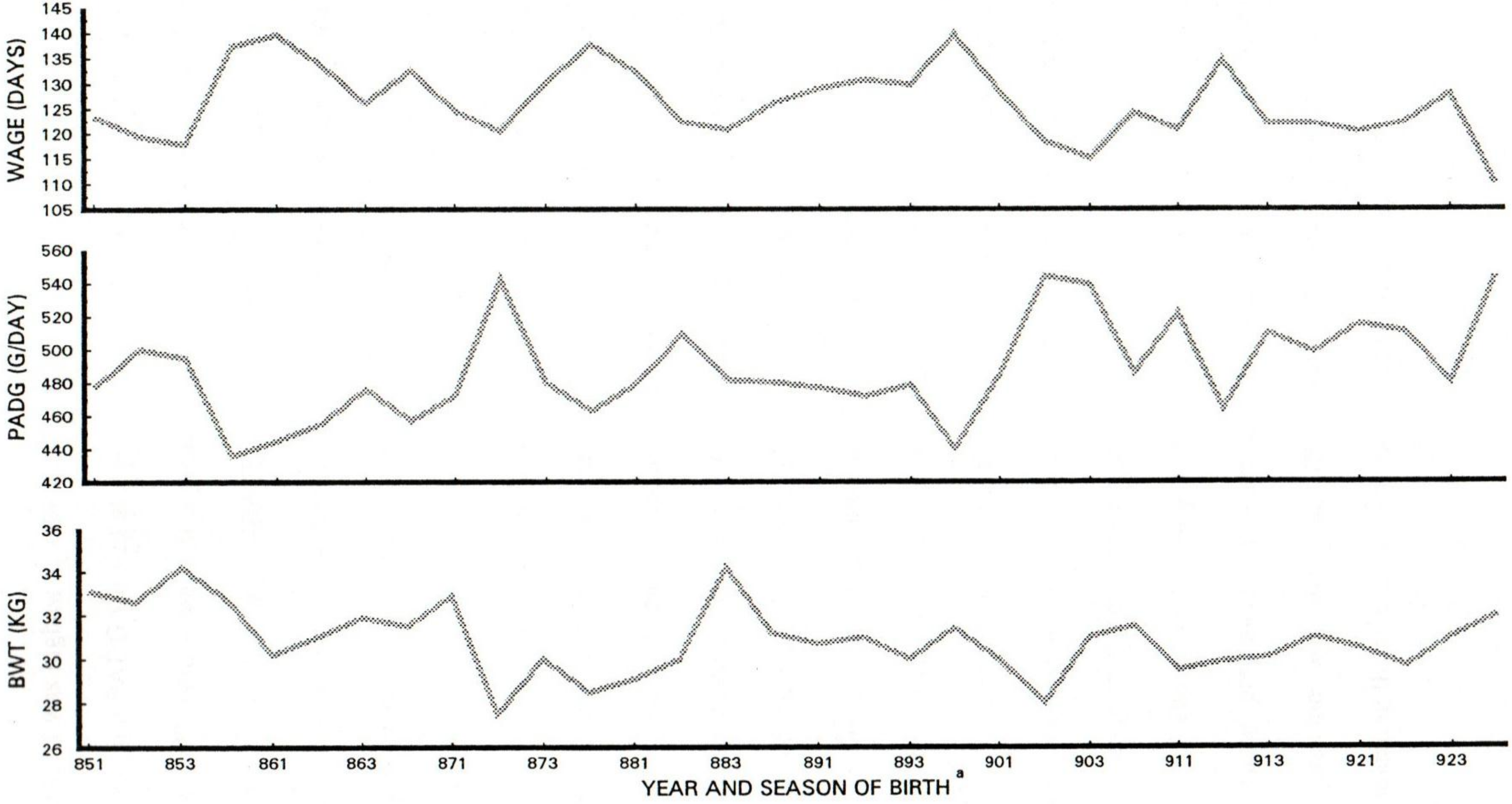


Figure 4.3 Relationship between BWT, PADG and WAGE by year and season of birth



[a] First two digits denote year and last digit denotes season

PADG was highest in 1990 and lowest in 1986. For WAGE those years that had high PADG weaned at a younger age and vice versa. Thus, calves born in 1990 were weaned at a younger WAGE, while those born in 1986 were weaned at a later age. SRATE were above 96% in the years 1985 and 1987. These were the years which recorded the highest and the lowest BWT, respectively. There was no clear trend over the years for these preweaning traits.

Season was a significant ($P<0.01$) source of variation for BWT, PADG and WAGE, but not for SRATE. BWT was highest in the second dry season (July-September) and lowest in the long wet season (April-June) with a least square difference of 1.6 kg. Generally the calves born in the second half of the year (i.e., from July to December) had higher BWT than those born during the first six months. PADG was highest ($P<0.001$) in the long wet season and lowest in the short wet season (500 vs. 476 g/day).

Calves born in the second dry season (which were heavier at birth) were weaned at a younger age. The effect of season on BWT is through its influence on the dam during gestation.

The interaction of year and season of birth was not fitted for SRATE because preliminary analyses showed that it was not significant. This interaction was significant ($P<0.001$) for BWT, PADG and WAGE indicating that for these traits the effect of season was not independent from that of the year. Calves born in the second dry season (July-September) of 1988 were the heaviest at 34.2 kg, while the lightest were born in the long wet season (April to June) of 1987 with a weight of 27.5 kg. PADG was highest in calves born in the 1990 long wet season (April to June) and lowest in those born in the 1985 short wet season (October to December). The year-season classes with the highest PADG tended to have youngest WAGE consistent with the expected negative relationship between PADG and WAGE.

4.2.2. Effect of dam parity and calf sex

Least squares means, standard errors and levels of significance for dam parity and calf sex are presented in **Table 4.1**. Parity of dam only significantly ($P<0.01$) affected BWT. The effect of dam parity followed the expected pattern whereby calves from early and later parity cows had the lowest BWT. There was a distinct reduction in the number of calves from first and second parity cows.

Sex of calf had a significant effect ($P<0.001$) on BWT and WAGE, but not on PADG and SRATE. Male calves were heavier than females at birth, with a least squares difference of 2.7 kg (9.2%), and males were weaned 6 days younger. When BWT was included as a covariate in the model, sex of calf significantly affected PADG ($P<0.001$) and SRATE ($P<0.05$).

4.3. Genetic factors

4.3.1. Effect of sire breed

Sire breed was not significant (P>0.05) for BWT and ranged from 31.2 kg for B-sired calves to 30.5 kg for S-sired calves **(Table 4.2)**. Sire breed approached significance (P<0.1) for PADG. The PADG ranged from 493 g/day for A-sired calves to 482 g/day for S-sired calves, a difference of less than 4% of the mean.

Similarly sire breed did not differ significantly (P>0.05) for WAGE, or for SRATE. The sire breed with the youngest, A, and oldest (B and S), WAGE differed by only 2 days, a difference of less than 2%. For SRATE the variation was also small, with a range of 3%.

4.3.2. Effect of dam genotype

Dam genotype was significant (P<0.001) for BWT but not for the other traits **(Table 4.2)**. B x Ar dams gave birth to the heaviest calves (32.0 kg) while the BWT of calves from Sr dams were the lightest (29.9 kg). When comparisons are made within dam mating system, no significant different was observed, i.e., there were no significant (P>0.1) difference in BWT between calves from Sr and Ar dams and no significant difference in BWT of calves from the B crosses.

Table 4.2. Least squares means (LSM) and standard errors (SE) for BWT, PADG, WAGE and SRATE by sire breed and da genotype.

	Traits[a]											
	BWT(kg)			PADG(g/day)			WAGE (days)			SRATE(%)		
Breed group[b]	n	LSM	SE	n	LSM	SE	n	LSM	SE	n	LSM	SE
Sire breed.												
Sahiwal(S)	596	30.5	0.28	561	490	3.2	561	127	0.84	596	95	1.4
Ayrshire (A)	454	30.9	0.29	418	493	3.4	418	125	0.89	454	94	1.4
Brown Swiss(B)	393	31.2	0.30	358	482	3.6	358	127	0.93	393	92	1.5
Dam genotype.												
Sr	326	29.9	0.33	301	494	3.8	301	127	1.0	326	93	1.6
Ar	444	30.2	0.29	409	488	3.4	409	128	0.9	444	93	1.4
B x Sr	234	31.4	0.36	218	485	4.2	218	126	1.1	234	94	1.8
B x Ar	439	32.0	0.28	409	484	3.3	409	125	0.9	439	93	1.4
Overall	1443	30.9	0.18	1337	488	2.1	1337	126	0.6	1443	93	0.9
Anova[c]												
Sire breed (B)		ns			+			ns			ns	
Dam genotype (D)		***			ns			ns			ns	
B x D		ns			ns			ns			-	
Year of birth(Y)		***			***			***			***	
Season of birth(S)		***			***			**			ns	
Parity		**			ns			ns			ns	
Sex		***			ns			***			ns	
Y x S		***			***			***			-	

[a b c] See footnote in Tables 3.3 and 4.1.

The B x Ar dams can be compared with Sr, because they are both from Ar dams; correspondingly the B x Sr dams can be compared with Ar. The B x Ar dams produced calves that had a 2.1 kg (7.0%) heavier ($P<0.001$) BWT than Sr dams, and the B x Sr dams produced calves that were 1.2 kg (4%) heavier at birth ($P<0.01$) than the calves born to Ar dams.

For WAGE and SRATE, there were no significant difference among the dam genotypes (**Table 4.2**). The WAGE ranged from 125 days for B x Ar dams to 128 days for Ar dams, a difference of less than 2% of the mean. Survival differences attributed to the dam genotype were low and insignificant.

Because of the two classes of the dam mating system (basically TWBR and THBC), it can be inferred that dam mating system significantly ($P<0.05$) influenced BWT and PADG (**Table 4.5**). The absence of large differences between TWBR and THBC dams showed that the introduction of the third sire breed, B, for matings with the TWBR dams, Ar and Sr, resulted in small changes in calf preweaning performance, and only the effect on BWT was significant ($P<0.001$).

4.3.3. Effect of calf genotype

The genotype of calf had a significant effect ($P<0.001$) on BWT and approached significance ($P<0.1$) for PADG (**Table 4.1**). The least squares means for the various genotypes are shown in **Table 4.3**, together with their

Table 4.3. **Least squares means (LSM) and standard errors (SE) by calf genotype for BWT, PADG, WAGE and SRATE[a].**

	Traits											
	BWT(kg)			PADG(g/day)			WAGE (days)			SRATE(%)		
Calf genotype[b]	n	LSM	SE	n	LSM	SE	n	LSM	SE	n	LSM	SE
S x Sr	54	29.5	0.70	50	492	8.1	50	128	2.1	54	93	3.5
S x Ar	228	29.6	0.36	209	496	4.3	209	127	1.1	228	92	1.8
S x (B x Sr)	74	31.2	0.59	73	484	6.7	73	127	1.7	74	99	2.9
S x (B x Ar)	240	31.8	0.34	229	487	4.0	229	125	1.0	240	95	1.7
A x Sr	139	30.0	0.46	131	504	5.4	131	125	1.4	139	96	2.4
A x Ar	73	30.6	0.60	67	488	7.1	67	126	1.9	73	95	3.1
A x (B x Sr)	114	31.1	0.49	103	488	5.8	103	126	1.5	114	91	2.5
A x (B x Ar)	71	32.4	0.61	63	475	7.2	63	126	1.9	71	91	3.1
B x Sr	133	30.3	0.45	120	488	5.4	120	127	1.4	133	91	2.2
B x Ar	143	30.5	0.43	133	481	5.1	133	129	1.3	143	93	2.2
B x (B x Sr)	46	31.8	0.76	42	484	8.9	42	125	2.3	46	93	3.8
B x (B x Ar)	128	31.8	0.47	117	491	5.5	117	124	1.4	128	93	2.4
Overall	1443	30.9	0.18	1337	488	2.1	1337	126	0.6	1443	93	0.9

[a] See footnote in Table 3.3.

[b] A, Ayrshire; B, Brown Swiss; S, Sahiwal; r, stabilized two-breed rotation; breed of sire shown before breed of dam.
NB For significance tests see Table 4.1.

standard errors. The A x (B x Ar) calves had highest BWT (32.4 kg) while the S x Sr calves were the lightest (29.5 kg). The BWT increased with the percentage of *B. taurus* genes. The proportion of *B. taurus* genes ranged from 92% in the A x (B x Ar) calves to 17% in the S x Sr calves. The PADG ranged from 504 g/day for A x Sr (Ar) calves to 475 g/day for A x (B x Ar), a difference of less than 6% the mean.

Similarly calf genotypes did not differ significantly ($P>0.05$) for WAGE, or for SRATE. The genotypes with the youngest, B x (B x Ar), and oldest, B x Ar, WAGE differed by only 5 days, a difference of less than 4%. Variation for SRATE was greater, a range of 8% units, but with no apparent trend associated with the proportion of *B. taurus* genes.

4.3.3.1. Mating system comparisons

Differences between mating systems were significant in the analyses of variance for BWT ($P<0.001$) and PADG ($P<0.01$) but not for WAGE and SRATE (**Table 4.4**). Several mating system comparisons were significant ($P<0.01$) for BWT and some for PADG, but few even approached significance for WAGE or SRATE (**Table 4.5**).

The absence of large differences between TWBR and THBC showed that the introduction of the third sire breed, B, for matings with the two-breed rotational crossbred dams, Ar and Sr, had no important effects on calf

Table 4.4. Least squares means (LSM) and standard errors (SE) by mating system for BWT, PADG, WAGE and SRATE.

	Traits[a]											
	BWT(kg)			PADG(g/day)			WAGE (days)			SRATE(%)		
Mating systems	n	LSM	SE	n	LSM	SE	n	LSM	SE	n	LSM	SE
Two-breed rotation	367	29.8	0.30	340	499	3.5	340	126	0.9	367	93	1.5
Two-breed backcross	127	30.1	0.46	117	489	5.4	117	128	1.4	127	94	2.3
Three-breed cross	276	30.4	0.32	253	484	3.8	253	128	1.0	276	92	1.6
Three-breed backcross	117	32.2	0.48	105	479	5.7	105	125	1.5	117	92	2.4
Three-breed rotation	556	31.6	0.23	522	488	2.7	522	125	0.7	556	94	1.2
Overall	1443	30.9	0.18	1337	488	2.1	1337	126	0.6	1443	93	0.9
Anova[b]												
Mating system		***			**			ns			ns	
Year of birth(Y)		***			***			***			***	
Season of birth(S)		***			***			**			ns	
Parity		**			ns			ns			ns	
Sex		***			ns			***			ns	
Y x S		***			***			***			-	

[a] [b] See footnote in Table 3.5 and 4.1.

Table 4.5. Linear contrasts of mating systems means.

	Traits[a]							
	BWT(kg)		PADG(g/day)		WAGE (days)		SRATE(%)	
Mating system[b]	LSM	SE	LSM	SE	LSM	SE	LSM	SE
Dam mating system								
TWBR minus THBC	-1.7***	0.31	8*	3.6	2	0.9	-1	1.6
Calf mating system								
TWBR minus TWBB	-0.3	0.52	10	6.1	-2	1.6	-1	2.7
TWBR minus THBC	-0.6	0.42	15**	5.0	-2	1.3	1	2.2
TWBR minus THBB	-2.4***	0.57	20**	6.7	1	1.8	1	2.9
TWBR minus THBR	-1.8***	0.36	11**	4.2	1	1.1	-1	1.9
TWBB minus THBC	-0.3	0.56	5	6.6	0	1.7	2	2.9
TWBB minus THBB	-2.1**	0.67	10	7.9	3	2.1	2	3.4
TWBB minus THBR	-1.5**	0.51	1	5.9	3+	1.6	0	2.6
THBC minus THBB	-1.8**	0.58	5	6.8	3	1.8	0	2.9
THBC minus THBR	-1.2**	0.39	-4	4.6	3+	1.2	2	1.2
THBB minus THBR	0.6	0.54	-9	6.4	0	1.7	2	2.8

[a] See footnote in Table 3.5.

[b] TWBR, Two-breed rotation; TWBB, Two-breed backcross; THBC, Three-breed cross; THBB, Three-breed backcross; THBR, Three-breed rotation.

\+ $P<0.1$

* $P<0.05$

** $P<0.01$

*** $P<0.001$

preweaning performance. Similarly the comparison of THBC and THBR, which estimated the difference between the second and third generations of the three-breed rotation crossbreds resulted in small changes in calf preweaning performance, and only the effect on BWT was significant ($P<0.01$).

An alternative mating system to the introduction of the third breed of sire is the backcrossing of the Ar and Sr. The contrasts examining this mating system comparison, TWBR minus TWBB, showed no significant change in calf performance. Similarly the comparison of the three-breed crosses with their backcrosses (THBC minus THBB) was significant only for BWT (-1.8 ± 0.58 kg).

4.4. Estimates of additive and heterotic effects

Table 4.6 shows the estimates for G_I, G_M, H_I and H_M effects on calf performance. The G_I and G_M for A and S were not significant for any of the calf performance traits. For the *B. taurus-B. indicus* comparision, G_I approached significance ($P<0.1$) for BW. Calves from *B. taurus* dams were 1.5 ± 1.4 kg heavier at birth than those from S dams. This is the equivalent of 28 % of the phenotypic SD and less than 5 % of the parental mean, confirming small differences for BW between the two breeds. The G_M effect was not significant for any of the preweaning traits.

Table 4.6. **Means and SD for BWT, PADG, WAGE and SRATE and parameter estimates and SE for the genetic effects[a].**

	BWT		PADG		WAGE		SRATE	
	(kg)		(g/day)		(days)		(%)	
	$\overline{X}$	SD	$\overline{X}$	SD	$\overline{X}$	SD	$\overline{X}$	SD
Phenotype	31.0	5.36	485	55.3	127	14.5	93	25.21
	Est.	SE	Est.	SE	Est.	SE	Est.	SE
Individual breed effect								
Ayrshire (A)[b]	-0.61	1.52	1	18.1	2	4.8	5.4	7.75
Sahiwal (S)[b]	-1.81	1.77	4	20.8	7	5.5	2.7	8.98
B. taurus-*B. indicus*[c]	0.76[+]	0.43	-2	5.0	-1	1.3	-0.0	2.16
Maternal breed effect								
Ayrshire[b]	-0.45	2.52	-24	30.2	8	7.9	-4.5	12.81
Sahiwal[b]	-1.07	2.89	2	34.5	6	9.1	-5.5	14.68
B. taurus-*B. indicus*[c]	0.72	0.53	-10	6.3	1	1.7	0.9	0.03
Individual heterosis[d]								
AS	-0.70	1.29	26[+]	15.1	-3	4.0	-7.0	6.54
AB	-1.01	1.02	3	12.1	4	3.2	-7.7	5.18
B. taurus-*B. indicus*	0.43	0.90	-7	10.6	-3	2.8	3.7	4.57
Maternal heterosis[d]								
AS	-0.31	2.46	25	29.2	-7	7.7	0.5	12.51
AB	1.51	1.41	16	16.5	-6	4.3	-2.1	7.15
B. taurus-*B. indicus*	-3.19[*]	1.25	-4	14.8	6	3.9	-0.0	6.35

[a] Derived from different models described in the text.

[b] Estimates (Est) represents the additive genetic breed effects.

[c] Estimates for breed effects represent half the additive genetic breed differences between *B. taurus* (Ayrshire and Brown Swiss) and Sahiwal.

[d] Estimates for heterosis effects represent the difference between the F_1 crosses and the average of the purebred calves for individual heterosis and the difference between the F_1 crosses and the average of the purebred dams for maternal heterosis.

[+] $P<0.01$. [*] $P<0.05$.

Surprisingly, none of the H_I effects estimated from the *B. taurus-B. indicus* heterozygosity were significant ($P>0.05$). However for the AS heterozygosity, H_I approached significance ($P<0.1$) for DG. F_1 AS calves gained an estimated 26 ± 15 g/day faster than the mean of the purebred A and S calves. This is the equivalent of about 47 % of the phenotypic SD and less than 6 % of the parental mean. H_M effects were significant for BW in the *B. taurus-B. indicus* heterozygosity. It was estimated that F_1 *B. taurus* x *B. indicus* dams produced calves that were 3.2 ± 1.3 kg lighter ($P<0.05$) at birth than the mean weight of calves born to purebred *B. taurus* and S dams.

4.5. Parameter estimates

4.5.1. Heritabilities

Paternal half sib heritability estimates are presented in **Table 4.7.** Univariate REML estimates of variance-covariance component and genetic parameter for the preweaning traits are presented in **Table 4.8**. Estimates of direct, maternal and total heritabilities and paternal half sib heritabilities (for comparison) are presented in **Table 4.9**. Paternal half sib heritabilities estimates were lower than the REML Model 1 estimates. These paternal half sib estimates were 0.10 for BWT and close to 0.19 for PADG and WAGE. Direct and total heritability estimates were higher in Model 1 than in the rest

Table 4.7. Heritabilities, genetic and phenotypic correlations of BWT, PADG, WAGE and SRATE from paternal half sib analyses[a].

Trait	BWT	PADG	WAGE
BWT	0.10 ± 0.06	−0.48 ± 0.48	−0.02 ± 0.43
PADG	−0.39	0.20 ± 0.07	−0.87 ± 0.49
WAGE	−0.32	−0.74	0.18 ± 0.07
SRATE	0.06	–	–

[a] Heritabilities along the diagonal, genetic correlations above diagonal, phenotypic correlations below. Heritabilities of BWT, PADG and WAGE were estimated from 1384, 1282 and 1282 observations, respectively. Correlations between BWT and PADG or WAGE and between and PADG and WAGE were estimated from 1282 observations, while that between BWT and SRATE was estimated from 1384 observations.

Table 4.8. Univariate REML estimates of (co)variance components and genetic parameters[a] for BWT, PADG, WAGE and SRATE[b] using different models.

	σ^2_A	σ^2_M	σ_{AM}	σ^2_E	σ^2_P	h^2	m^2	C_{AM}	r_{AM}	h^2_T
				BWT						
Model 1	3.375			21.226	24.601	0.14				0.14
Model 3	1.971	1.558		20.908	24.438	0.08	0.06			0.11
Model 4	1.952	1.543	0.022	20.932	24.448	0.08	0.06	0.001	0.01	0.11
				PADG						
Model 1	655.619			2448.096	3103.715	0.21				0.21
Model 3	587.785	56.225		2455.327	3099.327	0.19	0.02			0.20
Model 4	590.102	50.979	3.407	2447.162	3091.651	0.19	0.02	0.001	0.02	0.20
				WAGE						
Model 1	50.987			162.226	213.828	0.24				0.24
Model 3	37.446	12.298		162.835	212.379	0.18	0.06			0.21
Model 4	37.338	11.392	0.801	162.269	211.800	0.18	0.06	0.004	0.04	0.21
				SRATE						
Model 1	0.036			6.200	6.236	0.01				0.01
Model 3	0.030	0.000		6.220	6.250	0.01	0.00			0.01
Model 4	0.030	0.000	0.000	6.230	6.260	0.01	0.00	0.000	0.15	0.01

[a] σ^2_A, direct additive genetic variance; σ^2_M, maternal additive genetic variance; σ_{AM}, direct-maternal genetic covariance; σ^2_E, error variance; σ^2_P, phenotypic variance; h^2, direct heritability; m^2, maternal heritability; C_{AM}: σ_{AM}/σ^2_P; r_{AM}, direct-maternal correlation; h^2_T, total heritability = $(\sigma^2_A + 0.5\sigma^2_M + 1.5\sigma_{AM})/\sigma^2_P$.

[b] See footnote in Table 3.5.

Table 4.9. Heritability estimates for BWT, PADG, WAGE and SRATE derived using restricted maximum likelihood (REML) and paternal half sib analyses (PHS).

	REML[a]						PHS[b]	
		Model 1	Model 4					
	n	h^2_D	h^2_D	m^2	r_{AM}	h^2_T	n	h^2
BWT	1443	0.14 ± 0.08	0.08 ± 0.06	0.06 ± 0.04	0.01	0.11	1384	0.10 ± 0.06
PADG	1337	0.21 ± 0.08	0.19 ± 0.09	0.02 ± 0.05	0.02	0.20	1282	0.20 ± 0.07
WAGE	1337	0.24 ± 0.09	0.18 ± 0.08	0.06 ± 0.05	0.04	0.21	1282	0.18 ± 0.07
SRATE	1443	0.01 ± 0.07	0.01	0.00	0.15	0.01	1384	n.e[c]

[a] h^2_D, direct heritability ; m^2, maternal heritability; r_{AM}, direct-maternal genetic correlation; h^2_T, total heritability; n = number of records analysed.

[b] Sires with more than three progeny were used. Total of 76df for sires within sire breed.

[c] PHS heritability not estimable (negative variance component).

of the Models. The direct heritabilities were higher than the maternal heritabilities. Because direct, maternal and total heritabilities from Models 3 and 4 were equal for these traits, only results from Models 1 and 4 are given in **Table 4.9**.

The direct heritability estimates were significant for all the traits except SRATE. Direct heritability estimates for Models 1 and 4 for BWT, PADG and WAGE were close to 0.18, while that for SRATE was 0.01. The maternal heritability estimates were not significant. The direct-maternal genetic correlations were close to 0 for BWT, PADG and WAGE. The corresponding estimates of heritability of total influences were 0.11, 0.20 and 0.21 for Model 4. The heritability estimates of total influence for Model 1 were similar to the corresponding direct heritabilities.

4.5.2. Correlations

Phenotypic and genetic correlations among BWT, PADG, WAGE and SRATE and the paternal half sib heritability estimates are shown in **Table 4.7.** Higher PADG were genetically associated (although not significant) with lower BWT. The genetic correlation between BWT and WAGE was close to zero (-0.02 ± 0.43). As expected from the dependency of WAGE on WWT, the genetic correlation between PADG and WAGE was high (-0.87 ± 0.49). The genetic correlation between BWT and SRATE was not estimable because of a negative genetic variance. While the phenotypic correlations among these traits showed the same negative relationship, the values were lower than the corresponding genetic correlations. The phenotypic correlation between SRATE and BWT was positive but the value was much closer to zero (0.06). The phenotypic correlation between BWT and PADG was negative (-0.39) meaning that high BWT was associated with lower PADG and thus an older age at weaning. This was reflected in the high and negative (-0.74) phenotypic correlation between PADG and WAGE.

5. DISCUSSION

5.1. Means and variances

The phenotypic performance reported in this study (**Table 4.1**) is higher than that reported generally in other tropical and sub-tropical studies. Kang'ethe (1990) reported a mean BWT of 26.1 ± 0.18 kg for mainly AS calves at Mariakani, a research centre in coastal lowland Kenya. The Mariakani mean was 4.8 kg lower than that reported in this study. This difference can be attributed in part to the contrasting genotypes and to the differences between the two herds in the plane of nutrition of the dams. The dams in this study received supplementation of various high protein and energy feeds. In contrast, supplements were not fed usually to the Mariakani cows.

The PADG in this study was superior to that reported at Mariakani by Kang'ethe (1990) (431 ± 8.0 g/day). This large difference (57 g/day) can be attributed mainly to the calf feeding regimes. At Kilifi Plantations, in addition to the high level of milk feeding (i.e., three times a day up to about 6-8 weeks of age), calves were fed a high energy and protein concentrate mixture. Calves in Mariakani, on the other hand, were fed twice a day with the quantity of milk increasing from 1 kg per feeding at 1 week to 2 kg at 8 weeks of age. They also had very little supplementation.

Because of the weaning criterion at Kilifi Plantations (i.e., on weight basis) WAGE will be used as a proxy for WWT. In this study the mean WWT of 92 kg was attained in 126 ± 0.6 days. This performance is superior to that reported by Kang'ethe (1990). He reported a mean WWT of 86.8 ± 1.13 kg at 140 days (20 weeks). The WAGE in present study is older than reported by Gregory and Trail (1981) in their studies for the years of birth 1972 to 1978 on the Kilifi herd. They reported a mean WWT of 90 kg which was attained at an age of 122 days. In the study by Gregory and Trail (1981), the calves were the contrasting two-breed rotational crosses, Ar and Sr. The difference could therefore be a result of period of study, fluctuations in weather conditions, disease incidences, sires used, different genotypes or changes in management.

The mean SRATE reported in this study is higher than that reported by Trail and Gregory (1981b) in the same herd in the earlier years. They reported a mean SRATE of 87% i.e., 6% lower than that estimated in this study. The improvement in SRATE can be attributed to changes in management, annual fluctuations in weather conditions and also to the mating system.

5.2. Environmental factors

5.2.1. Year and season of birth

The year of birth significantly influenced all the preweaning traits, but there was no clear trend over the years for these traits (**Table 4.1**). The year effect in this study could therefore be a result of annual climatic variations and the resultant fluctuations in forage quality and quantity and any confounding effects due to management changes, sires and breeds used and year of birth. As far as grazing conditions are concerned, weather conditions is the most crucial since it is the most important determinant of feed availability to the dams. The same kind of fluctuations seen for BWT were also seen for PADG, WAGE and SRATE. Similar significant effects of year of birth on these traits have been reported by Gregory and Trail (1981) and Thorpe et al. (1993). But in the analyses of performance records from Deloraine Estates in Kenya, Trail and Gregory (1982) reported an insignificant effect of year of birth on BWT. This was attributed to the supplementary feeding of dams during periods of feed scarcity.

The significant effect of year on SRATE was expected because years were classified into periods according to the level of mortality. Significant effects of year of birth on SRATE have been reported by Trail and Gregory (1982) and Morris et al. (1993a). Year of birth effects on SRATE will result from stress related to seasonal and annual variations in whether conditions and concomitant effects on disease incidences.

There was a clear advantage for calves born during the dry season in terms of their BWT, PADG and WAGE. The effect of season on BWT is through its influence on the dam during the gestation period. Calves born in the second half of the year (i.e., from July to December when the weather is relatively drier) had heavier BWT than those born during the first six months. Those dams with their last trimester of gestation occurring when pasture growth was good, gave birth to heavier calves. Calves born during the drier, hotter seasons spent the later part of their preweaning period in the subsequent cooler wet seasons, when forage is abundant and is of better quality. It is therefore, advantageous to have calving during the end of the dry season and start of the rains because supplementary feeding may not be necessary. However, while it would be possible to implement such a management change at Kilifi Plantations, it would be counterproductive because it would prevent year-round milk production. Its implementation under traditional smallholder management will be precluded by lack of controlled breeding in communal grazing areas. On the other hand, calves born in the wet season are weaned on poor pastures in the dry season when temperatures are high. They therefore gain less and are weaned later. Trail and Gregory (1981b) in their analyses of performance data from ranches in Kenya reported that calves born during the drier periods were often significantly lighter than those calves born in the wetter periods. Gregory and Trail (1981) also reported a significant effect of season of birth on BWT and WWT. Despite the supplementary feeding of pregnant cows, calves born in the hotter (drier) seasons were lighter at birth than those born in the cooler seasons. The temperature could have influenced the cow performance, possibly by reducing their feed intake.

The absence of any seasonal variation in SRATE in this study can be attributed to the type of management (housing, feeding and health) at Kilifi Plantations. Calves were bucket-fed in the calf houses and they were therefore less exposed to the extremes of weather. Calves were also vaccinated against viral diseases, sprayed regularly with acaricide for ticks and dewormed at about 6-8 weeks of age and again immediately before weaning. The subsequent reduction in seasonal disease risks most likely contributed to the absence of any effect of season of birth on SRATE. These results are consistent to those reported by Gregory and Trail (1981).

5.2.2. Dam parity

The distinct difference in the number of calves from first parity and second parity cows is due to the intensive herd culling policy at Kilifi Plantations. Because reproductive rates were relatively high and very little culling of heifers took place prior to their first mating, heavy culling was necessary in the first and second lactations to avoid increasing herd size. The herd policy on culling can be summarised as making decisions to maximise herd milk yield based primarily on the cow's yield relative to that of contemporaries. The significant effect of parity on BWT (**Table 4.1**) is consistent with reports elsewhere (DeNise et al., 1988; Agyemang et al., 1991), where first parity cows produced significantly lighter calves. Trail and Gregory (1982) also reported that calves born to the first parity cows were 1.2 kg lighter ($P<0.05$) than the mean BWT (28.0 kg) of calves born from the fourth parity cows. The results can be attributed to the fact that young dams utilize part of their nutrient intake for growth and thus energy needed for maintenance of pregnancy was also used for growth purposes. The foetus therefore receives less nutrients for its growth and is also limited by the smaller body size of the heifer. Non-significant parity effects were reported by Kang'ethe (1990). The non-significant effect of parity on PADG, WAGE and SRATE reported in the present study can possibly be due to the management system. Calves were bucket fed and reared in calf houses. In cases where a significant effect has been reported (Mwandotto, 1978; Crockett, et al., 1978b; Gregory et al., 1978b; DeNise et al., 1988, Sacco et al., 1989), this has been attributable to the fact that primiparous cows give birth to lighter calves and also have a poorer mothering ability because they have less milk. This has been reported in situations where dams nurse their calves. Non-significant parity effects have also been attributed to advanced age at first calving by Willis and Wilson (1974).

5.2.3. Calf sex

The significant difference between male and female calves for preweaning performance was consistent with most other reports in the literature (Koch et al., 1959, 1973; Lowell, 1973; Trail and Gregory, 1982; Nelsen et al., 1984, 1986; Mwandotto, 1986b; Sacco et al., 1989; Gregory et al., 1991; Tawah et al., 1992, 1993). The heavier male BWT is due to hormonal differences between males and females which result in differential abilities to grow prenatally. The difference reported in the present study (9.2%) is however, higher than the 5.6%, 3% and 6.3% reported by Boston et al. (1980), Estrado-Arteage et al. (1990) and Thorpe et al. (1993), respectively.

The non-significant effect of calf sex on PADG conforms with the findings of Gregory and Trail (1981) and Kang'ethe (1990). Generally it is recommended that a bucket reared calf is fed according to its body weight. Since males in the present study had heavier BWT, on average, than female calves, then it follows that they should have received more milk than the females. This was not the case because the quantity of milk fed daily was dictated by a time scale with no distinction according to live weight or calf sex. This may have deprived the males of the ability to express their potential in PADG. This is reinforced by the fact that when BWT was included as a covariate in the analytical model for PADG, sex of calf was highly significant ($P<0.001$). A feasible explanation for this is that inclusion of BWT accounted for both genetic and environmental differences among calves in PADG. This then enabled differences in PADG due to sex of calf to be expressed. When the BWT covariate was not included in the model, calf sex was not a significant influence on PADG. This implies that sex of calf effects on PADG are attributable to BWT differences.

The resultant WAGE was statistically different between the sexes with male calves being weaned 6 days (4.9%) younger than female calves. This is consistent with the results reported by Rege and Famula (1993). The meaning of the present results is that assuming that males and females were weaned at a constant age, say 123 days, the males would have attained an average WWT of 92 kg while the female would have had a WWT of 86 kg. This difference (6 kg or 7%) could have resulted in a significant effect of sex of calf on WWT. Trail and Gregory (1982) reported that males were 18 kg (10.5%) heavier ($P<0.01$) at weaning than females. Singh et al. (1970) reported a 10.7 kg higher WWT in males than in females. In the N'dama cattle, Agyemang et al. (1991) reported that males were weaned 5% heavier than females. In contrast, a non-significant effect of sex on WWT has been reported by Thorpe et al. (1993) although males were, numerically, heavier than females by 2.2 kg. They attributed this lack of significance to the fact that calves in their study were fed on a fixed milk (time scale) ration, thus some calves, especially the bigger ones at birth, were probably not able to express their potential for growth.

Male calves had a 2% lower SRATE than female calves, although the difference was not significant. In some studies, especially when calves experienced dystocia, higher SRATE have been reported in females. Gregory et al. (1978a) reported a 1.1% higher ($P<0.05$) level of perinatal mortality in males. This was attributed to the fact that more than twice (11.6% vs. 5.0%) as many male calves required major assistance ($P<0.01$) at birth. In the present study, this differences cannot be attributed to dystocia because there were no recorded dystocia cases. The higher SRATE in females in this study is consistent with the reports of Sacco et al. (1989), Kang'ethe (1990) and Gregory et al. (1990) who reported 3, 4.8 and 2% higher SRATE in females, respectively. When SRATE was adjusted for BWT in this study, sex of calf significantly ($P<0.05$) affected SRATE. This implies that calf sex effects on SRATE are attributable to BWT differences. The male calves in this study were born significantly heavier ($P<0.001$) and this could explain the higher SRATE in females. The implication of these findings is that environmental factors need to be corrected for in order to improve the efficiency of selection.

5.3. Genetic factors

5.3.1. Sire breed

Although not statistically significant, the effect of sire breed was not consistent across traits, in that there was a shift in the breed rankings. The sire breed which produced the heaviest calves at birth (B) tended to have the lowest SRATE. For PADG and WAGE the ranking changed with the A-sired calves having the highest rate of gain and a younger age at weaning. Apart from SRATE, A-sired calves were superior to S-sired calves.

The ranking of sire breeds in this study agrees with the finding of Kang'ethe (1990) as far as A and S are concerned, but does not agree with the finding of Gregory and Trail (1981) in the same herd as this study, who reported that S-sired calves were 2.9 kg heavier ($P<0.05$) at birth than A-sired calves. Gregory and Trail (1981) did not report a significant interaction of sire breed and dam genotype. Their results could have been due to the fact that A sires were mated to Sr dams while S sires were mated to Ar dams. The heavier BWT of the S-sired progeny were attributed by Gregory and Trail (1981) to the fact that the Ar dams had a maternal additive genetic superiority over the Sr dams. Lack of significant effect of sire breed on BWT has also been reported by Trail and Gregory (1982) in their studies with A, S and Simmental sire breeds at Deloraine Estates.

The effect of sire breed approached significance ($P<0.1$) for PADG. The finding on the A and S sires are inconsistent with those of Gregory and Trail (1981) for the years of birth 1972 to 1978 in the same herd. They reported a 45 g/day greater PADG from birth to 90 kg for the A- than for the S-sired calves. The large difference in the study by Gregory and Trail (1981) was attributed in part to the greater difficulty in training S-sired calves to drink milk from the pail during the first few days after birth. Thus, low intake of colostrum resulted in low intake of antibodies which had a long term detrimental effect on subsequent development of the progeny. In this study, however, there were no differences in the behaviour of calves. This is because calves in present study were allowed to suckle colostrum direct from their dams for about 24 hours after which they were confined in movable calf pens within the cow paddock.

As expected from the dependency of WAGE on PADG, there was a 2 days difference in WAGE between the A-sired calves and those sired by B or S (125 vs. 127 days). This represents less than 2% of the mean indicating that the three sire breeds were basically the same in WAGE. However, in other studies where calves have also been weaned at a constant WAGE, significant effect of sire breed on WWT has been reported. Kang'ethe (1990) reported that calves sired by F and A (both *B. taurus*) were on average 7.5 kg and 4.3 kg heavier, respectively, at weaning than those sired by S (*B. indicus*). A non-significant effect of sire breed on WWT has been reported by Trail and Gregory (1982) in their studies with A, S and Simmental sire breeds. The lack of significance in the present study could be due to the management practice. Calves were bucket fed and this would have allowed the calf of poor condition to receive a similar amount of milk as a calf of good (heavy BWT) condition. This practise would have limited the opportunity for differences in transmitted effects between sire breeds to be expressed.

The SRATE of S-sired calves were marginally better than A- and B-sired calves. These results are consistent with those of Gregory and Trail (1981) who reported that S-sired calves had better survival than A-sired calves. The implication of this result is that even under high level of management, S genes have a favourable effect on SRATE in the relatively stressful climate that characterizes Kilifi Plantations.

Since A-sired and B-sired calves had similar BWT, PADG, WAGE and SRATE, B is viable alternative to A as the sire breed when selection is solely based on calf preweaning performance. But for postweaning performance, it could imply that the use of B as the sire breed would be more effective than A. This is in view of the mature live weights of these sire breeds. The mature live weight of A sire is about 700 kg while that of a mature B sire is about 1100 kg (Felius, 1985). But because of the present objective (milk production) of the production system, this would have a negative effect on cow size in that it would result in heavier cows which will tend to eat more and thus increase the production costs. At Kilifi Plantations, a consequence of this lack of any major variation for preweaning performance among sire breeds is that preweaning performance should be given little emphasis when selecting among these sire breeds. These decisions will be determined by relative lactation and reproductive performance. Analyses of milk production and calving interval in the same herd have shown B to be superior to A (Thorpe et al., 1994), while a comprehensive review of crossbreeding of *B. taurus* and *B. indicus* for dairy production in the tropics showed that F-sired crosses were superior to B-sired crosses (Cunningham and Syrstad, 1987). Thus, choice of *B. taurus* sire breed should consider breed effects on cow productivity per unit metabolic weight and longevity traits, the genetic variation for which will be important in tropical dairy production.

5.3.2. Dam genotype

The ranking (highest to lowest) of the four breed crosses on BWT was B x Ar, B x Sr, Ar and Sr (**Table 4.2**) with a significant ($P<0.001$) breed cross range of 2.1 kg or 6.8% of the overall herd least squares mean. For

PADG, the ranking reversed with Sr ranking first and B x Ar last. WAGE followed nearly the same ranking as BWT. The B x Sr had the highest SRATE while the others had similar SRATE. When comparing the TWBR **(Table 4.3)**, Ar ranked first for BWT but was second for the other traits.

The range between the dam genotype means for calf BWT was 2.1 kg. This could be attributed to the higher proportion of exotic genes in the B x Ar dams, that is, due to additive maternal effects. The fact that Ar and Sr dams gave birth to calves that had similar BWT (a difference of 0.3 kg) implies that there was little genetic variation, possibly due to the management standards (nutrition). This was surprising considering that the Ar dams have 67% *B. taurus* genes while Sr dams have 33% *B. taurus* genes. If this were not the case, it would, on the basis of transmitted effects, be expected that calves from Ar dams would be heavier than those from Sr dams. Kang'ethe (1990) reported that Ar dams gave birth to calves that were 2.8 kg heavier at birth than the Sr dams.

The small difference in PADG between calves born to Sr (33% *B. taurus*) dams and those born to B x Ar (83% *B. taurus*) dams cannot be attributed to additive maternal effects. This is because calves in this study were bucket fed so that calf's performance in rate of gain was almost wholly dependent on its own genetic potential (genotype) and not on that of its dam's potential for milk production except possibly residual dam effects on BWT.

Presumably, had calves been suckled as they are in beef herds, calves from B crosses dams could have performed better than those from either Sr or Ar dams because they produce more milk (Thorpe et al., 1994).

Although calves from THBC dams had lower PADG than those born to the TWBR dams, these calves were weaned 2 days younger. This possibly could be a result of the BWT because calves from the B crosses were 1.7 kg heavier than the corresponding TWBR dams. This was proved by fitting BWT as a covariate in the model for WAGE. BWT highly significantly ($P < 0.001$) influenced WAGE indicating dam genotype effect on WAGE could be attributable to BWT differences.

The small variation among dam genotypes and mating systems in this study shows that the maternal breed effect of these dam genotypes summed to give very similar aggregate preweaning performance for all traits but BWT. Therefore when selecting among these dam genotypes in this herd, preweaning performance should be given little emphasis. The decision will be determined by the major objective of the production system which for this herd is lactation and reproductive performance.

5.3.3. Calf genotype and mating system

The ranking of the calf genotypes for BWT was such that calf genotypes with the high percentages of *B. taurus* genes were heavier than those with low percentages of *B. taurus* genes. The difference between the calf genotypes with the highest and lowest BWT, A x (B x Ar) and S x Sr, respectively, was 2.9 kg (9.8%). Based on both the calf's additive genetic composition and that of the dam, this was expected since A x (B x Ar) calves were born to B x Ar dams, while S x Sr were from Sr dams. Thus the results could be attributed to differences in maternal and individual additive genetic effects. As A x (B x Ar) calves were born to dams with a higher proportion of exotic genes, they had a superior additive maternal effect than the S x Sr calves. This difference could also be due to the fact that A x (B x Ar) calves possess a higher degree of heterozygosity than the S x Sr calves because they were derived from three different breeds. The superior performance of the THBC, THBR and THBB relative to the TWBR could be attributed to higher heterozygosity in the crosses having three breeds.

The Sr calves had a higher rate of gain than the B x Ar calves. The calf genotype that had the highest BWT ended up having the lowest weight gain, i.e., A x (B x Ar). As has been alluded to (**section 4.2**), had these calves been reared as in beef herds, that is, running with their dams until weaning, they could have suckled as much milk as their dams could produce and in so doing realise a larger proportion of their genetic potential. In this study it is possible that some of the calves, especially the relatively heavier ones received less milk than their requirements. Their full genetic potential could then not have been expressed and these results may have underestimated the relative performance of the B crosses and overestimated the performance of A and S crosses.

The non-significant calf genotype effect on SRATE reported in this study is inconsistent with studies elsewhere when data were from a wide array of sire breeds including biological types of large size e.g., Charolais. Laster and Gregory (1973) and Smith et al. (1976a) attributed the significant effect of calf genotype on SRATE on BWT. They reported that calf breeds heavier at birth had higher rates of mortality, but this was mainly in situations where dystocia was important. However, Kang'ethe (1990) reported a significant effect of calf genotype on SRATE where there were no recorded dystocia cases. The high-grade S calves had the lowest SRATE. This was not attributed wholly to mortality. There was a tendency by the management to cull calves that had BWT below 18 kg and these were mostly calves in the high-grade S group. Gregory and Trail (1981) compared two-breed rotational crosses in Kilifi Plantations, and reported that calves with a higher proportion of S genes had higher SRATE.

Calf preweaning performance was good, indicating that management standards were high. At this high level of performance, variation among calf genotypes was small. This was surprising considering that the calf genotypes represented a wide range (8 to 83%) of gene proportions from S (*B. indicus*), and that eight out of the twelve calf genotypes had genes from two *B. taurus* breeds (A and B). The small variation among calf genotypes shows that the individual and maternal breed and heterotic effects of the sire breeds and dam genotypes summed to give very similar aggregate preweaning performance for all traits but BWT. Consequently dairy producers in the areas of Kenya where these crossbreds are popular have great flexibility when combining these three breeds in terms of their expected performance from birth to weaning under favourable management standards.

5.4. Genetic effects

5.4.1. Additive genetic effects

This study shows a relatively small difference in G_I and G_M between the *B. taurus* (A and B) and S breeds for calf performance. The lack of a significant difference in G_I between the *B. taurus* and S breeds for BWT is in agreement with the results reported by Thorpe et al. (1993) for A, F and S. Significant G_I for BWT have been reported elsewhere (Olson et al., 1993) in temperate beef cattle with a wider range of mature sizes (Angus, Brahman and Charolais). In contrast to the large and significant G_I for PADG and WWT reported by Thorpe et al. (1993), G_I for these traits were not significant in this study. In the study reported by Thorpe et al. (1993), the production environment had a lower nutritional level than that in the present study. The contrasting G_I estimates in the two studies may therefore be the result of genotype x environment interactions.

The non-significant G_M for all traits in the *B. taurus-B. indicus* contrast is consistent with the finding of Thorpe et al. (1993) but inconsistent with the study of Olson et al. (1993) in temperate beef calves. Beef calves are suckled and therefore preweaning growth is a direct indicator of the dam's milk production and mothering abilities. The calf's rate of live weight gain will therefore be partly determined by the dam's potential for milk production and any other maternal behaviour. Meyer et al. (1994) in their studies on milk production of Australian beef cows (Hereford and Wokalup) reported that milk production is the major component of maternal effects on preweaning growth of beef calves with breed differences for maternal effects being largely attributable to differences in milk yield. In the present study, the bucket feeding and calf house rearing contributed to the absence of the expression of G_M variation for PADG, WAGE and SRATE. The non-significant G_I and G_M between A and B (not shown) has important consequences in production systems in which milk production is the major objective. Under these conditions, the A and B become nearly equal in preweaning performance so that evaluation of lactational and reproductive traits become more important.

5.4.2. Heterotic effects

The absence of H_I and H_M effects in the *B. taurus* - *B. indicus* heterozygosity may have been due to the good production environment (Barlow, 1981; Cunningham and Syrstad, 1987; Bondoc et al., 1989). Sheridan (1981) suggested that reduced heterosis could be due to either parental epistasis (involving complementary genes) and/or to the presence of unlinked additive epistatic gene combinations in at least one of the parental lines. Heterosis is most marked for dairy cattle in the harsh environments of the tropics when adapted cattle (e.g., S) are mated to exotic stock (e.g., A, B, F etc.) that are adapted to the specialised environment of industrialised and intensive systems of management (Hickman, 1982). A model for the performance of crosses of *B. taurus* and *B. indicus* cattle in poor and good environments has been proposed by Cunningham (1981). A high-potential adapted Zebu breed (e.g., S breed) and an exotic breed may not differ greatly in production in good conditions. However, heterotic effects for the *B. taurus* x *B. indicus* crosses are expected to be larger in poor environments (Cunningham, 1981).

Although high nutrition systems result in much higher phenotypic production the expression of heterosis may be reduced (Ahlborn-Breier and Hohenboken, 1991). Gregory et al. (1966a, 1966b) reported higher level of heterosis in heifers than in steers when the heifers were on a lower plane of nutrition than steers. The significant H_I effect for BWT, PADG, WWT and SRATE reported by Thorpe et al. (1993) could have been due to the suboptimal nutrition provided at Mariakani. Non-significant H_I effect has been reported by Gregory et al. (1991), who reported a deterioration in preweaning performance from F_2 to F_3. This deterioration was attributed to a reduction in heterozygosity. The present results and reports from the literature suggest that the utilization of *B. taurus* x *B. indicus* heterosis effects may provide a useful tool to increase preweaning performance in nutritionally restricted production systems.

In the *B. taurus* - *B. taurus* heterozygosity, H_M effects were of a higher magnitude and of opposite sign to that reported by Thorpe et al. (1993) for crosses of *B. taurus* (A and F) and S breeds. In general, and especially in beef cattle, any large advantage in preweaning performance of calves (especially SRATE) will affect herd's reproductive and replacement rates, which, in turn, will determine the profitability of the herd. This will be one of the factors determining the practicability of implementing alternative breeding systems.

5.5. Genetic and phenotypic parameters

5.5.1. Heritabilities

Woldehawariat et al. (1977) summarized many of the numerous estimates of genetic parameters in beef cattle. Their weighted average value for the heritability of BWT was 0.45, PADG, 0.30 and WWT, 0.24. Compared with these estimates and those from other studies on beef cattle **(Table 2.1)**, estimates in this study are lower for BWT, PADG and WAGE. These paternal half sib heritability estimates indicate that additive genetic variance constitutes a moderate proportion of the phenotypic variance of these traits. The lower paternal half sib estimates relative to the REML estimates were expected, because REML estimates are considerably less biased by selection than corresponding paternal half sib estimates. This is because selection of parents reduces the genetic variance in the progeny by generating gametic phase disequilibrium (Falconer, 1982). The reduced additive variance therefore results in a reduced heritability among the progeny.

Because of the low maternal heritability estimates, genetic improvement in these traits would be more rapid if efforts were concentrated on the individual (direct effects). Considerably more opportunity exists for the improvement of the average gene effects in the calf than in the dam. The low maternal heritability estimates reported in the present study relative to those reported elsewhere (Mackinnon et al., 1991; Tawah et al., 1993) are attributed to the calf feeding regime. In the present study calves were bucket fed in calf houses. Therefore this practice limited the expression of maternal effects (**section 5.4.1**). However, the low estimates of maternal heritabilities for preweaning traits of progeny have also been attributed to negative covariances among component traits (e.g., maternal behaviour, milk yield and composition and immune transfer) by Trus and Wilton (1988) in their studies with Simmental.

The non-significant genetic correlations between direct and maternal effects for these traits indicates that selection for increased preweaning direct additive performance of the calf will not affect the maternal genetic ability of the female. It may be argued that under favourable nutritional conditions, the direct-maternal genetic correlations for these traits should be lower (Cantet et al., 1988). However, high and negative genetic correlations between direct and maternal effects have been reported in temperate countries by Bertrand and Benyshek (1987), Trus and Wilton (1988) and Meyer (1992b) for BWT, PADG and WWT, respectively (**Table 2.1**). In tropical countries high and negative genetic correlations between direct and maternal effects have been reported by Tawah et al. (1993). A possible explanation for this is that females which are small as calves grow up to become small dams which are better able to utilize the suboptimal production environment for their maintenance and for growth of calves than females which are born big and thus grow up as big dams under similar conditions. The big dams are therefore unable to meet their maintenance requirements and support the growth needs of their calves from the poor pastures. Consequently, their calves tend to be smaller at birth and weaning than those of the small dams at similar ages.

Estimates of direct heritability for BWT from Model 4 (**Table 4.9**) are lower than the majority reported in the literature (**Table 2.1**), although the Model 1 estimate (0.14) is similar to that for Simmental breed reported by Quaas et al. (1985). Higher estimates of this heritability have been reported by Bertrand and Benyshek (1987) (**Table 2.1**) for the composite Brangus compared with the purebred Limousin. They ascribed this result to increased genetic variation due to gene frequency differences between the original foundation breeds, namely, Brahman and Angus.

Heritability estimates of direct additive effects of PADG were moderate in both the Models (Model 1, 0.21; Model 4, 0.19). These estimates were similar to the 0.21 reported by Hetzel et al. (1990) in Hereford-Shorthorn crosses and to those reported by Tawah et al. (1992) in Gudali using paternal half sib analyses (**Table 2.1**). However, the estimated direct heritability values for this trait are much lower than the estimates given by Trus and Wilton (1988) (0.39) and Brown et al. (1990) (0.58) in Shorthorn and

Hereford breeds, respectively.

Heritability estimates of direct additive effects for WAGE were moderate but higher in Model 1 (0.24) than in Model 4 (0.18). The Model 1 estimate was similar to that reported by Meyer (1992b) for WWT in Hereford cattle using the same model, while the Model 4 estimate was similar to that reported by Meyer (1992b) again using the same model (i.e., Model 4). However, Meyer (1992b) reported higher estimates (0.60) in Zebu-crosses using Model 4. The current estimates were also lower than those reported for other genotypes in similar tropical environments (Tawah et al., 1993) and elsewhere (Robinson, 1990).

The non-significant direct heritability estimate for SRATE (0.01) is equal to estimate given by Baker et al. (1990) for crosses of Angus and Hereford breeds. These results clearly show that SRATE is largely under environmental influence. In the absence of large phenotypic variation and as herd performance for SRATE was good, there is no justification for attempting to improve SRATE through intra-population selection. But for BWT, PADG and WAGE, opportunity exists for improvement through selection.

5.5.2. Genetic and phenotypic correlations

The moderate negative genetic correlation between PADG and BWT (although not significant) indicates that favourable additive genes for PADG are associated with low BWT and that selection for PADG would yield a favourable correlated response in BWT. This was surprising in view of the known strong positive genetic correlation of BWT with PADG and BWT with WWT reported in the literature (Koch et al, 1973; Koots et al., 1991; Mackinnon et al., 1991; Meyer, 1994). Consequently this estimate needs substantiating, and the genetic correlations of BWT and SRATE estimated to allow the implications of selection for WWT (or PADG) to be assessed. Consistent with estimates in the literature for PADG and WWT (DeNise et al., 1988; Reynolds et al., 1991; Tawah et al., 1992), and as a result of their biological dependency, there was a high and negative genetic correlation between PADG and WAGE, indicating that a high PADG resulted in a desirable younger age at weaning.

The phenotypic correlation between BWT and PADG was negative. Thus, high BWT were associated with low PADG and subsequently an undesirable older WAGE because the phenotypic correlation between PADG and WAGE was high and negative (-0.74). This relationship was most likely due to the feeding regime. A heavier animal requires more feed than a lighter animal to maintain its weight and add more. At Kilifi Plantations, calves were fed on a time scale and not on live weight basis, meaning that heavier calves at birth were not able to express their potential in weight gain and consequently younger age at weaning. Other studies have reported high and positive phenotypic correlations between BWT and PADG (Pahnish et al., 1964; Koch et al., 1973; Nelsen and Kress, 1979; Massey and Benyshek, 1981a, 1982) and between PADG and WWT (Massey and Benyshek, 1981b; Reynolds et al., 1991; Tawah et al., 1992). The phenotypic correlation between BWT and SRATE in this study was similar to the estimate reported by Cundiff et al. (1982). The low and non-significant phenotypic correlation between BWT and SRATE indicates that there is no relationship between BWT and SRATE in this herd.

6. CONCLUSIONS AND RECOMMENDATIONS

The calf preweaning traits analysed in this study were highly influenced by the environmental factors (calf sex, dam parity, and calf year and season of birth). There was a clear advantage in these traits for calves born at the end of the dry season. For preweaning performance, it is therefore, advantageous to have calving during the end of the dry season and start of the rains. However, while it would be possible to implement at Kilifi Plantations, it would be counterproductive because it would prevent year-round milk production. Its implementation under traditional smallholder management will often be precluded by the difficulties of controlled breeding in communal grazing areas.

The results suggested that the heavier calves at birth were not able to express their full genetic potential for growth. Therefore there is the need for Kilifi Plantations to reconsider their calf rearing system so far as the quantity of milk offered is concerned. It is recommended that a calf is fed according to its body weight and not on a time scale. In this situation therefore, this will call for recording of live weight performance at weekly intervals. The weights would then be used to determine the amount of milk to be fed to a calf. The amount should be an equivalent of about 10% of the body weight of the calf. It could be fed on a twice a day basis. This amount should be increased on a performance. As variation among these crosses for lactation and reproductive traits is known to be large (Thorpe et al., 1994), selection decisions will be determined by the relative performance of mating systems for these traits, and not by their preweaning performance. Dairy producers in the areas of Kenya where these crossbreds are popular have great flexibility when combining these three breeds for preweaner production. Choice of sire breeds, however, should consider breed effects on cow productivity per unit metabolic weight and longevity traits, the genetic variation for which, will be important in tropical dairy production.

Therefore further study is required of the lactational and reproductive performance of some of the calf genotypes represented in this study at Kilifi Plantations. F_1 and two-breed rotational crosses involving B and S breeds should be studied for preweaning, lactational and reproductive performance for a valid conclusion to made about the comparative performance of A and B breeds.

The relatively low and insignificant ($P > 0.05$) individual and maternal additive genetic and heterotic effects in the *B. taurus* - *B. indicus* heterozygosity for preweaning traits found in this study, relative to larger differences found in other studies (e.g., Thorpe et al., 1993) is possibly due to the favourable feeding and management conditions at Kilifi Plantations.

The relatively large standard errors associated with the heritability and correlation estimates could be due to the large sampling variation resulting from the limited data set in terms of the number of sires and observations per sire. The magnitude of heritability estimates, especially of direct effects, indicates that the opportunity exists to improve preweaning growth through selection. Estimates of the genetic and phenotypic correlations between preweaning traits and postweaning, reproduction or lactational traits are required to show if any performance advantage during the preweaning period will be maintained in the postweaning performance. The correlations with lactational and reproductive traits will indicate the overall effect of selection for lactational and reproductive traits of dams on the subsequent performance of the progeny.

While crossbreeding results in improvement in the performance of the current generations, continued improvement of performance will require an efficient within-breed selection programme for the economically important production traits.

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