CHARACTERIZATION OF BREED ADDITIVE AND HETEROSIS EFFECTS IN BEEF CATTLE USING EXPERIMENTAL RESULTS

BY

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Chapter 1

GENERAL INTRODUCTION

1.1 BACKGROUND

South African livestock producers play an important role by using around 87% of the country's non-arable land for agricultural production. The country is mostly characterized by semi-arid climate with erratic rainfall. It is believed that total cattle numbers in South Africa ranged from 13.6 to 13.8 million head over the past 5 years (RMRD SA, 2010). Cognisance should be taken that the cattle sector is highly dualistic with communal/emerging and commercial farmers co-existing. The current estimate is that there are 6.7 million beef cattle and 1.5 million dairy cattle in the commercial sector as well as approximately 5.5 million cattle in the communal and emerging sector. Research on several aspects of the communal and emerging sector has shown that this sector has not reached its full potential. For example, the voluntary exits, internationally referred to as off-take (number of animals sold, slaughtered, donated, exchanged as a percentage of total herd size) in the communal sector is estimated to be 6 percent, which is significantly lower than the estimated 32 percent in the commercial sector (Scholtz & Bester, 2010).

Commercial farmers mostly find formal markets for their calf crops in the large feedlot sector in South Africa (75% of cattle are finished through feedlots). Only 5% of the beef cattle from subsistence farmers go through formal marketing channels. This is because current animals from the subsistence sector do not meet requirements of the feedlots. This market requires animals that are earlier maturing, are efficient converters of high quality feed and possess superior carcass attributes. In its comprehensive agricultural development program, the South African government lists the development of feedlots and market access for emerging and communal beef cattle farmers as a means to make significant contributions towards poverty alleviation and economic development in the rural areas (MacNeil & Matjuda, 2007; RMRD SA, 2010).

The type of production strategy to be followed in developing countries of the southern hemisphere will depend primarily on the environment and level of management. The availability of diverse cattle breed resources with large adaptive and productive differences allow breed types to be matched with the different environments, management capabilities

and markets - thereby maximizing the opportunity for high productivity and profitability. In the more developed areas, where managerial skills may be better, but conditions are often harsh, with relatively low levels of natural nutrition, crossbreeding with small framed indigenous cows may succeed in improving the output of beef cattle farming (Calegare *et al.*, 2007).

No single pure cattle breed excels in all areas that affect profitability or "is best in all environments" (Anderson 1990; Burrow, 2006). It is important for cattle producers to optimize economically important traits whilst trying to reduce costs of production in their respective environments. This can be done by applying genetic principles of selection and crossbreeding. Selection is an excellent tool with traits of moderate to high heritability such as growth rates and carcass traits. However, some of the most important traits related to beef production, such as reproductive rate and calf survival, are of low heritability. This means the success of selection programs for these traits is expected to be limited, but can be improved faster with crossbreeding (Miller, 2010). Crossbreeding is one of the oldest and most fundamental animal breeding technologies that can be used to reduce costs and enhance productivity. A more detailed discussion on the advantages of crossbreeding are presented in Chapter 2. Many crossbreeding trials have been conducted in South Africa. However, none were analyzed in such a way that heterosis effects were quantified.

Furthermore, MacNeil & Matjuda (2007) simulated breeding objectives for Angus and Charolais terminal sires to be used in breeding Afrikaner, Bonsmara, and Nguni cows. They developed an aggregated simulation model that is reliant on user inputs for the phenotypic characterization of the germplasm and economic characterization of the production environment. However, owing to a lack of data they assumed specific values for fitness traits in the purebreds and derived heterosis values for the crossbreds based on results from the USA.

1.2 AIM OF THE STUDY

This study was initiated owing to the need for characterization of breed additive and particularly heterosis effects under South African conditions. The aim of the study is to characterize and quantify breed additive and heterotic effects on growth, fitness, and feedlot traits of South African beef cattle using results obtained from Vaalharts Research Station. A total of 29 breed combinations were produced previously (Els, 1988; De Bruyn, 1991) and provide the basis for this study. It is envisaged that these results will supply valuable

information that can be used to develop crossbreeding systems under South African conditions in future.

1.2.1 Objectives

The specific objective of this study is to partition phenotypic values of crossbred animals in the studies of Els (1988) and De Bruyn (1991) into breed additive and heterotic effects for the South African beef industry. Estimates of these effects can then be used to predict performance of a particular cross and to maximize hybrid vigor in effective crossbreeding systems.

The outcomes of this study are aligned to the Strategic Plan for South African Agriculture (NDA, 2001) and addresses the following two core goals, namely:

- 1. to maintain and increase international competitiveness and profitability
- 2. to ensure the sustainable use and management of the natural resource base.

This study will ultimately assist commercial, emerging and communal beef producers to make better use of available beef breed resources and to capitalize on the favourable effects of heterosis.

1.3 SOURCE OF THE DATA / EXPERIMENTAL DESIGN

Comparative research studies were initiated in 1967 as a national project after the importation of live animals of exotic breeds into South Africa (Mentz, 1977). These studies were terminated in the 1970's. However, the need to fully evaluate the potential of these 'new' breeds remained. It was believed that good quality animals were imported. From then onwards only importation of semen of exotic breeds was allowed.

Another purpose of the research was to evaluate the basic principles on which crossbreeding systems could be based and presented in practice.

The first crossbreeding experiment using the Afrikaner as dam line was started by Mentz (1977), and was followed by research on crossbreeding with increased numbers of genotypes for extensive beef production by Els (1988) and intensive beef production by De Bruyn (1991).

Mentz (1977) started a project that evaluated Afrikaner, Bonsmara, Brahman, Charolais, Hereford and Simmentaler as sires in crosses with Afrikaner dams. The objectives of the research were to evaluate postweaning growth of the F1 male progeny as slaughter animals and F1 cows as maternal breeding stock. Els (1988) repeated the research work, but also extended the study to include crossbreeding with the F1 dams. Els (1988) and De Bruyn (1991) used the same sire breeds in crossbreeding with the Afrikaner in specific two-breed crosses (½ Afrikaner), F1 back-crosses to the dam lines (¾ Afrikaner) and crosses to the other sire lines (¼ Afrikaner). Whilst Els (1988) evaluated production characteristics of pure-and crossbred beef cattle on veld, De Bruyn (1991) evaluated the production characteristics of these breed-types under feedlot conditions where individual feed intake was measured.

Chapter 2

CROSSBREEDING IN BEEF CATTLE WITH REFERENCE TO THE SOUTHERN AFRICAN SITUATION – A REVIEW

2.1 INTRODUCTION

The beef cattle industry has moved towards national and international beef cattle evaluation with multiple pure breeds and crossbred animals (Garrick, 2006; Pollak, 2006), whilst breeding objectives have adopted a more economical orientation (Ritchie & Coran, 1996). Breeding programs mainly focus on weighting beef cattle traits with their economic values and profitability (Barwick & Yeats, 1998; Graham *et al.*, 1998) in selection indices with today's sophisticated genetic prediction systems (Green, 2009) in a genome-enabled era. Prediction models use existing breeding values to model total herd productivity. For crossbreeding, information on breed composition and heterosis are incorporated into multi-breed genetic evaluation models to predict phenotypic performance (Cardoso & Templeton, 2004; Pollak, 2006). This comes as more commercial cattle producers direct themselves towards crossbreeding systems in which crossbred animals have higher merit in reproduction, growth and end product (Spangler, 2007).

South African technology development endeavors to follow suit. Currently, the country has good multi-trait systems for intra-breed evaluation to evaluate the genetic potential of its many purebred and composite cattle breeds. However, a national (multi-breed) evaluation system will have to be developed which will allow the estimation of heterosis and the development of breed adjustment tables. Experimental results can enhance the development of the multi-breed database. Breeding objectives could then include crossbred animals in order to create an equitable and enabling environment that allows producers to be highly competitive and market responsive.

It is believed that improved indigenous cattle and crosses of indigenous breeds with exotic breeds probably have the greatest potential for sustainable red meat production in South Africa (Schoeman, 1989; Scholtz & Theunissen, 2010).

Various studies (Bonsma, 1980; 1983; Scholtz, 1988; Prayaga, 2003a; 2003b; 2004; Prayaga *et al.*, 2006) indicate that Sanga and Zebu cattle have the ability to survive, grow and reproduce in the presence of endemic stress factors such as ecto- and endo-parasites, diseases, climatic conditions characterized by high heat and humidity, and poor seasonal nutrition. However these cattle generally have lower reproductive rates and poorer meat quality attributes than the *Bos taurus* breeds that are less adapted to the stress factors of the tropical areas.

Schoeman (1989) claimed the high calving rate of Sanga cattle, indigenous to Africa, as an outstanding feature, while Scholtz (1988) demonstrated their adaptation to harsh environments. Strydom (2008) indicated small or no differences in meat quality between Sanga cattle and exotic European/British breeds in South Africa. These breeds are recommended for crossbreeding systems due to their outstanding maternal performance. For example, McManus et al. (2002) showed that the locally adapted Pantaneiro cattle had approximately double the reproductive rate of Nellore cattle in the harsh environment found in the Brazilian Pantanal. It is therefore expected that improved taurine genotypes will be matched with different environmental challenges (Mirkena et al., 2010), management capabilities and markets in order to maximize the opportunity for high productivity and profitability (Frisch and O'Neill, 1998; Prayaga, 2003a, 2003b; Burrow 2006). The usually larger weaner offspring, from smaller breeding dams, is expected to be more efficient (Calegare et al., 2007; Scholtz, 2011). Indigenous cattle breeds, however, have to be conserved to ensure their ongoing availability for beef production in the (sub) tropics (Ntombizakhe, 2002; Burrow 2006; Scholtz & Theunissen, 2010). It is imperative that these base populations of cattle should also be improved (Garrick, 2006).

A properly designed crossbreeding system takes advantage of appropriate combinations of superior traits of different breeds, referred to as complementarity. Experimental results and computer simulation indicate that differences in additive genetic merit of breeds for specific characters can be used to properly combine genetic resources and to provide for complementarity through the use of terminal sire breeds. Usually maternal breeds (breeds that excel in maternal traits of fertility, limited dystocia, milk production, maintenance efficiency and mothering ability) are crossbred with paternal breeds (breeds strong in paternal traits such as rate and efficiency of gain, meat quality and carcass yield) (Dickerson, 1973; Scholtz, 1988; Scholtz *et al.*, 1990; Scholtz & Theunissen, 2010).

It has furthermore been claimed that heterosis in a sound crossbreeding program could increase productivity in the beef cow herd by as much as 26% over a comparable straight

breeding program (Cundiff et al., 1974; Koger et al., 1975; Gregory & Cundiff, 1980; Lamb et al., 1982; MacNeil et al., 1991; MacNeil, 2005; MacNeil & Matjuda, 2007; Miller, 2010).

No one production system is optimal for all beef cattle producers (Lamberson *et al.*, 1993; Miller, 2010). Small herd size, in particular, puts extra limitations on the suitability of particular mating systems - in which case hybrid bulls offer an alternative to rotational crossbreeding.

While the supply of performance tested F1 bulls from selected and proven purebred parents (with EBVs) are available in the USA, they are limited or non existent in many developing countries. It is believed that crossbreeding will gain importance in many developing countries of southern Africa, as climatic changes stand to affect the African continent more substantially than the other continents (Anitei, 2006; Appel, 2006; Romanini *et al.*, 2008).

Vercoe & Frisch (1992), Prayaga (2003a; 2003b) and Prayaga *et al.* (2006) demonstrated that productivity differences between genotypes exist in terms of their resistance to environmental stresses and production potential. The two-way cross between genotypes with high production potential (e.g. European *Bos taurus* breeds) and those with high resistance to environmental stress (e.g. Asian and African *Bos indicus* and Sanga breeds) is considered an exceptional genotype with a unique combination of these two sets of attributes. Estimates of heterosis for growth traits are also dependent on the environment in which they are measured (Dadi *et al.*, 2002). Skrypzeck *et al.* (2000) claimed that the level of heterosis is larger under poor environmental conditions than under good environmental conditions (crossbreeding x environment interaction), making crossbreeding the obvious breeding practice under unfavourable conditions. This is in contrast to results on heterosis for weaning percentage from all seven *Bos taurus* breeds that were mated with *Bos indicus* Boran cows at two sites in Tanzania (Said *et al.*, 2003) where the level of performance in the trait improved linearly with improved pasture conditions.

2.2 CROSSBREEDING SYSTEMS

As has been stated earlier, variation amongst environments requires the use of different breed combinations. Sprinkle (2001) and Spangler (2007) are among authors who advised producers to take all complexities into consideration in the outline of their production goals. Possible limitations include feed and forage resources, labour, rainfall, ability to supplement cattle, number of camps, size of the herd, herd (heifer) replacement strategy, temperament desired, adequacy of corral facilities and commitment to a certain management level.

Daley (2006) cites ten factors confusing USA producers about crossbreeding and declares that crossbreeding in beef production is still untapped. It can certainly be argued that South Africa is in the same situation.

Crossbreeding systems fall into three main categories, viz. rotational crossbreeding-, terminal crossbreeding- and composite or synthetic systems.

2.2.1 Specific and Rotational crossbreeding

2.2.1.1 Specific crossbreeding systems (two- or three-breed specific or backcross)

The use of a two breed cross involves maintaining purebred cows and mating all dams to a (purebred) sire of another breed in systems where greater heterosis favours crossbreeding (Dickerson, 1973). The system is easy and realizes maximun heterosis but since the dams that produce calves are not crossbreeds, the offspring are not able to take advantage of any maternal heterosis. In a three-breed specific system another unrelated sire-line, is incorporated which is mated to the first generation dam line. This system realizes the highest level of heterosis. Backcrossing involves the breeding of crossed dams to the same sire line as was used for their breeding and decreases the heterosis by half (Lamberson *et al.*, 1993). Specific crossbreeding systems require one or two breeding camps, but are dependant on a source of replacement heifers if continuance of the breeding program is desired (Anderson, 1990).

2.2.1.2 Rotational (spatial and time) crossbreeding systems

Rotation systems should involve breeds with comparable characteristics such as birth weight, growth and lactation potentials, and those that are well adapted to the feed and other resources of the production environment (MacNeil *et al.*, 1988).

The classic form of a rotational crossbreeding sytem is spatial crossbreeding. In spatial rotations, all breeds are used at the same time but are separated spacially. In a two-breed system sires of two breeds are used in two breeding pastures. Replacements leave the group into which they were born to join the other breeding group as a replacement. Thus, dams sired by a sire line of a particular breed are mated to a sire line of another breed for their entire lives. The system realizes 72% heterosis in the offspring and 56% in the dam (Lamberson *et al.*, 1993).

In a three-breed (spatial) rotational system dams sired by sires of breed A are mated to sires of breed B, dams sired by sires of breed B are mated to sires of breed C and dams sired by sires of breed C are mated to sires of breed A (MacNeil *et al.*, 1988); thus dams are mated to the sire line of the breed that is least related to them (the sire breed of their maternal grand dam). This crossbreding system realizes 91% of the possible heterosis in the offspring and 70% in the dam and breed complementarity (Lamberson *et al.*, 1993). The system may be prohibitive in herds of less than 100 cows because it involves three sire line breeds. Unless artificial insemination is practiced, at least three breeding camps are required and a uniform cowherd is unlikely (Anderson, 1990).

After seven generations the additive genetic composition reaches equilibrium in both systems. The two-breed rotation will render two genotypes, fluctuating at a ratio of 67:33 in the different cows. In the three-breed rotation the additive genetic composition will be 57:29:14 (Schoeman, 1999).

Another commonly used form of rotational crossbreeding is rotating sire breeds across time e.g. two-breed rotation or criss-cross and three-breed rotation. Typically breeding sires are rotated every one or two breeding cycles. This system is simpler to manage than spatial rotation but the level of observed heterosis is less due to increased backcrossing to a limited number of breeds. Over time the breeding dams also become very inconsistent in their breed makeup and performance (Lamberson *et al.*, 1993).

Due to shifting markets which demand similar change to new breeds and breeding objectives 'equilibrium hybrid vigor' is seldom reached in beef cattle. Higher-way rotations are also unusual because of the demand of a higher management level and the difficulty in finding more than three compatible breeds with comparable characteristics and genetic merit (Anderson, 1990) and adapted to the feed and other resources of the production environment (MacNeil *et al.*, 1988). Dickerson (1973) claimed that lower reproduction rate favours rotational crossbreeding or synthetics rather than specific crossbreeding.

2.2.1.3 Rotaterminal crossbreeding systems

In these systems two- or three-breed specific and rotational crossbreeding systems of dams with superior maternal traits are mated to sires from a terminal sire breed. Young (replacement) dams in a three-breed single sire crossbreeding system are bred to sires superior in maternal traits for three calving opportunities (approximately 60 to 65% of the cow herd), after which they are bred to terminal sires. Breeds typified by relatively high genetic

potentials for growth rate and a lean-to-fat ratio of the carcass can be used as sire breeds on the older dams. Heterosis and breed complementarity can be maximized. Two- and three-breed single sire rotaterminal systems realize 59 and 77% of the maximum heterosis in the offspring respectively, while the dams have 47 and 60% of the expected heterosis. A three-breed two sire rotaterminal system realizes 59% of the potential heterosis in the offspring and 47% in the dams in the rotational phase and 100% and 59% in the offspring and dams in the terminal phase respectively (MacNeil *et al.*, 1988, Anderson, 1990, Lamberson *et al.*, 1993).

2.2.2 Terminal crossbreeding

In this system the cowherd (which consists mostly of F1 females or adapted dam lines) is mated to bulls of a unrelated terminal sire breed, especially in systems where there is a divergence in maternal vs. individual performance and epistatis (Dickerson, 1973). No crossbred heifers are held back and all calves are marketed. Herd sires are selected on terminal traits such as average daily gain, feed conversion, muscling, external fat, marbling, tenderness, carcass weight, quality and yield grade. No consideration is given to maternal traits (e.g. milk production, early maturing, etc.) since no replacements are retained.

Producing and retaining quality replacement heifers with terminal crossbreeding systems can be a challenge (Casas *et al.*, 2010) unless all cows are straight bred to dam-breed bulls during the first part of the mating season, and thereafter to terminal-breed bulls (Scholtz & Theunissen, 2010). Since the most fertile cows tend to come on heat early in the mating season, replacement heifers will be bred from these more fertile cows. Alternatively, F1 or purebred replacement females can be procured.

Craig (2011) specified the following criteria for evaluating a crossbreeding program: merit of component breeds, level of hybrid vigor produced, complementarity, consistency of performance/genetic antagonisms and meets end-product target. Simplicity, replacement considerations and accuracy of genetic prediction are certainly also factors to be considered.

According to Dickerson (1969) and Schoeman (1999) the phenotypic values of a two-breed animal can be partitioned into its crossbreeding parameters, when it is assumed that there is no epitasis between loci and no interaction between effects (parameters), in a model as follows:

$$P_{X(AB)} = \frac{1}{2} A_A + \frac{1}{2} A_B + M_B + D^I_{AB} + E_X + E_M$$

where:

 $P_{X(AB)}$ = the phenotypic value of individual X

 A_A and A_B = the direct (additive) genetic effects of the sire breed (breed A) and dam (breed B), respectively

M_B = direct maternal effect from dam B

 D_{AB}^{I} = dominance effect giving expression to individual heterosis expressed in P_{X}

 $\mathbf{E}_{\mathbf{X}}$ = the environmental effect to which the calf is subjected

 E_{M} = the environmental effect the dam is subjected to

This is similar to Dickerson's model (1969), which was used by MacNeil *et al.* (1982) to estimate individual and maternal additive and heterosis effects in beef cattle. A maternal granddam effect can also be included in the formula if the granddam was a crossbred animal (MacNeil *et al.*, 1988).

In the case of a three-breed cross, e.g. sire of breed C mated to an AB crossbred dam, the above-mentioned formula can be extended to include an additional parameter, namely the maternal heterosis effect (D^{M}_{AB}), contributing to the fact that the mother is a crossbred. The model then becomes:

$$P_{X(CAB)} = \frac{1}{2}A_C + \frac{1}{4}A_A + \frac{1}{4}A_B + M_{AB} + D^{I}_{CAB} + D^{M}_{AB}$$

where:

 $P_{X(AB)}$ = the phenotypic value of individual X

 A_C , A_A and A_B = the direct (additive) genetic effect

M_{AB} = direct maternal effect

D^I_{CAB} = individual heterosis effect

 D_{AB}^{M} = maternal heterosis effect

(with E_X and E_M ignored – assumed to be the same for all the breeding groups)

Dickerson (1969) explained that the quantities ($\frac{1}{2}$ $A_A + \frac{1}{2}$ A_B) and ($\frac{1}{2}$ $A_C + \frac{1}{4}$ $A_A + \frac{1}{4}$ A_B) form the basis for assessing genetic change in crossbreeding systems between breeds A, B and C. Similarly, different breed compositions can be calculated for each of the crossbreeding systems and/or for each of the composite breeds.

2.2.3 Composite or synthetic systems (and composite/terminal systems)

Composites have at least two breeds in their background and often more. Composite cattle are hybrid cattle that breed to their own kind and are similarly managed as purebreds. Composites are subject to maximum recombination effects (Dickerson, 1973), but a level of the original heterosis can be maintained as long as adequate numbers of sires are used in each generation to avoid inbreeding. Using a composite bull on composite cows reduces the need for separate breeding camps or rotating breeds of sire (Miller, 2010).

According to Gregory & Cundiff (1980) and Lamberson *et al.*, (1993) retention of initial heterozygosity after crossing and subsequent random mating within the crosses is proportional to:

$$1-\sum_{i=1}^{n} \mathbf{P}_{i}^{2}$$

where P_i is the fraction of each of the component of n breeds in the pedigree of a composite breed.

This implies that retention of heterozygosity favours the inclusion of an optimum number of breeds; taking into account that average additive merit may be lost when additional breeds are included (Kinghorn, 1982; MacNeil, 1987). For successful composite breeding the following needs to be determined:

- a. linearity of association of loss of heterosis with loss of heterozygosity
- additive gene variation relative to the parental breeds that contribute to them (particularly fitness related characters)
- c. the production environment must be characterized to provide for adaptability and inbreeding must be avoided

Composite cows can also be used in conjunction with a terminal sire breed in a system where replacement heifers are either procured from outside the system or bred with a proportion of the dam herd.

2.3 PREDICTING PERFORMANCE IN A CROSSBREEDING SYSTEM

To predict performance of a cross, estimates of the merit of pure breeds and estimates of the magnitude of individual and maternal heterosis must be available. Lamberson *et al.* (1993) predicted the weight of the progeny of two cattle breeds with heterosis as follows:

(Breed A weight + Breed B weight)/2 x (1 + individual heterosis)

If a third breed C was mated to A x B F1 cows, calf weights would be predicted by adding individual and maternal heterosis to the genetic merit of the crossbred calf. The genetic merit of the calf would be calculated as ½ the genetic merit of breed C plus ¼ of the genetic merit of breed A and plus ¼ of the merit of breed B or

[
$$\frac{1}{2}$$
 C + $\frac{1}{4}$ A + $\frac{1}{4}$ B] x (1 + individual heterosis) x (1 + maternal heterosis)

Phenotypic performance of other types of crossbred progeny can be calculated similarly.

2.4 CONCLUSIONS

Experimental results and computer simulations indicate that differences in additive genetic merit of breeds for specific traits can be used to synchronize genetic resources and to provide for complementarity through terminal sire breeds. However, excessive variation in additive genetic composition in economically important traits between generations reduces the number of breeds that should generally be compatible. This reduces the use of complementarity other than in a combined breed-rotation, terminal-sire system. Such a static terminal-sire crossbreeding system provides opportunity to synchronize germ plasm resources with production resources in about 50 percent of the cow herd and to use maximum first cross heterosis in approximately 67 percent of the calves marketed and to use complementarity in more than 50 percent of the calves marketed. Thus a breed-rotation system involving young cows to meet replacement requirements combined with a terminal-sire system on mature cows can use individual and maternal heterosis from rotation crossing plus complementarity and individual heterosis from terminal crossing (Gregory & Cundiff, 1980).

Many producers believe that heterosis is most easily maximized with a three breed crossing system, mating a crossbred cow with a bull of a third breed.

Alternative to continuous crossbreeding systems, especially for smaller herds or those with fewer management capabilities, are the periodic rotation (Bennett, 1987a and 1987b) or composite systems (MacNeil, 1987; Spangler, 2007).

No one system is optimal for all beef cattle producers (Lamberson *et al.*, 1993; Miller, 2010). Small herd size presents extra limitations and suitability of particular systems, and in which hybrid bulls offer an alternative to rotational crossbreeding. While the supply of performance tested F₁ bulls from selected and proven purebred parents (some with EBV) are plentiful in the USA, it is very limited or may not even exist in South Africa.

Contrary to developments elsewhere, and particularly in the USA and Australia, there are no crossbreeding studies currently active in South Africa involving several genotypes and/or backcrossing. Research on the indigenous Afrikaner breed to evaluate the performance of crossbreeding for beef production was conducted in the Northern Cape Province approximately 25 years ago by Mentz (1977), Els (1988) and De Bruyn (1991).

More recent outcomes from crossbreeding research include the breeding of Nguni cows with Charolais and Simmentaler breeds (Scholtz & Lombard, 1992); and a crossbreeding experiment conducted between 1972 and 1984 at Mara Research Station in the Limpopo Province (Schoeman *et al.*, 1993).

It is therefore essential that crossbreeding studies be conducted and that previous studies be re-analyzed properly to supply the necessary information needed for efficient use of breed resources by South African beef producers. This holds promise for reducing unit cost of beef production, and for increased profitability and sustainability amongst all beef farmers.

Chapter 3

DATA USED FOR CHARACTERIZATION OF BREED ADDITIVE EFFECTS AND HETEROSIS

3.1 INTRODUCTION

Apart from the mentioned study on the indigenous Afrikaner breed in the Northern Cape Province at Vaalharts Research Station more recent outcomes from crossbreeding research include the breeding of Nguni cows with Charolais and Simmentaler breeds (Scholtz & Lombard, 1992); the current Nguni x Angus crossbreeding at Vaalharts and a crossbreeding experiment conducted between 1972 and 1984 at Mara Research Station in the Limpopo Province (Schoeman *et al.*, 1993). The least squares mean results obtained in the study of Els (1988) and De Bryun (1991) were utilized in the current study.

3.2 MATERIALS AND METHODS

3.2.1 Experimental terrain

Crossbreeding experiments were carried out at Vaalharts Research Station, situated near Jan Kempdorp. The station is located fairly in the middle of South Africa at 2751' South and 2450' East at an altitude of 1 175 meters and is in an area with sandy red soil with lime rock underneath. These soils form part of the Hutton form and represents mainly the Manganese series (Van der Merwe, 1962; Laker, 2003). The veld type is mixed *Tarchonanthus* veld, Veld type No 16b, 4 (Acocks, 1975). The research station has a carrying capacity of 10 ha/LSU.

The climate at the Vaalharts Research Station is classified as semi-arid. It is characterized by hot summers and cold winters with frost a common occurrence. The highest monthly average temperature is 32°C and is experienced during December and January and the lowest monthly average temperature is -0.5°C and is experienced during July.

The average precipitation is 450 millimeters per annum of which 88% is experienced during the summer months from October to April in the form of thunderstorms (Els, 1988).

The research station experienced above average annual precipitation of 497 millimeters during the period when this experiment was conducted (1976 to 1980).

3.2.2 Experimental animals

3.2.2.1 The Afrikaner

The Afrikaner (A) is among the oldest indigenous breeds in South Africa. The breed had developed from Hottentot (San) cattle, which Els (1988) had believed belonged to the Sanga group of bovine. By the end of the 18th century the settlers around the southern Cape had developed the Afrikaner into a well-defined breed which was primarily adapted to extensive production systems and valued for its exceptional draught purposes, meat, milk and good leather (Scholtz, 2010). The Afrikaner Cattle Breeders' Society, founded in 1912, was one of the first breed societies to be established in South Africa. Traditionally the Afrikaner was regarded as a *Bos taurus* breed. However, a separate domestication site cannot be excluded (Bradley & Cunningham, 1999).

The Afrikaner is used in crossbreeding programs, especially in the more harsh and extensive beef producing regions. The breed is characterized by its hardiness, easy calving, rounding-off ability on natural grazing and efficient conversion of grazing into good quality beef. The small to medium size Afrikaner dam line can increase cow productivity when mated to large frame bulls to produce heavy weaners. In South Africa, the Afrikaner played a role in the development of six composite breeds namely Bonsmara, Afrigus, Afrisim, Hugenoot, Sanganer and S.A. Braford. Cattle of this breed served as a control group in the study.

3.2.2.2 The Brahman

The name Brahman (B) refers to the American developed *Bos indicus* breed, and not collectively to all *Bos indicus* breeds, while the word Zebu is descriptive of *Bos indicus* breeds. The introduction of the Brahman to South Africa occurred in 1954. Over the past five decades, the Brahman has dramatically changed the composition of the national commercial herd in this country. The reason for this is its ability to cross well with virtually any other breed of cattle. In addition, the breed's versatility allows it to perform well in an environment that changes frequently, due to unforeseen climatic conditions (Scholtz, 2010).

3.2.2.3 The Charolais

The first Charolais (C) herd was established in 1773 in Nievre in France. It became a common breed in the country in the 19th century where it was primarily kept and selected for beef production, but a milk strain was also developed in Vendeé. The first Charolais cattle were imported to South Africa in 1955. The Charolais Cattle Breeders' Society of South Africa was founded in 1966. Since then the breed has made a significant contribution to the improvement of the county's beef production. Charolais cattle are considered a large framed beef breed with good adaptation to intensive systems (Scholtz, 2010).

3.2.2.4 The Hereford

The Hereford (H) had its origin in Herefordshire in England. The early development of the breed was towards an animal of superior grazing qualities. The first two bulls were imported to South Africa during 1892 and the Hereford Breeders' Society of South Africa was founded in 1917 (Scholtz, 2010).

The animals used in this study were regarded as a small framed beef breed that was developed for temparal environmental conditions and believed to be of an early maturing type. Cows were considered to have high fertility and low milk production (Els, 1988).

3.2.2.5 The Simmentaler

Simmentaler (S) cattle had their origin near the Simmerom river of Switzerland. The first bulls and heifers were imported to Namibia in 1895 and then to South Africa in 1905 as dual purpose milk/beef cattle. The Simmentaler Breed Society was formed in 1964. A descendant of the Aurochs (*Bos taurus primigenius*), Simmentaler is genetically 'unrelated' to Zebu, Sanga and British breeds, and thus has seen sustained popularity for crossbreeding (Scholtz, 2010). Simmentaler cattle have large frames, cows have high milk production and weaners/steers are fast growing.

3.3 METHODOLOGY

The study of Els (1988) involved the evaluation of purebred Afrikaner (A), Brahman (B), Charolais (C), Hereford (H), and Simmentaler (S); and A as dam line in crosses with B, C, H and S sire lines. Els (1988) mainly focused on production potential of calves born over a four

year period that extended from 1976 to 1980 and the production potential of first cross heifer genotypes from the A dam line between 1979 and 1983.

3.3.1 Management practices

In the experiment by Els (1988), the experimental cows were kept on natural veld. Each cow herd consisted of 60 animals and was subjected to a 6 camp (90 hectares each) rotational grazing system. A phosphate-salt lick (6% phosphate) was available *ad libitum* throughout the year. All female animals were immunized against symptomatic anthrax, botulism, splenic fever, lumpy skin disease and three-day sickness (ephemeral fever) annually. Heifers were also immunized against anaplasmosis and brucellosis before weaning. A regular dipping program was followed throughout the year and animals were also additionally hand dressed for ticks when handled.

The mating season stretched over a ten week period (usually from 15 January to 31 March or two weeks earlier). During the first six weeks of the mating season artificial insemination (AI) was practiced. The semen of five bulls per sire line was used. Only calves born from AI bulls were evaluated as crossbred animals.

During the last four weeks 'round up' bulls were used to mate cows that did not conceive with AI. The calves born from these bulls were declared surplus animals and were not evaluated as crossbred animals. Cow weights at partus were taken within 4 to 11 days after calving.

Cow herds were vicited twice daily during the calving season to ensure that calf weights were taken within 24 hours post partum. All calves were dehorned with a warm dehorning iron shortly after birth and male calves were castrated at six weeks of age with rubber bands. At weaning, calf weights were taken with a 14-day interval before and after the age of 210 days. These weights were then interpolated to be the weights at 210 days of age. Calf weights were only taken after feed and water were withdrawn for a period of 15 hours (Els, 1988).

All genotypes of heifers that were born during the four year period were studied for post weaning growth. They were weighed on a monthly basis. At an age of 24 - 27 months heifers were mated. The heifers were mated from December to middle March, one month earlier than the cows.

For the production characteristics produced under feedlot conditions De Bruyn (1991) used weaner steers of about 7 months and 220 kg in individual feeding pens, where they were intensively fed (10.47 MJ ME/kg and 11.86% crude protein). All animals were individually weighed at the commencement of the trail and bi-weekly afterwards until slaughter. Animals were again withdrawn from feed and water about 15 hours prior to weighing. The individual feed intake of each animal was recorded over each 14-day period. At slaughter the final live weight of each animal was recorded. A standard slaughter procedure was then applied. Feedlot and carcass characteristics such as average daily gain, feed conversion ratio, meat and leather quality and carcass average daily gain were determined.

3.3.2 Statistical analysis

A factorial experimental design was used with sire and dam breeds as the two factors. A linear model was assumed and the data were analyzed using Harvey's (1972; 1976) programs for mixed models. Tests were done using a program (P/FKTRL) developed by Jooste as cited by Els (1988), to test the effect of linkage in the data. The data met all the necessary requirements. All relevant parameters were analyzed and had residual effects, but none of these effects were found to be significant (P < 0.05), except cow weight at calving within dam line genotype. This effect was subsequently included in the model.

Least squares means were estimated using Harvey (1972; 1976). Least significant differences (Tukey) were adapted for uneven numbers according to the method used by Winer (1962) as cited by Els (1988).

For the evaluation of different breeds as dam lines, body weights and relevant parameters were used. Els (1988) analyzed the data with three different methods. The results of the following two analysis were used:

- a. A 'Principle effects linear model' where no interactions were removed in the various analysis
- b. Factorial analyses with sire genotypes (A, B, C, H, S) and dam genotypes (A, BA, CA, HA, SA) where the first letter of a crossbred animal always indicates the sire line and the second letter the dam line, as per convention. Hereby included were interactions of sire x dam genotype, sire genotype x age of cow and dam genotype x age of cow

De Bruyn (1991) analyzed feedlot characteristics of steers by means of the least-squares analysis of variance (Harvey, 1988). Carcass results (e.g. carcass weight) were submitted to an analysis of covariance, using fat (%) as covariant. Subcutaneous fat (%) is used as basis of carcass classification in South Africa.

Chapter 4

ADDITIVE AND NON-ADDITIVE EFFECTS ON WEIGHT TRAITS

4.1 INTRODUCTION

Crossbreeding systems are mainly employed to improve the efficiency of beef production. Beef producers derive income from the total weight of calves weaned. Net income is associated with costs of maintenance of the production unit minus the expence; and can be maximized when the optimum number of cows with correct genetic potential (size and milk production) is in harmony with the production environment (MacNeil *et al.*, 1988; Burrow 2006). Weight traits are not equally important for improved efficiency (MacNeil & Matjuda, 2007), but they form integral parts of composite traits such as weaning weight per cow exposed to mating and are indicative of biological and economic efficiency of a cow-calf enterprise.

Today's sophisticated genetic prediction systems (Green, 2009) enable prediction systems to use existing breeding values to model total herd productivity. For crossbreeding, information on breed composition and heterosis are incorporated into multi-breed genetic evaluation models to predict phenotypic performance (Cardoso & Templeton, 2004; Pollak, 2006). This comes as more commercial cattle producers direct themselves to crossbreeding systems in which crossbred animals have higher merit in reproduction, growth and end product (Spangler, 2007) in a changing environment (Anitei, 2006; Appel, 2006).

South African technology development will follow this trend. Currently, the country has good multi-trait evaluation systems for intra-breed evaluation to evaluate the genetic potential of its many purebred and composite cattle breeds. In crossbred genotypes direct and maternal (and paternal) non-additive effects can be estimated and used to calculate phenotypic values for additional herd productivity.

The aim of this chapter is to characterize and quantify crossbreeding breed additive and heterosis effects in South African beef cattle using results obtained from the Vaalharts Research Station in South Africa in respect of four weight traits in 24 crossbred genotypes from five pure breeds.

The objective is to partition the phenotypic values of crossbred animals in the study of Els (1988) into crossbreeding parameters for the South African beef industry.

4.2 MATERIALS AND METHODS

Crossbreeding experiments were carried out at the Vaalharts Research Station, situated near Jan Kempdorp. For a complete description of the experimental terrain and animals as well as environmental conditions and management practices see Chapter 3.

Least squares means for weight traits in different breed group combinations were published by Els (1988). Genotype, contemporary group (year of birth, calving season, age of dam) and sex were significant (P < 0.05) sources of variation for all the traits. The least squares means for birth weight (BW), weaning weight (WW), 19 month heifer weight (HW) and cow weight at partus (CW) are presented in Tables 4.1 to 4.4.

Table 4.1 Least squares means and standard errors for birth weight (kg) for bull and heifer calves combined in the different sire and dam breed groups

	Sire breed				
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)
Α	34.5 ± 0.75	41.1 ± 0.88	41.5 ± 1.07	36.1 ± 0.85	39.6 ± 0.85
	(41)*	(29)	(24)	(31)	(32)
В	-	32.7 ± 1.10	-	-	-
		(24)			
С	-	-	46.8 ± 0.94	-	-
			(40)		
Н	-	-	-	35.6 ± 0.91	-
				(44)	
S	-	-	-	-	43.2 ± 1.14
					(31)
ВА	32.5 ± 1.17	34.4 ± 1.17	37.6 ± 1.13	35.2 ± 1.05	34.9 ± 1.14
	(23)	(17)	(20)	(21)	(19)
CA	40.0 ± 0.98	45.3 ± 1.07	45.7 ± 1.04	42.1 ± 1.11	46.1 ± 0.97
	(29)	(22)	(23)	(24)	(26)
HA	36.7 ± 1.05	40.8 ± 1.13	41.0 ± 1.26	36.0 ± 1.23	38.9 ± 1.02
	(21)	(19)	(16)	(16)	(26)
SA	39.0 ± 1.10	42.6 ± 0.92	42.5 ± 1.09	38.1 ± 1.16	39.4 ± 1.00
	(20)	(28)	(25)	(20)	(28)

Tukey's least significant difference (P≤0.05) for unequal numbers is 3.0 kg *Number of animals with recorded birth and weaning weights

Table 4.2 Least squares means and standard errors for weaning weight (kg) for bull and heifer calves combined in the different sire and dam breed groups

	Sire breed				
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)
Α	184.0 ± 3.47	206.2 ± 4.04	218.5 ± 4.94	195.0 ± 3.92	209.8 ± 3.92
В	-	198.8 ± 4.50	-	-	-
С	-	-	222.4 ± 3.90	-	-
Н	-	-	-	179.1 ± 3.70	-
S	-	-	-	-	234.0 ± 4.70
ВА	199.5 ± 4.87	207.4 ± 5.42	238.0 ± 5.20	223.6 ± 4.85	237.0 ± 5.28
CA	216.2 ± 4.50	244.2 ± 4.95	234.8 ± 4.78	232.5 ± 5.11	240.7 ± 4.48
НА	202.4 ± 4.86	221.1 ± 5.23	227.6 ± 5.82	209.6 ± 5.66	229.8 ± 4.72
SA	219.8 ± 5.10	236.5 ± 4.25	244.8 ± 5.04	230.9 ± 5.37	228.5 ± 4.63

Tukey's least significant difference (P≤0.05) for unequal numbers is 12.3 kg

Table 4.3 Least squares means for 19 month weight (kg) of heifers in the different sire and dam breed groups

_	Sire breed				
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)
Α	303.9 (28)*	351.9 (17)	367.2 (21)	331.3 (12)	362.3 (18)
В	-	332.7 (14)	-	-	-
С	-	-	364.6 (35)	-	-
Н	-	-	-	301.1 (31)	-
S	-	-	-	-	359.1 (20)
ВА	313.4 (14)	324.4 (8)	389.8 (10)	337.5 (8)	382.8 (11)
CA	341.9 (20)	396.9 (13)	383.4 (14)	372.3 (12)	379.0 (14)
НА	330.2 (15)	370.9 (7)	374.6 (11)	333.5 (14)	370.1 (13)
SA	339.6 (15)	373.4 (15)	385.4 (20)	369.0 (12)	363.0 (14)

Tukey's least significant difference (P≤0.05) for unequal numbers was 30.7 kg

^{*}Number of animals with 19 month weights

Table 4.4 Least squares means for cow weights (kg) at partus in the different sire and dam breed groups

	Sire breed				
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)
Α	435 (114)*	488 (64)	497 (66)	438 (50)	481 (50)
В	-	449 (45)	-	-	-
С	-	-	502 (106)	-	-
Н	-	-	-	407 (99)	-
s	-	-	-	-	459 (78)
ВА	422 (45)	456 (31)	516 (30)	442 (24)	487(42)
CA	460 (75)	536 (45)	508 (47)	487 (46)	509 (54)
НА	420 (45)	490 (33)	487 (30)	445 (49)	485 (45)
SA	457 (54)	507 (47)	510 (65)	457 (32)	456 (46)

Tukey's least significant difference (P≤0.05) for unequal numbers was 40.0

The information in Tables 4.1 to 4.4 was used to estimate the additive and heterosis effects for weight traits.

Dickerson (1969, 1973) modeled two-breed and three breed production systems as follows:

Two breed:
$$\mathbf{A} \times \mathbf{B} = \frac{1}{2} \mathbf{G}_{A}^{I} + \frac{1}{2} \mathbf{G}_{B}^{I} + \mathbf{h}^{I} + \mathbf{G}_{B}^{M}$$
 (0 recombination loss)

Three breed: C x AB =
$$\frac{1}{2}G_{c}^{I} + \frac{1}{4}G_{A}^{I} + \frac{1}{2}G_{B}^{I} + h_{CxAB}^{I} + h_{AB}^{M} + \frac{1}{4}r^{I}$$

where $\mathbf{G^I}_A$, $\mathbf{G^I}_B$ and $\mathbf{G^I}_c$ represented direct additive effects of the specialized sire and dam breeds respectively; $\mathbf{h^I}$ is the average heterosis (dominance: interactions within loci) effect, $\mathbf{G^M}$ is the maternal effect of the specialized dam breed and $\mathbf{r^I}$ is the recombination effect. The \mathbf{r} parameter is intended to measure deviation from linear association of heterosis with degree of heterozygosity and describes the average fraction of independently segregating pairs of loci in gametes of both parents which are expected to be non-parental combinations, or breakdown in favorable epistatic interactions.

These models formed the basis for this study, and were also used to analyse backcrosses to dam and sire lines.

^{*}Number of animals with cow weights

a. Pure breeds

e.g.
$$C = G_{C}^{I} + G_{C}^{M}$$

b. Two-breed crosses

$$A \times B = \frac{1}{2}G_{A}^{I} + \frac{1}{2}G_{B}^{I} + H_{AB}^{I} + G_{B}^{M}$$

c. Backcrosses

$$A \times BA = {}^{3}\!\!/\!\!/ G^{I}_{A} + {}^{1}\!\!/\!\!/ G^{I}_{B} + {}^{1}\!\!/\!\!/ H^{I}_{BA} + {}^{1}\!\!/\!\!/ G^{M}_{B} + {}^{1}\!\!/\!\!/ G^{M}_{A} + H^{M}_{BA}$$

d. Three-breed crosses

$$A \times BC = \frac{1}{2}G_{A}^{I} + \frac{1}{4}G_{B}^{I} + \frac{1}{4}G_{C}^{I} + \frac{1}{2}H_{AB}^{I} + \frac{1}{2}H_{AC}^{I} + \frac{1}{2}G_{B}^{M} + \frac{1}{2}G_{C}^{M} + H_{BC}^{M}$$

where A, B and C are different breeds, G^I and G^M are the direct and maternal additive effects respectively and H^I and H^M the individual and maternal heterosis effects respectively. The heterosis effects were assumed proportional to expected heterozygosity.

The single model is:

$$Y = Gm + \beta G^{I} + \beta G^{M} + \beta H^{I} + \beta H^{M} + \epsilon$$

where Y is the vector of least squares means for the trait of interest, Gm is the intercept (additive effect of the Afrikaner) for the trait of interest. βG^I and βG^M are the partial regression coefficients of individual and maternal breed composition representing additive effects expressed as deviation from the A breed mean and βH^I and βH^M the regression coefficients of individual and maternal heterosis effects proportional to expected heterozygosities in the crossbred progeny. ϵ is random error (not estimated).

The GLM procedure of SAS (2010) was used for the analysis of the data set. Each trait was analyzed separately. Breed solutions for each trait were expressed relative to the Afrikaner breed. A similar method was followed by Williams *et al.* (2010) in the analysis of a number of cattle breeds from an extensive literature review of crossbreeding studies.

For each trait, the least squares means were equated to their respective expectations and the resulting system of equations was solved by weighted least squares, wherein the weight given to each mean was the reciprocal of its standard error. Constraints were imposed such that $\mathbf{G}_A^I = \mathbf{G}_A^M = 0$. Thus, the intercept was interpreted as the mean for A.

According to Kahi *et al.* (2000) genetic models may either ignore epistasis effects, assume the effects to be equal for all breed combinations, or estimate these effects for each breed combination. In this study, individual recombination effects were confounded with maternal effects (only in three-way crossbreeding) similar to that of MacNeil *et al.* (1988).

4.3 RESULTS AND DISCUSSION

Although this data have been collected some years ago it is believed to be reliable and accurate but was never analyzed in such a way that heterosis effects could be characterized. Some of the breeds involved may also have undergone changes in their base line populations due to selection (with a change in inbreeding coefficients and additive effects). The results are therefore not necessarily directly applicable in the current South African beef industry circumstances. However, no other more recent crossbreeding results of this scope are currently available in South Africa. Therefore the analyses of this data will supply useful information, albeit may be somewhat outdated.

The additive and heterosis effects for the weight traits in pure- and crossbred animals that were estimated are shown in Tables 4.5(a) and (b).

Table 4.5(a) Additive effects and standard errors on weight traits for pure- and crossbred animals

Effect	Breed	Birth weight (kg)	Weaning weight (kg)	19 month heifer weight (kg)	Cow weight at partus (kg)
Intercept	Α	34.5 ± 0.9*	184.0 ± 10.8	303.9 ± 13.3	435.0 ± 12.0
Individual (direct)	S	1.8 ± 2.8	27.3 ± 12.9	46.8 ± 25.0	10.2 ± 20.5
	В	3.0 ± 3.0	12.4 ± 12.2	16.3 ± 21.3	62.6 ± 18.0
	С	19.6 ± 5.6	64.1 ± 26.0	159.0 ± 52.4	180.1 ± 43.7
	Н	0.1 ± 3.0	24.7 ± 13.8	15.3 ± 24.6	48.8 ± 20.3
Maternal	S	7.0 ± 3.2	22.7 ± 13.3	8.4 ± 30.4	13.8 ± 25.7
	В	-4.8 ± 3.3	2.4 ± 12.6	12.5 ± 26.8	-48.6 ± 22.9
	С	-7.3 ± 5.8	-25.7 ± 26.2	-98.3 ± 56.1	-113.1 ± 46.8
	Н	1.0 ± 3.3	-29.6 ± 14.1	-18.1 ± 31.2	-76.8 ± 26.1

^{*}All standard errors are expressed in measured units and represent a lack of fit to the genetic model, rather than variation amongst animals in the same genotype

From Tables 4.5(a) and (b) it can be seen that all the breeds involved in the study had positive individual (direct) additive (breed) effects on all the weight traits over that of the A breed, whereas maternal additive effects were mostly negative; the S breed being an exception. This is in accordance with results reported by Schoeman *et al.* (1993) in a study which involved H, S and A breeds at Mara Research Station (and where breed effects were also expressed as deviation from A). Dickerson (1969, 1973), Wilson *et al.* (1972) and Schoeman (1989) suggested a possible negative correlation between direct and maternal effects on pre-weaning growth and suggested that those breeds with high estimated individual additive effects would be most suitable as terminal sire breeds in production systems designed to maximize weaning weight, while breeds with high estimated maternal additive effects would be most useful as dam breeds.

Table 4.5(b) Heterosis effects and standard errors on weight traits for pure- and crossbred animals

Effect	Breed	Birth weight (kg)	Weaning weight (kg)	19 month heifer weight (kg)	Cow weight at partus (kg)
Individual	ВА	4.8 ± 2.1	14.7 ± 6.9	36.4 ± 20.5	17.9 ± 17.8
(direct)	CA	-3.7 ± 3.3	1.8 ± 13.8	-18.0 ± 33.6	-30.7 ± 28.3
	НА	2.2 ± 2.1	-0.5 ± 7.8	23.2 ± 20.8	-22.1 ± 18.1
	SA	4.6 ± 2.0	13.0 ± 7.4	35.0 ± 21.7	46.5 ± 18.3
	ВС	-2.1 ± 3.0	24.0 ± 14.6	39.7 ± 25.2	44.6 ± 20.9
	ВН	5.7 ± 2.3	28.0 ± 11.0	51.2 ± 15.3	30.2 ± 13.1
	BS	3.8 ± 2.2	36.7 ± 10.6	71.7 ± 17.3	82.2 ± 14.5
	СН	-3.5 ± 3.1	0.0 ± 14.8	-10.2 ± 25.9	-27.1 ± 21.4
	CS	-1.3 ± 3.0	6.1 ± 14.3	-23.1 ± 26.9	9.5 ± 22.4
	HS	1.6 ± 2.2	22.7 ± 10.8	43.1 ± 18.3	39.5 ± 14.7
Maternal	ВА	-2.4 ± 1.4	5.5 ± 5.8	-16.2 ± 9.5	-10.6 ± 8.1
	CA	6.9 ± 2.5	30.7 ± 11.4	58.2 ± 23.6	54.8 ± 19.4
	НА	-0.2 ± 1.4	22.1 ± 5.9	15.6 ± 12.3	22.8 ± 10.2
	SA	-2.2 ± 1.3	6.2 ± 5.4	2.3 ± 11.8	-16.8 ± 9.7

*All standard errors are expressed in measured units and represent a lack of fit to the genetic model, rather than variation amongst animals in the same genotype

4.3.1 Birth weight (BW)

Studies have shown that 75% of calves lost before weaning are lost at or near birth and that 80% or more of the deaths result from dystocia or calving difficulties (Sprott & Troxel, 2008). Older cows are bigger, have larger pelvic openings and consequently, have much less calving difficulties than younger cows. Most calving difficulties occur in heifers calving for the first time. Factors affecting calf BW are breed or genotype of the sire and dam or calf and generally have the greatest influence on calving difficulties (Anderson & Plum, 1965). For BW (Table 4.5(a)) the C had the highest direct breed (individual additive) effect on the A dam line; +19.6 kg or +56.8%. This undesirable increase implicated that C sires could only be used on older cows (MacNeil *et al.*, 1988), but not on heifers. Purebred C dams however, had a negative/desirable maternal additive contribution of -7.3 kg or -21.2%.

Long (1980) stated that heterosis, resulting in increased BW, is generally 6 to 7% when *Bos taurus* breeds are crossed, less (0 or negative) when *Bos taurus* sires are crossed on *Bos indicus* dams, but considerably higher (20 to 25%) when the reciprocal mating is made. Cundiff *et al.* (1986) and Arthur *et al.* (1999) however, stated that direct heterosis effects for BW generally range from 1 to 11% with values for *Bos indicus* x *Bos taurus* at the upper end of the scale. Results from this study could not confirm most of these findings. Two-breed *Bos taurus* x *Bos taurus* genotypes (CA, HA, SA, CH, CS and HS) had an average negative direct (individual) heterosis contribution of -0.1 kg or -0.3% to the BW of the A, the CA genotype being the largest (-3.7 kg or -10.7%). *Bos indicus* x *Bos taurus* (Sanga included) genotypes (BA, BC, BH, and BS) had an average positive direct heterosis contribution of +3.1 kg or +8.8%, which is higher than that given in the literature. The CA dam however, had the highest maternal heterosis effect of +6.9 kg or +20% on the trait out of the four A crossbred dam lines (BA, CA, HA and SA). The combined heterosis effect (individual and maternal as deviation from the A breed) for the CA genotype was +3.2 kg or +9.3%.

On the other hand the S had a small direct breed effect on BW (+1.8 kg or +5.2%), but the highest maternal additive effect (+7.0 kg or +20.3%) of all the breeds involved in the study. This is contrary to findings of Skrypzeck *et al.* (2000) who obtained a negative maternal effect (-7.2%) in a study which involved the S, H and A breeds on the Johannesburg farms and who ascribed calving difficulties with S genotypes most likely the result of the positive breed (individual additive) effect on BW.

The result from Table 4.5(a) however, suggests that the direct maternal effect could be nearly four times larger. Schoeman *et al.* (1993) also obtained positive direct maternal effects for S. The combined additive contributions of S to increased BW were +25.5% and substantially higher than the +10.9% obtained by Skrypzeck *et al.* (2000), but closer to the +17.3% found by Schoeman *et al.* (1993). Two-breed S genotypes (SA, BS and HS) also had positive individual heterosis effect on BW (an average of +3.3 kg), the only exception being the CS genotype that was mentioned earlier. SA crossbred dams cancelled almost half of their direct heterosis effect with a maternal contribution of -2.2 kg. This small effect was in accordance with findings by Skrypzeck *et al.* (2000) who had found that the maternal heterosis effects of the S breed on BW compared with A and H was non-significant, though the breeds were managed in a higher environmental level.

The B sire had an undesirable positive individual additive contribution on BW (+3.0 kg or 8.7%), but the B dam had a -4.8 kg (-13.9%) effect on BW. The combined additive contributions were -5.2%. The study reinforced the views that B sired calves have increased

BW (Gregory *et al.*, 1979; Barkhouse *et al.*, 1998) and that B dams produce small calves (Prayaga, 2003a). Out of the ten different two-breed combinations involved in the study, the BH had the highest individual heterosis effect (+5.7 kg or +16.5%) on the trait. Other B two-breed genotypes (BA and BS) also had positive values (+4.8 and +3.8 kg respectively), an exception being the BC genotype (-2.1 kg). However, half of individual heterosis effect of the BA dam line was cancelled by the maternal effect; resulting in a combined heterosis effect of +2.4 kg for the genotype. The data suggested that all B pure- and crossbred sire lines could only be used to breed with mature cows and not with heifers. In this study individual heterosis effect for BW was highest between B x H (+16.5%) and B x A (+13.9%). The results are in accordance with Franke (1994) who also reported that the direct heterosis from crosses made between B sires and Angus, C and H breeds resulted in an increase in BW over the other breeds.

The combined additive values for the H breed were relatively small for BW (+1.1 kg). This also applied to the average individual heterosis contribution (+0.1) kg for the H two-breed genotypes (HA, CH and HS). The maternal heterosis effect of the HA genotype was favorable (-2.2 kg) for BW. Skrypzeck *et al.* (2000) suggested the inclusion of higher levels of H contributions in crossbreeding systems for the prevention of dystocia. It must be stressed that data such as that shown in Table 4.5 represented the average breed performance at a specific time.

Individual bulls in the small breed groups can cause as many or more problems than the average of the larger group. Also, some bulls of the larger type cause fewer problems than the breed average. Such bulls (larger breeds, minimum calving problems) nearly always have a record of light BW, as do many of their ancestors (Sprott & Troxel, 2008).

4.3.2 Weaning weight (WW)

Although higher WW can alter feed requirements due to amongst other factors, an increased milk production of cows (Garrick, 2006), cattle breeders usually aim for higher weaning weights. However, the primary objective of applied animal breeding programs is assumed to be a reduction of total costs per value-unit of products under varying management and marketing situations (Dickerson, 1973). Cundiff *et al.* (1974) had found that the maternal effect of heterosis did reflect greater and more persistent milk production in favour of crossbred cows over straight bred cows in a study which involved three British breeds.

The C had the highest positive direct breed effect (+64.1 kg or 34.8%) on WW (Table 4.5(a)). However, +25.7 kg of this contributions was cancelled by the direct maternal effect of the C dam line (which might be the consequence of lower milk production); totaling a combined additive contribution of +38.4 kg or +20.9%. This combined additive contribution was exceeded by the S dam line with +27.3 kg individual additive effect and +22.7 kg maternal heterosis effect (Table 4.5(b)); totaling +50.0 kg or +27.2 %; compared to +21.9% reported by Schoeman *et al.* (1993) and +12.2% by Skrypzeck *et al.* (2000). These results suggested that the C and S breeds not only makes the breeds logical choices as terminal sire lines, but that the SA would most likely make an appropriate dam line under favorable conditions such as the sweet veld conditions of Vaalharts Research Station. This was also suggested by Neser *et al.* (2003).

Table 4.5(a) shows that the B sire line had the lowest direct effect (+12.4 kg or +6.7%) on WW out of the four purebred sire lines bred to the A dam line. Contrary to the findings of Roberson *et al.* (1986) that has indicated a superior maternal ability, results of the B dam line involved in this study indicated only on a small positive maternal breed effect (+2.4 kg). The two-breed BH and BS genotypes had the largest direct heterosis effects of +24.0 and +36.7 kg on WW (Table 4.5(b)) respectively, suggesting that hybrid sire lines could increase WW in the A dam line. The BA dam however, had a slightly larger maternal heterosis effect (+5.5 kg).

The H had a direct breed contribution of 24.7 kg on WW (Table 4.5(a)). Out of all the purebreds the H dam line showed the lowest maternal additive effect (-29.6 kg or 16.1%) on WW. Schoeman et al. (1993) also found that the H's additive contribution to WW was small positive (+3.9%), though not negative, when compared to the A genotype, while Skrypzeck et al. (2000) obtained a -6.7% combined additive contribution for WW in the H breed. In studies Alenda et al., (1980), MacNeil et al. (1982); Schoeman et al., (1993); Skrypzeck et al., (2000) and Franke et al., (2002) also obtained negative estimates of direct breed effects for H, mainly explained by the negative direct maternal effect. The results suggested that the H dams involved in MacNeil's study had low milk production which had affected WW. Table 4.5(b) shows that the HA genotype had a small negative direct heterosis effect (-0.5 kg), but this negative value was cancelled with a positive maternal heterosis effect of +22.1 kg or +12.0%. This is contrary to the result of Skrypzeck et al. (2000) who only obtained +2.1% maternal heterosis effect for WW in HA dams. Schoeman et al. (1993) also found the S maternal ability to exceed both that of the A and H, while the A maternal ability was superior to that of H for WW. The H should therefore not be considered as dams in crossbreeding systems.

The individual heterosis contribution of the CS genotype was +6.1 kg for WW (Table 4.5(a)). The other two-breed C and S genotypes (CA, BC, CH and SA, BS, SH) had average individual heterosis effects of +8.6 kg and +24.1 kg respectively. The maternal heterosis contribution of the CA dam line was the highest of all A crossbred dam lines (+30.7 kg or +16.7%) (Table 4.5(b)). The total combined heterosis effect of the CA dam line was +32.5 kg versus the +19.2 kg effect of the SA dam line. Schoeman *et al.* (1993) found the direct maternal effect for SA, to be non-significant, but found that the maternal breeding values for WW increases linearly with an increase in S proportion in later generations.

4.3.3 Heifer weight (HW)

Most breeding systems that produce weaner calves must also produce replacement heifers. To produce a consistent set of replacement heifers, it is essential that the appropriate crossbreeding system with a particular set of breeds be consistently maintained (Olsen, 2002). A substantially large individual additive effect on HW was brought about by the C sire; +159.0 kg or +52.3% (Table 4.5(a)). This effect was largely cancelled in the C dam line (-98.3 kg) with a combined additive effect of +60.7 kg or +20.0%.

The S and B purebred genotypes had positive values for individual and maternal additive effects of +55.2 and +28.8 kg respectively. The H breed had a combined additive effect of -2.8 kg, mainly due to the large negative direct maternal contribution.

Out of the two-breed genotypes in this study, the BS genotype had the largest individual heterosis effect of +71.7 kg or +23.6% for HW, while other B genotypes (BA, BC and BH) also had positive values (+36.4, +39.7 and +51.2 kg respectively) (Table 4.5(b)). However, the C genotypes (CA, CH and CS) had negative values (-18.0, -10.2 and -23.1 kg respectively). The remaining genotypes (SA, HA and HS) also had positive values (+35.0, +23.3 and +43.1 kg respectively). The BA dam line was the only A crossbred dam line with a negative maternal heterosis value (-16.2 kg) for HW, while the other crossbred dam lines (CA, HA and SA) showed positive values (+58.2, +15.6 and +2.3 kg respectively), with that of SA being the smallest.

4.3.4 Cow weight (CW)

Results from this study also indicated that even for CW breed and heterosis effects still exists. Although CW at weaning is the more reliable and practical measure to record, Crook et al. (2010) had found an estimated genetic correlation of 0.95 ± 0.03 between CW at calving and at weaning of the calf. In this study CW was measured at calving (partus). CW impacts on maintenance requirements, the larger the animal, the greater its maintenance requirement, especially energy and protein. Therefore, an indicator of cow size may be important in the evaluation of alternative breeding objectives (MacNeil et al., 1984; Garrick, 2006). Postpartum is the period of greatest nutritional demand (Hall et al. 2009). However, Greiner (2009) suggested that cows that have increased mature size are able to give birth to heavier calves without increases in calving difficulty.

The A breed is well adapted to harsh environmental conditions, with relatively low maintenance requirements (Moyo *et al.*, 1996). Table 4.5(a) indicates that the C purebred sire line increased CW of the A genotype the most (+180.1 kg or +41.4%) and that the S breed had the smallest individual additive effect (+10.2 kg or + 2.3%) of the four purebred genotypes involved in the study. The combined additive effects for the C and S breeds were +67.0 and +24 kg respectively. The combined additive effects for the two remaining purebreds (B and H) were +14 and -28.0 kg respectively; mainly the result of negative direct maternal effect.

The substantial (positive and negative) maternal additive effects of the purebreds involved in the study on post-weaning traits were contrary to belief that these weight traits are not influenced by the maternal merit of the dam line. Prayaga (2003a) and Pico *et al.* (2004) are among authors who also found that maternal effects still exist in post weaning traits; and were observed up to final (mature) weight.

The BS genotype had a substantial higher individual heterosis effect on CW (+82.2 kg or +18.9%) than the other two-breed genotypes (Table 4.5(b)). The remaining two-breed B genotypes also contributed positively to the trait with an average direct heterosis effect of +30.9 kg, the largest of all sire lines. The C genotypes had the lowest average individual heterosis effect of -17.6 kg (-4.0%) of all four sire lines. However, the CA dam line was responsible for the highest maternal heterosis effect of +54.8 kg or +12.6%. The SA dam line however, contributed the highest combined heterosis effect (+29.7 kg or +6.8%) to CW out of the four crossbred dam lines. The BA, CA, and HA genotypes had total heterosis effects of +7.3, +24.1 and +0.7 kg respectively.

4.4 PREDICTION OF PERFORMANCE IN CROSSBRED GENOTYPES

For the estimation of net breed effects, proportional contributions for the various dam breeds in their two- and three-breed and backcross combinations were derived. The genetic model was adapted because of the dependencies of the B, C, H and S breeds on the A breed direct and maternal effects (which were set to zero and not included in the model). The genetic components of the other breeds were estimated as deviations from the A breed mean. Hence, composite estimates of all production trait averages of all 24 crossbred genotypes could be derived using the contributions as shown in Tables 4.6 with the following models:

Two-breed crosses

$$A \times B = I_B + (DG_B^I = 0) + \frac{1}{2}DG_A^I + H_{AB}^I + (DG_B^M = 0)$$

b. Backcross to dam

$$B \times AB = I_B + (\sqrt[3]{DG}_B^I = 0) + \sqrt[1]{DG}_A^I + \sqrt[1]{H}_{BA}^I + H_{AB}^M + \sqrt[1]{DG}_A^M + (\sqrt[1]{2}DG_B^M = 0)$$

c. Backcross to sire

$$A \times AB = I_B + \sqrt[3]{4}DG_A^I + (\sqrt[4]{4}DG_B^I = 0) + \sqrt[4]{4}I_{BA}^I + H_{AB}^M + \sqrt[4]{2}DG_A^M + (\sqrt[4]{2}DG_B^M = 0)$$

d. Three-breed crosses

A x BC =
$$I_B + \frac{1}{2}DG^I_A + (\frac{1}{4}DG^I_B = 0) + \frac{1}{4}DG^I_C + \frac{1}{2}H^I_{AB} + \frac{1}{2}H^I_{AC} + H^M_{BC} + (\frac{1}{2}G^M_B = 0) + \frac{1}{2}G^M_C$$

where I_B is the intercept or individual additive effect of the dam breed, DG^I_A is the individual additive deviation of sire breed A from the dam breed, DG^I_C is the individual additive deviation of sire breed C from the dam breed A, H^I_{AB} and H^I_{AC} and are the individual heterosis effects of genotypes AB and AC, H^M_{BC} is the maternal heterosis effect of genotype BC and G^M_C is the maternal additive effect of dam breed C.

The expected phenotypic means for growth traits in two- and three-breed genotypes were subsequently calculated and are presented in Tables 4.7 to 4.10.

Table 4.6 Proportional contributions of genetic effects from various dam breed combinations to trait values in respect of the A breed

Crosses	additiv	vidual /e effect /) of:	Materr	nal additi	ve effect (G ^M) of:		heterosis (H ^l) of:		eterosis (H ^M) f:
Crosses	Dam breed	Sire breed 1	Sire breed 2	Dam breed	Sire breed 1	Sire breed 2	Sire breed 1 x Dam breed	Sire breed 1 x Sire breed 2	Sire breed 1 x Dam Breed	Sire breed 2 x Dam breed
Two-way cross e.g. BA	0	0.5	0	0	0	0	1	0	0	0
Back cross to dam e.g. ABA	0	0.25	0	0	0	0.5	0.5	0	0.5	0
Back cross to sire e.g. BBA	0	0.75	0	0	0.5	0	0.5	0	0.5	0
Three-way cross e.g. BCA	0	0.5	0.25	0	0	0.5	0.5	0.5	0	1

4.4.1 Birth weight

Table 4.7 Expected phenotypic values for birth weight (kg) for bull and heifer calves in the different sire and dam groups

	Sire breed					
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)	Average
Α	(34.5)	40.8	40.6	36.7	42.6	40.2
ВА	34.1	35.6	40.1	35.5	35.4	35.6
CA	37.4	45.5	47.1	42.1	45.2	43.5
НА	35.0	41.5	37.7	36.8	35.9	38.7
SA	41.8	46.5	44.8	37.8	40.5	41.4
Average	37.1	41.1	42.2	37.8	40.6	

⁽⁾ Not included in the calculation of the average

The probability of dystocia and lower survival is affected by the calf BW (Skrypzeck et al., 2000). The results (Table 4.7) indicate that A sire line genotypes provided the smallest average composite estimate of the phenotypic value for BW (37.1 kg) of all five sire line combinations which also involved the B, C, H and S sire breeds, but on average BA crossbred cows proofed to limit BW to the biggest extent in crosses with all the sire lines (35.6 kg). This was in accordance with findings by Els (1988). Backcrossing two-breed genotypes to the dam line decreased BW; the ABA genotype provided the smallest expected phenotypic value of BW in all 19 crossbred combinations of the five breeds involved in the study. Backcrossing two-breed genotypes to the sire line decreased BW in BBA and SSA genotypes, remained constant in the HHA genotype, but increased in the CCA genotype. The phenotypic values suggested that all genotypes of two- and three-breed crosses of the A dam line showed increased BW; the only exceptions being the ABA genotype. Since the least squares means of the BA and BBA genotypes (Table 4.1) also showed an increasing effect on BW, the results indicated that the B and C sire lines had a true ability to increase BW. The C sire line had the heaviest calves (42.2 kg), followed by the B sire line (41.1 kg). Though their study was performed under an intensive production system at farms in the Johannesburg area, Dadi et al. (2002) also found that C sired calves were 5 kg heavier than H sired calves. Progeny of CA crossbred cows also had the largest BW of all two-breed dams.

4.4.2 Weaning weight

Table 4.8 Expected phenotypic values for weaning weight (kg) for bull and heifer calves in different sire and dam groups

			Sire breed			
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)	Average
Α	(184.0)	205.0	217.9	196.1	210.7	207.4
ВА	198.4	204.7	239.2	224.9	232.4	219.9
CA	203.4	243.4	235.9	229.9	241.1	230.7
НА	186.2	225.0	230.8	198.6	229.1	213.9
SA	211.8	251.9	245.3	231.9	225.5	233.3
Average	200.0	226.0	233.8	216.3	227.8	

() Not included in the average

All crossbred genotypes weaned heavier than purebred A calves (Table 4.8). The results indicate that the C sire line had the highest expected phenotypic value for WW (233.8 kg). SA dam line provided the largest phenotypic value for WW (233.3 kg) in genotypes which involved crosses of C, B, H and S sire breeds with the A dam. On average, the A sire line had the lightest calves at weaning (200 kg). Results for the respective dam lines had the same trends than the sire lines. The BSA genotype provided the highest expected phenotypic value for WW (251.9 kg). Backcrossing two-breed genotypes to the A dam line decreased WW in ABA, ACA and AHA, but not in ASA. Backcrossing these genotypes to their sire lines increased WW, an exception being the BBA genotype. This indicated that the B genotype used in the study did not have a true superior ability to increase WW in the A breed. It is suggested that the genotype of the calf was a primary variable in WW in two-breed crosses, instead of the mothering ability of cow in crossbred dam genotypes; SA dams on average weaned the heaviest calves.

4.4.3 Heifer weight

Table 4.9 Expected phenotypic values for 19-month weight (kg) of heifers in different sire and dam groups

			Sire breed			
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)	Average
Α	(303.9)	348.5	365.4	334.8	362.3	352.8
ВА	324.3	332.5	388.4	342.9	374.8	352.6
CA	314.6	398.9	394.1	363.0	382.1	370.5
НА	318.1	366.2	379.7	325.8	376.7	353.3
SA	338.5	384.3	381.1	358.7	361.9	364.9
Average	323.9	366.1	381.7	345.0	371.6	

⁽⁾ Not included in the average

The expected phenotypic values (Table 4.9) indicate that all sire line genotypes of A crossbred heifers weighed heavier than purebred heifers at nineteen months of age; the continental breeds (C and S) being heaviest, followed by B, H and A breeds. The BA dam line did not change the average expected HW compared to the average HW of the A dam line. However, HW in the BBA decreased from BA genotypes in this study. Backcrossing other two-breed genotypes to the A dam line decreased HW in all genotypes. Backcrossing two-breed genotypes to their sire lines increased HW in CCA and HHA but did not change HW in the SSA genotype.

4.4.5 Cow weight

Table 4.10 Expected phenotypic values for cow weight (kg) at partus in different sire and dam groups

			Sire breed			
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)	Average
Α	(435.0)	484.2	494.4	437.3	486.6	475.6
ВА	427.2	458.5	512.8	444.2	533.8	475.3
CA	435.5	540.8	525.6	478.1	511.4	498.3
НА	405.6	487.0	492.8	430.0	479.7	459.0
SA	468.9	509.0	507.1	455.8	474.0	483.0
Average	434.3	495.9	506.5	449.1	497.1	

⁽⁾ Not included in the average

The results (Table 4.10) indicate that all genotypes involved in the study had increased expected phenotypic values for CW at partus compared to purebred A dams (435 kg); the only exception being the AHA and HHA genotypes (405.6 and 430.0 kg). The BCA had the largest heterosis of all genotypes with a CW of 540.8 kg. On average, the B, C, H and S sire line genotypes had 14.2, 16.6, 3.4, and 14.5% increased CW respectively, compared to A sire line genotypes.

Backcrossing two-breed genotypes to the A dam line decreased CW in all genotypes, indicating that the A had a true ability to decrease CW in all the breeds involved in the study. Backcrossing two-breed genotypes to the sire lines decreased CW in all genotypes (SSA, BBA and HHA), except in the CCA genotype.

4.4.4 Calf/cow weight ratio

The average expected calf/cow weight ratio (WW/CW) for weaning weight in the different sire and dam groups are presented in Table 4.11.

Table 4.11 The average expected phenotypic calf/cow weight ratios for the different sire and dam groups

			Sire breed			
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)	Average
Α	(0.423)	0.423	0.441	0.448	0.433	0.436
ВА	0.464	0.446	0.466	0.506	0.435	0.463
CA	0.467	0.450	0.449	0.481	0.471	0.463
НА	0.459	0.462	0.468	0.462	0.478	0.466
SA	0.452	0.495	0.484	0.509	0.476	0.483
Average	0.461	0.456	0.462	0.482	0.458	

⁽⁾ Not included in the average

The five dam breeds (A, BA, CA, HA and SA) had average expected calf/cow weight ratios of 0.436, 0.463, 0.463, 0.466 and 0.483 respectively (Table 4.11). All crossbred genotypes, except for the BA genotype, increased the calf/cow weight ratio. These results suggested that production efficiency could increase when *Bos taurus* sire lines were crossbred to A purebred and crossbred dam lines, provided that the breeding system is sustainable in the specific environment. All the three-breed genotypes except the SBA and BBA, had larger ratios than two-breed genotypes.

The H sire line and the SA dam line had the best expected calf/cow weight ratios. The introduction of S genes in crossbreeding systems was also suggested by Schoeman *et al.* (1993). Backcrossing the two-breed genotypes to the all sire lines improved the expected calf/cow weight ratio. The HSA, HBA and BSA, genotypes had the largest calf/cow weight ratios of 0.509, 0.506 and 0.495 respectively.

4.5 THE CORRELATION BETWEEN THE ESTIMATED PHENOTYPIC VALUES AND THE LEAST SQUARES MEANS

In order to validate the predicted breed additive and heterosis effects, Pearson's correlations (r) were calculated between the estimated phenotypic values and least squares means for all the weight traits and are presented in Table 4.12.

Table 4.12 Pearson's correlation between expected phenotypic values and least squares means for growth traits

Growth traits	Correlation
Birth weight	0.93
Weaning weight	0.87
19 Month heifer weight	0.94
Cow weight	0.93

The values (Table 4.12) were all above 0.86 for the growth traits. A shortcoming was that biological replicates were averaged before correlations were calculated due to a lack of the raw data of the experiment.

Possible explanations for the < 1 correlations are:

- The model did not account for all the effects
- Heterosis from multiple groups and their variation. Variation in group means due to sampling (the fact that the s.e. is not zero) implies that the correlation cannot be unity
- Epistasis or recombination effects.

4.6 NON-ADDITIVE EFFECTS

The average non-additive effects for the weight traits in two-breed and three-breed genotypes was calculated by expressing the performance of the crossbred animals in relation to the average of the parents (Newman & Reverter, 2000; Greiner, 2009) and are shown in Table 4.13.

Table 4.13 The average percentage heterosis effects for growth traits in two- and three-breed crosses

	Birth weight (kg)	Weaning weight (kg)	19 month heifer weight (kg)	Cow weight at partus (kg)
Individual heterosis				
Bos indicus** x Sanga*	13.9%	8.0%	12.0%	4.1%
Continental** x Sanga*	2.6%	4.0%	2.8%	18.1%
British** x Sanga*	4.6%	-0.3%	7.6%	5.1%
Bos indicus*** x Bos taurus	21.4%	16.1%	17.8%	12.0%
Bos taurus*** x Bos taurus	-9.3%	5.2%	3.2%	1.7%
Maternal heterosis				
Bos indicus** x Sanga*	-7.0%	3.0%	-5.3%	-2.4%
Continental** x Sanga*	13.6%	10.0%	10.0%	4.4%
British** x Sanga*	-1.0%	12.0%	5.1%	5.2%

^{*} Sanga was represented by the Afrikaner breed

The heterosis effect on BW (Table 4.13) of the two-breed *Bos indicus* x *Bos taurus* differed largely from other genotypes.

In different crossbreeding experiments in beef cattle, MacDonald & Turner (1972) and McElhenney *et al.* (1986) found the influence of maternal heterosis on BW is either non-existing or negligible. The individual non-additive effect of B on BW differed largely from other genotypes. However, on average the effect in B x *Bos taurus* genotypes was 7.5% larger than in the BA genotype (13.9%) (Table 4.13). Continental x A genotypes had a small individual non-additive effect of 2.6%, but a large maternal effect of 13.6% on BW. On the contrary, B and H sires cancelled some of the undesirable individual non-additive effect on BW with maternal values of -7.0 and -1.0%, respectively in the A dam line.

The current study found a large maternal heterosis effect in the Continental breeds; mainly in the C breed. All breeds, except the Hereford, had increased heterosis effects on WW in the A breed. The maternal heterosis of crossbred dams validated the value of crossbred dams in producing heavier WW, which may be associated with improved milking abilities of

^{**} Continental breeds were represented by the Simmentaler and Charolais breeds, British was represented by the Hereford breed and *Bos indicus* was represented by the Brahman breed *** *Bos indicus* x *Bos taurus* and *Bos taurus* x *Bos taurus* values were derived, because these progenies were not produced (The Afrikaner was not included as a *Bos taurus* in this calculation)

crossbred dams (Dadi *et al.*, 2002). The maternal non-additive effect for the BA on WW was only 3.0%, compared to 10 and 12%, respectively for Continental x Afrikaner and HA genotypes respectively. The combined (individual plus maternal) non-additive effect for WW was highest in Continental x Afrikaner genotypes (14.0%).

Gregory *et al.* (1987) found that maternal heterosis effects on post weaning growth were not important. Their study involved Brown Swiss, Red Poll, Hereford and Angus cattle, while Prayaga (2003a) indicated that indicine crossbred cows had a positive effect on post-weaning growth rates of their calves. Positive individual non-additive effects of 17.8% and 12.0%, respectively were found for 19 month HW and CW at partus when the B was crossed the *Bos taurus* breeds. While *Bos taurus* x A crossbred genotypes had positive maternal non-additive effect, the BA dams had negative maternal non-additive effects of -5.3% and -2.4% respectively on these post weaning traits. The results suggest that that the combined non-additive effect of the B (1.7%) on cow weight at partus was smaller than in Continental x A (22.5%) and HA (10.3%) genotypes.

4.7 CONCLUSIONS

The C sire line had the heaviest expected calf birth weights (42.2 kg), followed by the B sire line (41.1 kg). C and B dams cancelled some of the undesirable direct additive effect on BW. Due to additive and non-additive effects of the C and B purebreds, these sires should only be bred to mature cows. C crossbred sires decreased BW, while B crossbred sires increased BW, the only exception being the BC genotype which had a small negative effect (-2.1 kg). The S breed however, had a small positive direct additive effect (+1.8 kg), but highest maternal additive effect (+7.0 kg or +20.3%) of the five breeds (A, S, B, C, and H) involved in the study. The additive and non-additive effects for the H breed on BW were small. On average the expected BW increased by +5.7 kg in two-breed genotypes, but only by another +0.7 kg in three-breed genotypes (backcrossings not taken into calculation).

Although the C had the highest direct breed effect of +64.1 kg or 34.8% for WW, it is suggested that the breed could only be used in a terminal-sire system. The combined additive effect of the C dam line was exceeded by the S dam line (+38.4 kg or +20.9% versus +50.0 kg or +27.2%). Although the B breed had positive genetic parameters for WW, backcrossing the BA genotype to the B sire line proved that the breed did not have a true superior ability to increase WW in the A breed. The study suggested the C and H dam lines could not transmit positive maternal additive effects to WW, while the B dam only had a small positive effect. The two-breed BH and BS genotypes had the largest average direct

heterosis effects of +24.0 and +36.7 kg on WW respectively. This gives opportunity for paternal heterosis to maximize WW in a weaner calf production system with these crossbred genotypes. The heterosis effect for WW obtained in the current study for CA and SA crosses was in accordance with the 4% assumed by MacNeil & Matjuda (2007) for South African conditions. The combined heterosis effect on WW of the CA dam line was highest (+32.5 kg) of the two-breed A dam lines. The maternal heterosis effect of the HA dam was the second largest (+22.1 kg) of the four two-breed combinations of A.

The A sire line had the lowest expected phenotypic values for HW and CW (323.9 and 434.3 kg respectively), indicating that these heifers would probably reach puberty earlier and that these cows would be smaller compared to genotypes from S, B, C and H genotypes. The latter genotypes are assumed to have the most delayed puberty of all the types evaluated.

Chapter 5

ADDITIVE AND NON-ADDITIVE EFFECTS ON FITNESS TRAITS

5.1 INTRODUCTION

In order to develop the most effective suckler cow replacement strategies, beef producers must have information about breed-specific direct and maternal effects for economically important traits. In the dam line the traits affecting maternal ability and calf production are of primary importance (Roughsedge *et al.*, 2001). A sire line that is appropriate for the ultimate use of progeny must optimize production in the dam line (Weaber, 2010).

Reproductive fitness has the greatest impact on profitability of a beef cattle enterprise in that a unit genetic increase in fertility influences the profit function to a greater extent, especially in extensive tropical production systems where calving rates are relatively lower. MacNeil & Matjuda (2007) developed an aggregated simulation model to facilitate breeding strategies in mating exotic sires to adapted dam lines in specific crossbreeding systems to produce value-added weaned calves to the large feedlot industry in South Africa. Apart from other important phenotypic traits, they found the relative emphasis of the calf survival trait alone to be equally important as direct weaning in the selection index.

Selection for easily measurable traits correlated to improve fertility traits and the exploitation of heterosis through crossbreeding are options to consider for additional herd productivity (Long, 1980; Skrypzeck *et al.*, 2000, Prayaga, 2004).

Composite traits such as weaning weight per cow exposed to breeding or number of calves weaned in relation to number of cows exposed to breeding are indicative of both biological and economic efficiency of a cow-calf enterprise (MacNeil *et al.*, 1988) provided that the beef production system is sustainable.

Reproduction as a trait has many components such as calving difficulty (dystocia), longevity and stayability, which manifest themselves as threshold traits, while other components such as calving date, calving interval and age at first calving are of continuous nature. Threshold traits are not continuous in their expression and exhibit distinct categorical phenotypes, but such traits must be visualized as having an underlying genetic merit and continuity. The heritability of some of these traits (e.g. calving difficulty) appears to be of such low magnitude that it seems unlikely that these traits could be improved through selection, but rather through crossbreeding (Smith, 2005; Van der Westhuizen *et al.*, 2001).

The aim of this chapter is to characterize and quantify crossbreeding heterosis of *Bos taurus* and *Bos indicus* bulls on South African Afrikaner (Sanga) cows using results obtained from Vaalharts Research Station in South Africa in respect of fitness traits in 24 crossbred genotypes. The objective is to partition the estimated phenotypic values of crossbred animals in the study of Els (1988) into crossbreeding parameters for the South African beef industry.

5.2 MATERIALS AND METHODS

The crossbreeding experiments were carried out at Vaalharts Research Station, situated near Jan Kempdorp. For a complete description of the experiment terrain and animals as well as environmental conditions and management practices see Chapter 3.

Least squares means for conception rate (CR: percentage of cows certified pregnant), mortality at birth (MB: percentage of calves that died at birth), pre-weaning mortality (MW: percentage of calves that died between birth and weaning) and weaning percentage (WP: calves weaned/cows certified pregnant) in the different breed group combinations were published by Els (1988). Genotype, contemporary group (year of birth, calving season, age of dam) and sex were significant (P < 0.05) sources of variation for all the traits. In addition to the traits published by Els (1988), weaning rate (WR; number of calves weaned in relation to number of cows exposed to breeding) was calculated. The least squares means for these fitness traits are presented in Tables 5.1 to 5.4 (Els.1988).

Table 5.1 Least squares means for conception rate (%) in the different sire and dam breed groups

	Sire breed					
Dam breed	Afrikaner	Brahman	Charolais	Hereford	Simmentaler	
	(A)	(B)	(C)	(H)	(S)	
Α	79.8 (114)*	89.1 (64)	92.4 (66)	96.0 (50)	90.0 (50)	
В	-	77.8 (45)	-	-	-	
С	-	-	83.0 (106)	-	-	
н	-	-	-	92.9 (99)	-	
S	-	-	-	-	89.7 (78)	
ВА	93.3 (45)	90.3 (31)	90.0 (30)	100.0 (24)	97.6 (42)	
CA	97.3 (75)	100.0 (45)	91.5 (47)	97.8 (46)	90.7 (54)	
HA	91.1 (45)	93.9 (33)	90.0 (30)	85.7 (49)	93.3 (45)	
SA	94.4 (54)	95.1 (47)	90.8 (65)	90.6 (32)	97.8 (46)	

^{*}The number of animals in their respective groups is indicated in brackets

Table 5.2 Least squares means for mortality at birth (%) in the different sire and dam breed groups

			Sire breed		
Dam breed	Afrikaner	Brahman	Charolais	Hereford	Simmentaler
	(A)	(B)	(C)	(H)	(S)
Α	2.2 (91)*	0 (57)	1.6 (64)	0 (48)	4.4 (45)
В	-	2.9 (35)	-	-	-
С	-	-	2.3 (88)	-	-
н	-	-	-	4.4 (92)	-
S	-	-	-	-	5.7 (70)
ВА	0 (42)	0 (28)	7.4 (27)	4.2 (24)	0.0 (41)
CA	2.7 (73)	2.2 (45)	2.3 (43)	6.7 (45)	2.0 (49)
HA	0.0 (41)	0.0 (31)	0.0 (27)	0.0 (42)	0.0 (42)
SA	2.0 (51)	2.5 (40)	3.4 (59)	0.0 (29)	0.0 (46)

^{*}The number of animals in their respective groups is indicated in brackets

Table 5.3 Least squares means for pre-weaning mortality (%) in the different sire and dam breed groups

	Sire breed					
Dam breed	Afrikaner	Brahman	Charolais	Hereford	Simmentaler	
	(A)	(B)	(C)	(H)	(S)	
Α	3.3 (89)*	5.3 (57)	3.1 (63)	2.1 (48)	6.7 (43)	
В	-	0.0 (34)	-	-	-	
С	-	-	8.0 (86)	-	-	
н	-	-	-	5.4 (88)	-	
s	-	-	-	-	4.3 (66)	
ВА	14.3 (42)	0.0 (28)	14.8 (25)	4.2 (23)	2.4 (41)	
CA	4.1 (71)	0.0 (44)	11.6 (42)	2.2 (42)	2.0 (48)	
HA	0.0 (41)	3.2 (31)	3.7 (27)	4.8 (42)	0.0 (42)	
SA	3.9 (50)	0.0 (39)	6.7 (57)	0.0 (29)	4.4 (45)	

^{*}The number of animals in their respective groups is indicated in brackets

Table 5.4 Least squares means for weaning percentage (%) in the different sire and dam breed groups

			Sire breed		
Dam breed	Afrikaner	Brahman	Charolais	Hereford	Simmentaler
	(A)	(B)	(C)	(H)	(S)
Α	75.4 (114)*	84.4 (64)	92.4 (66)	94.0 (50)	80.0 (50)
В	-	75.6 (45)	-	-	-
С	-	-	74.5 (106)	-	-
Н	-	-	-	83.8 (99)	-
S	-	-	-	-	80.8 (78)
ВА	80.0 (45)	90.3 (31)	70.0 (30)	91.7 (24)	95.2 (42)
CA	90.7 (75)	97.8 (45)	78.7 (47)	89.1 (46)	87.0 (54)
HA	91.1 (45)	90.9 (33)	86.7 (30)	81.6 (49)	93.3 (45)
SA	88.9 (54)	83.0 (47)	81.5 (65)	90.6 (32)	93.5 (46)

^{*}The number of animals in their respective groups is indicated in brackets

Weaning rate was determined by using information in Tables 5.1 to 5.4. These averages are presented in Table 5.5.

Table 5.5 Average for weaning rate (%) in the different sire and dam breed groups

	Sire breed						
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)		
Α	66.7 (114)*	79.7 (64)	81.8(66)	84.0(50)	76.0(50)		
В	-	68.9 (45)	-	-	-		
С	-	-	67.0 (106)	-	-		
н	-	-	-	74.7 (99)	-		
S	-	-	-	-	67.7 (78)		
ВА	73.3 (45)	74.2 (31)	60.0 (30)	83.3 (24)	73.8 (42)		
CA	76.0 (75)	75.6 (45)	66.0 (47)	73.9 (46)	72.2 (54)		
HA	80.0 (45)	78.8 (33)	80.0 (30)	67.3 (49)	80.0 (45)		
SA	68.5 (54)	68.1 (47)	63.1 (65)	65.6 (32)	84.8 (46)		

^{*}The number of animals in their respective groups is indicated in brackets

The models used for the estimation of additive and heterosis effects in this Chapter have already been described in Chapter 4.

The GLM procedure of SAS (2010) was used for the analysis of the data set. The data set was formed by recording each least squares mean along with breed composition, maternal breed composition and direct and maternal heterozygosities as covariates on a weighted (number of animals) LS regression. Each trait was analyzed separately. Breed solutions for each trait were expressed relative to the Afrikaner breed, similar to a method used, by amongst others, Williams *et al.* (2010).

5.3 RESULTS AND DISCUSSION

The proportional contributions from the various genotyes that were used for the estimation of genetic effects in two- and three-breed and backcross combinations were described in Chapter 4.

The additive and heterosis effects for the fitness traits in pure- and crossbred animals were estimated and are shown in Tables 5.6(a) and (b).

Table 5.6(a) Additive effects and standard errors on fitness traits for pure-and crossbred animals

Effect	Breed	Conception (%)	Calving difficulty (%)	Pre- weaning mortality (%)	Weaning percentage (%)	Weaning rate (%)
Intercept	Α	79.8 ± 2.8*	2.2 ± 1.5	3.3 ± 2.1	75.4 ± 6.0	66.7 ± 2.8
Individual	S	11.9 ± 1.3	-6.2 ± 5.6	-2.7 ± 7.4	4.2 ± 23.8	36.9 ± 11.2
(direct)	В	-5.3 ± 13.1	-1.1 ± 6.6	-26.5 ± 8.8	17.6 ± 7.7	3.4 ± 13.0
	С	-28.6 ± 1.5	1.7 ± 10.9	36.3 ± 14.4	-64.1 ± 45.2	-45.4 ± 21.3
	Н	-13.1 ± 11.5	0.9 ± 6.0	6.6 ± 7.8	-230 ± 24.1	-27.4 ± 11.4
Maternal	S	-2.0 ± 12.1	9.7 ± 6.1	3.6 ± 8.1	1.2 ± 25.6	-35.9 ± 12.0
	В	3.3 ± 14.2	1.7 ± 7.2	23.2 ± 9.7	-17.4 ± 29.9	-1.2 ± 14.1
	С	31.8 ± 21.8	-1.6 ± 11.1	-31.6 ± 14.7	63.2 ± 46.0	45.7 ± 21.7
	Н	26.2 ± 12.2	1.2 ± 6.3	-4.4 ± 8.3	31.4 ± 25.7	35.4 ± 12.1

^{*} All standard errors are expressed in percentage units and represent a lack of fit to the genetic model, rather than variation amongst animals in the same genotype

The heritability of reproduction traits are low (MacNeil *et al.* 1984; Van der Westhuizen *et al.*, 2001; Weaber, 2009) and variation in them are largely due to environmental factors. Therefore a small portion of additive variation in fitness traits were expected, but heterosis was expected to significantly improve the productivity of cows regarding fitness traits (Weaber, 2009). Dickerson (1973) suggested that lower reproductive rates favour rotational crossbreeding or synthetics rather than specific crossbreeding.

Table 5.6(b) Heterosis effects and standard errors on fitness traits for pure- and crossbred animals

Effect	Breed	Conception rate (%)	Calving difficulty (%)	Pre- weaning mortality (%)	Weaning percentage (%)	Weaning rate (%)
Individual	ВА	12.2 ± 8.5	-2.1 ± 4.3	15.9 ± 5.7	-0.9 ± 17.8	11.8 ± 8.4
(direct)	CA	30.0 ± 12.1	-0.5 ± 6.0	-16.6 ± 8.1	44.5 ± 25.5	36.3 ± 12.0
	HA	21.7 ± 8.1	-2.3 ± 4.1	-5.8 ± 5.5	28.3 ± 17.0	30.1 ± 8.0
	SA	7.0 ± 7.9	4.0 ± 3.9	2.5 ± 5.4	11.7 ± 16.7	-6.8 ± 7.9
	ВС	17.4 ± 12.8	6.0 ± 6.4	-6.5 ± 8.5	18.6 ± 27.0	8.8 ± 12.7
	ВН	17.9 ± 10.6	3.9 ± 5.3	3.4 ± 7.1	10.1 ± 22.4	18.9 ± 10.5
	BS	-5.8 ± 9.5	2.5 ± 4.8	-2.1 ± 6.3	-6.5 ± 20.0	-17.3 ± 9.4
	СН	18.1 ± 12.4	10.4 ± 7.1	-19.2 ± 8.4	30.8 ± 26.1	30.8 ± 12.3
	CS	-0.3 ± 11.8	1.9 ± 7.0	-16.2 ± 7.9	12.2 ± 24.8	-4.1 ± 11.7
	HS	1.2 ± 9.3	-0.1 ± 4.7	-9.1 ± 6.2	9.5 ± 19.6	-5.7 ± 9.2
Maternal	ВА	6.7 ± 6.1	-1.2 ± 3.1	-3.0 ± 4.1	10.8 ± 12.9	-0.2 ± 6.1
	CA	-4.9 ± 9.7	0.3 ± 5.7	14.3 ± 6.6	-18.5 ± 20.5	-19.0 ± 9.7
	HA	-8.2 ± 4.9	-2.4 ± 2.5	1.6 ± 3.4	-6.4 ± 10.4	-11.6 ± 4.9
	SA	6.6 ± 5.1	-4.4 ± 2.5	0.0 ± 3.4	8.5 ± 10.7	11.8 ± 5.1

^{*} All standard errors are expressed in percentage units and represent a lack of fit to the genetic model, rather than variation amongst animals in the same genotype

5.3.1 Conception rate (CR)

The results in Table 5.6(a) indicate that the S was the only breed that had a desirable individual additive contribution to the A breed for conception rate (CR) (+11.9% percentage units or 14.9%), but had a negative maternal additive effect (-2.0% percentage units). The B, C and H breeds had a combined (individual plus maternal) additive effect of -1.9, +3.6 and +13.1% percentage units respectively, the latter mainly due to large maternal effects. Since CR is not a trait that is frequently used in beef cattle, articles relating to calving rate were considered. Theoretically, there should not be a big difference between CR and calving rate. Long (1980) reported direct heterosis for calving rate in the range of 3 – 15%. Table 5.6(b) indicates that the CA genotype had the largest positive individual heterosis effect (+30.0% percentage units or 37.6%) on CR and the BS the largest negative (-5.8% percentage units or -7.3%) out of the ten two-breed genotypes involved in the study.

The only other genotype with a negative individual heterosis effect on CR was the CS genotype. The BA and SA genotypes had positive maternal heterosis effects (+6.7 and +6.6% percentage units, respectively) and CA and HA genotype negative maternal heterosis effects (-4.9 and -8.2% percentage units respectively). Weaber (2010) reported 4.4% and 3.7 % average individual and maternal heterosis for calving rate in beef cattle in the USA.

5.3.2 Mortality up to birth (MB)

Williams et al. (1991) estimates genetic effects for calving success by treating it as a trait of the calf. They stated that this procedure gave scope for equal emphasis to the genotype of the sire and dam. Cundiff et al. (1982) stated that the incidence of dystocia, considered as a calf trait, has a heritability of 0.30. However, Gregory et al. (1991) and Prayaga (2004) treated the calving difficulty as a trait of the dam. In the current study the genetic effects were also derived after adjustment for the fixed effects affecting mortality up to birth (MB) including breed of the bull, similarly to the method of the latter mentioned authors. Table 5.6(a) indicates that the direct effects on MB of the S and B genotypes (-6.2 and -1.1% percentage units respectively) were desirable on the A dam line, the H had a small positive effect (+0.9% percentage units), but the C breed had an undesirable +1.7% percentage units or +77.3% contribution. It is suggested that C sire should not be mated to small or young A dams and that care should be taken that the expected breeding value for birth weight for C sires should be small. However, the negative maternal additive effect (-1.6% percentage units) almost cancelled the entire positive direct breed effect in the C genotype. The combined additive effects of the S, B and H dam lines were +2.7, +0.6 and 2.1% percentage units respectively. Roughsedge et al. (2001) claimed that breeds with greater mature weight have greater maternal genetic effects for calving ease, but negative direct genetic effects. This study confirmed the statement for the S, but not for the C continental breeds. Table 5.6(b) indicates that the CH genotype had the highest individual heterosis effect of +10.4% percentage units, while the BA had the lowest effect (-2.1% percentage units). All crossbred cows (BA, HA and SA) except CA, improved calving success with -1.2, -2.4 and -4.4% respectively when compared to purebred A cows.

5.3.3 Pre-weaning mortality (MW)

Pre-weaning calf survival is closely associated with and influenced by the maternal capability of the dam and is known to vary among genotypes (Williams *et al.*, 1990; Peacock *et al.*, 1999; Weaber, 2010). In a crossbreeding experiment that involved British, Sanga derived,

Zebu and Continental breeds in a tropical environment, Prayaga (2004) found that about 50% of pre-weaning calf mortalities were due to abortion, 14% between birth and 1 week after birth due to unknown reason, 9% due to dystocia and 17 % due to unknown reasons between one week after birth and weaning. Inadequate mothering ability (e.g., bottle teats, abandonment of calf), killed by predators, and premature and accidental death were additional causes of pre-weaning mortality. This study found results (Table 5.6(a)) contradicting Prayaga (2004), who found no strong additive genetic differences among breeds involved in his study and hence his recommendation that no strong emphasis on calf survival traits need to be given while planning crossbreeding programs. The C breed had the largest undesirable additive effect on pre-weaning mortality (MW) (+36.3% percentage units). The H also had an undesirable breed effect (+6.6% percentage units). The combined additive effects for the S, B, C and H breeds were +0.9, -3.3, +4.7 and +2.2% percentage units respectively. It is thus suggested that only the B genotype might have complementary genes to increase the pre-weaning calf survival rate in the A. However, Table 5.6(b) shows that out of the ten two-breed combinations the BA genotype had a substantially larger undesirable direct heterosis contribution (+15.9% percentage units or +482%) on MW, while other combinations had an average contribution of -7.7% percentage units or -234%. The BA dam line (with a maternal heterosis effect of -3.0% percentage units, outperformed the HA, SA and CA dam lines and the CA dam line had the highest undesirable effect (+14.3% percentage units). The combined heterosis effects (individual plus maternal) for MW in BA, CA, HA and SA were +12.9, -2.3, -4.2 and +2.5% percentage units respectively. Weaber (2010) however reported 1.9 and 1.5% average individual and maternal heterosis effects for survival to weaning in the USA.

5.3.4 Weaning percentage (WP)

Breeds that excel in a combination of fitness traits such as CR and calf survival also contribute to calf weaning weights when calf weaning weights are expressed on a per cow exposed basis. Breeds that sire cows that excel in this combination of traits will also have higher weaning weights per cow exposed (Greiner, 2009). The weaning percentage (WP) of the A breed was 75.4% (Table 5.6(a)). Only the S and B breeds had desirable positive direct contributions: +4.2 and +17.6% percentage units respectively, while the C and H breeds had undesirable negative contributions: -64.1 and -23.0% percentage units respectively. The individual and maternal additive contributions were once again negatively correlated in the dam lines. The combined additive contributions were +5.4, +0.2, +0.9 and +8.4% percentage units for the S, B, C and H breeds respectively. Table 5.6(b) shows that the individual heterosis effect of the CA genotype cancelled the large undesirable individual additive effect

by more than half, resulting in a direct breed and heterosis effect of -19.6 % percentage units or -30.0%. Other two-breed genotypes (HA, SA, BC, BH, CH, CS and HS) had desirable contributions averaging +16.0% percentage units, the only exception being the BA and BS genotype with -0.9 and -6.5% percentage units effect respectively. The maternal heterosis effect of the CA and HA dams were undesirable (-18.5 and -6.4% percentage units respectively), while those of the BA and SA dams were desirable (+10.8 and +8.5% percentage units respectively). The combined heterosis effects for the BA, CA, HA and SA dam lines were +9.9, +26.0, +21.9 and +20.2% percentage units respectively; averaging +19.5% percentage units or +25.9%.

5.3.5 Weaning rate (WR)

The S genotype had a substantial larger individual additive desirable contribution (+36.9% percetage units) than any of the other purebred genotypes on the weaning rate (WR) of the A breed, which had a WR value of 66.7% (Table 6). The C had the largest undesirable direct breed effect (-45.4% percentage units or -68.0%). However, the maternal additive effects of the S and C breeds (-35.9 and +45.7% percentage units respectively) cancelled their direct breed effects, resulting in the combined additive contribution of the H being the largest (+8.0% percentage units or +12.0%). The B and H genotypes had values of +3.4 and -27.4% percentage units respectively. The individual heterosis effects (Table 5.6(b)) for two-breed combinations varied between -17.3 (for the BS genotype) and +36.3% percentage units (for the CA genotype). In this regard only CA, HA and CH paternal heterosis would increase WR in the A breed (the latter two genotypes with 30.1 and 30.8% percentage units respectively).

The BA dam had a small undesirable maternal heterosis effect of (-0.2% percentage unit) on the WP of the A, the CA and HA genotypes had values of -19.0 and -11.6% percentage units respectively. The only crossbred dam line that had a desirable maternal heterosis contribution to the A genotype was the SA breed (+ 11.8% percentage units or +17.7%).

5.4 PREDICTION OF PERFORMANCE IN CROSSBRED GENOTYPES

The expected phenotypic values for the different fitness traits in two- and three-breed genotypes were subsequently calculated and are presented in Tables 5.7 to 5.10.

5.4.1 Conception rate (CR)

The two cases where the expected conception rates are higher than 100, may be the result of the lack of fit of the model or an artifact of the assumed normal distribution of the trait. Johnson & Notter (1987) studied the problem of assuming normal distributions for binominal traits and found that parameter estimates on binominal scale were slightly lower than those on the underlying normal scale, thus indicating that the use of linear models to analyze binominal reproduction data is satisfactory.

Table 5.7 indicates that all crossbred sire line genotypes had improved CR when they were compared to their respective pure breeds and the A breed; the least squares means for the A, B, C, H, and S breeds were 79.8, 77.8, 83.0, 92.9 and 89.7% respectively (Table 5.1). While Williams *et al.* (1990) found that straightbred B cows had lower calving rates than Angus, C and H in Louisiana, USA, Cartwright (1973), Williams *et al.* (1990) and Prayaga (2004) found that rotational systems which involved combinations of B genotypes had increased calving rates compared to purebred British and Continental breeds in subtropical environments. Mpofu (2002) claimed that none of several crossbred cows could surpass the calving rate of indigenous Mashona cattle in Zimbabwe and that the fertility rate of the A was low in comparison with indigenous, Zebu, British and Continental breeds on natural pastures.

Table 5.7 Expected phenotypic values for conception rate (%) in the different sire and dam groups

	Sire breed						
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)	Average	
Α	(79.8)	89.4	95.5	94.9	92.8	93.2	
ВА	89.6	86.9	96.3	100.2	93.5	93.3	
CA	101.1	95.7	86.8	97.0	93.3	94.7	
НА	96.4	93.8	91.2	89.8	97.9	93.8	
SA	88.6	88.9	89.3	87.3	94.6	89.7	
Average	93.9	90.9	91.8	93.8	94.4		

() Not included in the average

In this study three-breed genotypes did not necessarily outperform the two-breed combinations, but CA and HA dam lines had the highest average expected CR (95.5 and 94.9% respectively). Backcrossing two-breed genotypes to the A sire line did not change the expected phenotypic CR in the ABA markedly (89.4 *versus* 89.6%), increased the CR in the ACA (95.5 *versus* 101.1%) and AHA (94.9 *versus* 96.4%) genotypes and decreased the CR in the ASA (92.8 *versus* 88.6%). The latter two genotypes had the highest and the lowest expected phenotypic values, respectively for CR of all genotypes involved in the study. Backcrossing two-breed genotypes to their respective sire lines decreased CR in all three-breed genotypes, an exception being the SSA genotype (92.8 *versus* 94.6%). These results suggested that although the A sire line had the highest average expected phenotypic value for CR (93.9%), it only outperformed the B, C and H sire lines, but not necessarily the S sire line.

5.4.2 Mortality at birth (MB)

Table 5.8 Expected phenotypic values for mortality at birth (%) in the different sire and dam groups

	Sire breed							
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)	Average		
Α	(2.2)	-0.5	1.8	0.4	3.1	1.2		
ВА	1.1	0.0	5.2	2.9	1.8	2.2		
CA	1.7	3.4	1.4	6.6	2.1	3.0		
НА	0.5	0.9	6.4	-0.7	-0.4	1.3		
SA	5.3	0.7	2.7	0.3	7.3	3.3		
Average	2.2	0.9	3.5	1.9	2.8			

⁽⁾ Not included in the average

A low calf survival rate may indicate problems with dystocia and a lack of vigor. According to Williams *et al.* (1990) the C breed is known to require more assistance at birth than other pure breeds such as Angus and H, while B require less. Among other, the environment to which the calf was exposed has been found to influence the degree of assistance at birth (Laster & Gregory, 1973).

The least squares means for MB (Table 5.2) in the A, B, C, H and S purebred genotypes were 2.2, 2.9, 2.3, 4.4 and 5.7% respectively. This is in accordance with Mpofu (2002) who found that indigenous breeds outperformed the exotic breeds on survival rates. Two-breed genotypes however had lowered MB (Table 5.8) compared to the purebred A. In three-breed genotypes the SSA had the highest average expected phenotypic value for MB (+7.3%) and the HHA the lowest (-0.7%). Backcrossing two-breed genotypes to the A genotype increased the expected phenotypic value for MB in ABA and ASA, but the values remained almost the same in ACA and AHA genotype. Conflicting results were however obtained when two-breed genotypes were backcrossed to their respective sire lines: the expected phenotypic value for MB in BBA and SSA also increased. There were decreases in the MB of CCA and HHA from their respective two-breed genotypes.

5.4.3 Pre-weaning mortality (MW)

Table 5.9 Expected phenotypic values for pre-weaning mortality (%) in the different sire and dam groups

			Sire breed			
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)	Average
Α	(3.3)	6.0	4.9	0.8	4.4	4.0
ВА	15.6	2.3	11.9	7.5	4.1	8.3
CA	-4.5	2.3	13.7	1.7	2.7	4.8
НА	0.7	0.9	4.6	4.0	-0.3	2.0
SA	5.7	-2.0	6.2	0.2	4.3	2.9
Average	4.4	1.9	8.3	2.8	3.0	

⁽⁾ Not included in average

Williams *et al.* (1990) found in a study which involved 3 729 crossbred calves that MW was similar and lower than MW of straightbred calves. In the current study the least squares means for MW (Table 5.3) in the A, B, C, H and S purebred genotypes were 3.3, 0.0, 8.0, 5.4 and 4.3% respectively. In a study by Prayaga (2004) in Australia pre-weaning mortality constituted up to 10% of total births. Table 5.9 indicates that out of all two-breed genotypes HA had the lowest MW (0.8%).

On average the C sire line and BA dam line had the highest average expected phenotypic value for MW (both with 8.3%), which were both substantially larger than the other lines of cattle. The low average MW of the B sire line was contradictory to findings by DeRouen *et al.* (1967), Koger *et al.* (1967), Cundiff (1970), Reynolds *et al.* (1980) and Wiliams *et al.* (1990) under different circumstances.

The BA, ABA and BBA genotypes had expected values for MW of 6.0, 15.6 and 2.3% respectively; which suggests that the A genotypes should not constitute more than 25% in the genetic make up of the cross. The ASA genotypes had increased expected values for MW (4.4 versus 5.7%), and almost the same value in the SSA genotype (4.4 versus 4.3%).

Results also indicate that the increases in A genotype decreased the expected MW in C genotype (4.9 versus -4.5%), but not in H crosses (0.8 *versus* 0.7%).

5.4.4 Weaning percentage (WP)

Table 5.10 Expected phenotypic values for weaning percentage (%) in different sire and dam groups

			Sire breed			
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)	Average
Α	(75.4)	83.3	87.8	92.2	87.8	87.8
ВА	76.0	84.8	81.4	89.7	86.1	83.6
CA	104.0	90.1	71.9	90.6	86.6	88.6
НА	96.3	92.4	84.5	84.8	91.7	89.9
SA	87.2	91.2	81.9	93.0	89.3	88.5
Average	90.9	88.4	81.5	90.1	88.3	

⁽⁾ Not included in the average

The least squares means for WP (Table 5.4) in the A, B, C, H and S purebred genotypes were 75.5, 75.6, 74.5, 83.8 and 80.8% respectively. Results in Table 5.10 indicate that all crossbred genotypes had improved expected WP, an only exception is the CCA genotype. William *et al.* (1990) also obtained an overall mean WP that was higher in crossbred cows than in purebred cows.

In the current study the average expected phenotypic values for WP in the crossbred sire lines were higher than their respective purebred sire lines. Crossbred *Bos taurus* dam lines had an advantage over the crossbred B dam line. The C sire line had the lowest expected WP (81.5%) of all sire lines. Since the BBA genotype (84.8%) had an advantage over the ABA genotype (76.0%), it could be suggested that increasing proportions of B would lead to increasing WP in the A genotype. The ACA and CCA genotypes had the highest and lowest expected WP (104.0 and 71.9% respectively) of all genotypes that were involved in the study. Similarly, the AHA and HHA genotypes had expected WP of 96.3 and 84.8% respectively.

This suggests that a maximum WP is expected when A constitute 75% in the crossbreeds with C and H. There was a small difference between the expected WP for ASA and SSA genotypes (87.2 *versu*s 87.8%) which might indicate that the S genotype had only a small contribution in crosses with less than 50% A.

5.4.5 Weaning rate (WR)

The expected phenotypic values for WR (%) in different sire and dam groups are indicated in Table 5.11.

Table 5.11 Expected phenotypic values for weaning rate (%) in different sire and dam groups

		Sire breed								
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)	Average				
Α	(66.7)	80.2	80.3	83.1	78.4	80.5				
ВА	72.8	74.5	66.6	77.7	73.2	73.0				
CA	86.9	71.0	64.2	76.0	72.2	74.1				
НА	86.8	83.0	76.8	73.1	78.1	79.6				
SA	60.4	68.6	63.1	68.2	78.9	67.8				
Average	76.7	75.5	70.2	75.6	76.2					

⁽⁾ Not included in the average

The calculated cumulative trait WR (Table 5.5) of the A, B, C, H and S were 66.7, 68.9, 67.0, 74.7 and 67.7% respectively.

These results are different from Mpofu (2002) who indicated the superiority of adapted indigenous cattle and the inferiority of exotic cattle for fitness traits which are known to suffer when adaptability is poor. It could be explained by the fact that the semi-arid environment of Vaalharts Research Station may be less tick and parasite invested than Matopos Research Station in Zimbabwe.

However, on average two-breed combinations ranked biologically more efficient than purebred genotypes (Table 5.11) in the semi-arid environment. Backcrossing C and H crossbred dam lines to A sire increased the expected WR from 80.3 and 83.1% to 86.9 and 86.8% respectively; while backcrossing the CA and HA two-breed genotypes to their respective sire lines decreased the expected WR (to 64.2 and 73.1% respectively); suggesting that the ACA and AHA genotypes maximized WR. These genotypes had the highest WR of all genotypes involved in the study and also suggested that the A genotype had a true ability to increase WR in crosses with C and H breeds. On average the SA dam line had the lowest average expected WR of all dam lines (67.8%); the WR in the ASA progeny being the lowest of all genotypes (60.4%). The results suggested that on average two-breed rotations of the A breed could outperform three-breed rotations.

5.5 THE CORRELATION BETWEEN ESTIMATED PHENOTYPIC VALUES AND LEAST SQUARES MEANS

The Pearson's correlation between the expected phenotypic values and the least squares means for fitness traits were calculated and are presented in Table 5.12. A shortcoming was that biological replicates were averaged before correlations were calculated due to a lack of the raw data of the experiment. Because the environmental variance is larger for these traits than for growth traits, one might expect these correlations to be lower, provided the number of animals contributing to a breed group mean remains constant.

Table 5.12 Pearson's correlation between expected phenotypic values and least squares means for fitness traits

Fitness traits	Correlation value
Conception rate (CR)	0.64
Calving difficulty (MB)	0.50
Pre-weaning mortality (MW)	0.80
Weaning percentage (WP)	0.60
Weaning rate (WR)	0.80

The values in Table 5.12 range from 0.5 to 0.8 for the traits. Traits such as CR, MB and WP showed a larger lack of fit to the genetic model than MW and WR. Possible explanations for the < 1 correlations have already been discussed in Chapter 4. The fact that these traits are on a binominal scale may exacerbate the lower correlations.

5.6 NON-ADDITIVE EFFECTS

The average non-additive effects for the fitness traits in two-breed and three-breed genotypes in the study were calculated and are shown in Table 5.13.

On average fitness traits with large effects, MW and WR (Table 5.11), could be maximized in two-breed genotypes of the A breed, the only exception being the *Bos indicus* x Sanga cross for the MW trait. The direct heterosis in WR was substantial, except for the *Bos indicus* x *Bos taurus* cross which had a lower phenotypic value than was expected. In Chapter 4 it was found that the cow weights of crossbred genotypes were larger than purebred genotypes. The results in Table 5.11 further suggest that the increased cow weight did not influence WR.

Table 5.13 The average heterosis effects for fitness traits in two-breed *versus* three-breed crosses (backcrosses included)

	Conception rate (%)	Pre-birth mortality (%)	Pre-wean mortality (%)	Weaning percentage (%)	Weaning rate (%)
Individual heterosis					
Bos indicus** x Sanga*	15.3%	-95.0%	481.8%	-1.2%	17.7%
Continental** x Sanga*	23.2%	159.0%	-427.3%	37.3%	18.1%
British** x Sanga*	27.2%	-104.5%	-175.8%	37.5%	22.1%
Bos indicus*** x Bos taurus	12.3%	187.9%	-347.7%	9.8%	5.2%
Bos taurus*** x Bos taurus	7.9%	554.5%	-135.9%	23.2%	10.5%
Maternal heterosis					
Bos indicus** x Sanga*	8.4%	-54.5%	-90.1%	14.3%	-0.3%
Continental** x Sanga*	1.1%	-186.4%	216.7%	-6.6%	-5.4%
British** x Sanga*	-10.3%	-109.1%	48.5%	-8.4%	-17.4%

^{*} Sanga was represented by the Afrikaner breed

5.7 CONCLUSIONS

Some caution is advisable in the interpretation of the specific heterosis effects as the number of observations contributing to each estimate is fairly small.

The current study suggest that breeding CA or HA crossbred dams to A sires would be the most optimal crossbreeding system with regard to reproduction rate in an environment similar to that of Vaalharts Research Station. The results also suggest that crossbreeding with B could be advantageous, but that it would not maximize the WR in the A breed and that the S and A breeds do not complement one another with regards to WR.

^{**} Continental breeds were represented by the Simmentaler and Charolais breeds, British was represented by the Hereford breed and *Bos indicus* was represented by the Brahman breed

^{***}Bos indicus x Bos taurus and Bos taurus x Bos taurus values were derived, because these progenies were not produced. (Sanga was not calculated as Bos taurus in this calculation)

The results suggest that one of a number of crossbreeding strategies would maximize fitness in an environment similar to Vaalharts Research Station; that either A or B sires are mated to HA dams or A sires mated to CA dams in a specific crossbreeding - combined terminal sire system. Ratational systems will not have the same advantage since backcrossing the CA or HA dams to their respective sire lines would decrease the WR. Alternatively, CA, HA or CH crossbred sires could be used on purebred A dams in a specific crossbreeding system. These genotypes had the largest direct heterosis effect on WR of two-breed genotypes. In a specific two-breed system the HA genotype would maximize WR.

However, it should be noted that the data did not take cogniances of the genetic trends in the traits and the effects on heterosis parameters in any of the breeds since the conduction of the crossbreeding experiments.

Chapter 6

ADDITIVE AND NON-ADDITIVE EFFECTS ON FEEDLOT AND CARCASS TRAITS

6.1 INTRODUCTION

The South African beef market has changed radically over the last four decades. In the past farmers could sell their cattle as oxen or old cows for a reasonable price, but the advent of a large feedlot sector in South Africa, has meant that the commercial market now requires animals that are earlier maturing, efficient converters of high quality feed and possess superior carcass attributes (Scholtz *et al*, 2008). Currently 75% of all beef cattle slaughtered in the formal sector in South Africa originate from commercial feedlots (RMRD SA, 2010).

Although British and European breeds represent only 25% of the seed stock industry in South Africa, they dominate the feedlot industry with 53% of cattle in the feedlots originating from these breeds (Scholtz *et al*, 2008). This demonstrates that these breeds are being used as sire lines in crosses. However, it is not clear how effectively this is being done.

Furthermore, breeding objectives for the production of crossbred cattle are largely lacking in South Africa. MacNeil & Matjuda (2007) developed an aggregated simulation model for a consistently applicable breeding objective related to traits that influence profitability in commercial beef production with crossbred cattle. Heterosis is captured in progeny of locally adapted (low input) maternal breeds that are mated to specialized sires lines for economic efficiency. Results indicate that all traits are not equally important to selection decisions. For carcass traits, post-weaning daily gain, post-weaning daily feed intake, dressing percentage and fat depth are included in the breeding objectives; the latter with a relatively small emphasis. In this regard the utilization of the later maturing Continental breeds (e.g. Charolais, Simmentaler) with their favourable growth rate and efficiency of feed conversion (Cundiff *et al.*, 1981; Baker *et al.*, 1987) is available to producers.

The aim of this chapter is to characterize and quantify crossbreeding heterosis in South African beef cattle using results obtained from the Vaalharts Research Station in South Africa in respect of the carcass traits in 24 crossbred genotypes from five pure breeds. The objective is to partition the phenotypic values of crossbred animals in the study of De Bruyn (1991) into crossbreeding parameters for the South African beef industry. The study targeted only feedlot performance, which is different to crossbreeding systems that target complete pasture-fed beef production. Although the data have been collected some years ago it is believed to be reliable and accurate, but was never analyzed in such a way that heterosis effects could be characterized. Some of the breeds involved may also have undergone changes in their base line populations due to selection (with a change in inbreeding coefficients and additive effects). The results are therefore not necessarily directly applicable in the current South African beef industry circumstances. However, no other more recent crossbreeding results are currently available in South Africa. Therefore the analyses of this data will supply useful information, albeit somewhat outdated.

6.2 MATERIALS AND METHODS

The crossbreeding matings were carried out at the Vaalharts Research Station, situated near Jan Kempdorp as described in Chapter 3. De Bruyn (1991) evaluated five purebred sire lines; Afrikaner (A), Brahman (B), Charolais (C), Hereford (H) and Simmentaler (S) in crosses with the A as dam line and their F1 crosses at the then Animal and Dairy Science Research Institute at Irene. All the steers from the different genotypes were weaned at approximately 7 months of age and/or 220 kg, where-after they entered the feeding trial at Irene. They were slaughtered at an average live weight of 440 kg. At slaughter each animal was submitted to a standard slaughter procedure and subjected to carcass evaluation procedures.

Prior to the feeding period all steers were dosed with a broad spectrum anthelmintic. No anabolic growth promoters were administered to these animals. They were intensively fed (10.27 MJ ME/kg and 11.86% crude protein) in individual feeding pens.

Least squares means for feedlot traits in different breed group combinations were published by De Bruyn (1991). The least squares means for feedlot gain (FG), carcass gain (CG) and feed conversion ratio (FCR) from that study are presented in Tables 6.1 to 6.3.

Table 6.1 Least squares means and standard errors for feedlot gain (g/day) for steers combined in the different sire and dam breed groups

_	Sire breed						
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)		
Α	809 ± 48	968 ± 49	1056 ± 60	1089 ± 49	1126 ± 50		
	(19)*	(15)	(10)	(16)	(16)		
В	-	849 ± 57	-	-	-		
		(12)					
С	-	-	1380 ± 49	-	-		
			(16)				
Н	-	-	-	1201 ± 49	-		
				(16)			
S	-	-	-	-	1171 ± 50		
					(16)		
ВА	735 ± 57	773 ± 57	1177 ± 52	1018 ± 49	1075 ± 54		
	(13)	(12)	(14)	(15)	(13)		
CA	868 ± 51	1085 ± 49	1201 ± 49	1099 ± 49	1160 ± 49		
	(15)	(16)	(15)	(16)	(16)		
НА	931±57	1002 ± 54	1087 ± 64	985 ± 76	1100 ± 49		
	(11)	(13)	(9)	(7)	(16)		
SA	951 ± 49	928 ± 49	1090 ± 51	1024 ± 49	1085 ± 49		
	(16)	(16)	(15)	(16)	(16)		

^{*} Number of animals involved in all feedlot and carcass traits

Table 6.2 Least squares means and standard errors for carcass gain (g/day) for steers combined in the different sire and dam breed groups

	Sire breed						
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)		
Α	497 ± 28	560 ± 29	636 ± 35	625 ± 29	652 ± 29		
В	-	497 ± 33	-	-	-		
С	-	-	730 ± 29	-	-		
Н	-	-	-	702 ± 29	-		
S	-	-	-	-	615 ± 29		
ВА	440 ± 33	474 ± 33	630 ± 30	554 ± 30	559 ± 31		
CA	453 ± 30	568 ± 29	677 ± 29	616 ± 29	637 ± 29		
НА	530 ± 33	606 ± 31	588 ± 38	562 ± 44	617 ± 29		
SA	509 ± 29	485 ± 29	637 ± 29	581 ± 29	613 ± 29		

The models used have already been described in Chapter 4.

The GLM procedure of SAS (2010) was used for the analysis of the data set. The data set was formed by recording each least squares mean along with breed composition, maternal breed composition and direct and maternal heterozygozyties as covariates on a weighted (inverse of standard errors) LS regression. Each trait was analyzed separately. Breed solutions for each trait were expressed relative to the Afrikaner breed, similar to a method used, by amongst others, Williams *et al.* (2010) in the analysis of a number of cattle breeds from an extensive literature review of crossbreeding studies.

Table 6.3 Least squares means for feed conversion ratio (kg weight gain/kg feed consumed) for steers in the different sire and dam breed groups

	Sire breed					
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)	
Α	7.9 ± 0.2	7.2 ± 0.2	6.7 ± 0.3	7.0 ± 0.2	6.9 ± 0.2	
В	-	7.6 ± 0.3	-	-	-	
С	-	-	6.1 ± 0.2	-	-	
Н	-	-	-	6.6 ± 0.2	-	
S	-	-	-	-	7.3 ± 0.2	
ВА	8.1 ± 0.2	8.2 ± 0.3	6.4 ± 0.2	6.8 ± 0.2	6.7 ± 0.2	
CA	7.6 ± 0.2	7.1 ± 0.2	6.4 ± 0.2	7.0 ± 0.2	6.6 ± 0.2	
НА	7.4 ± 0.3	7.2 ± 0.2	7.0 ± 0.3	7.4 ± 0.3	7.2 ± 0.2	
SA	7.4 ± 0.2	7.8 ± 0.2	6.9 ± 0.2	7.0 ± 0.2	7.1 ± 0.2	

6.3 RESULTS AND DISCUSSION

The breed additive and heterosis effects for the carcass traits in pure- and crossbred steers that were estimated are shown in Table 6.4(a) and 6.4(b).

Table 6.4(a) Additive effects and standard errors for carcass traits in crossbred steers

Effect	Breed	Live ADG (g)	Carcass ADG (g)	Feed conversion ratio (kg/kg)***
Intercept	Α	809.0 ± 37.9*	497.0 ± 27.4	7.9 ± 0.3
Individual	S	335.4 ± 100.0	223.1 ± 72.8	-1.0 ± 0.8
(direct)	В	-18.9 ± 106.8	62.3 ± 77.1	0.8 ± 0.8
	С	1335.9 ± 202.2**	839.0 ± 147.1**	-4.3 ± 1.5
	Н	122.4 ± 116.9	83.9 ± 84.4	-0.2 ± 0.9
Maternal	S	27.6 ± 113.7	-105.1 ± 82.7	0.4 ± 0.9
	В	58.9 ± 120.5	289.7 ± 90.7	-1.1 ± 0.9
	С	-764.9 ± 209.2**	-606.0 ± 152.2**	2.6 ± 1.6
	Н	269.6 ± 128.7	121.1 ± 93.0	-1.1 ± 1.0

^{*}All standard errors are expressed in measured units and represent a lack of fit to the genetic model, rather than variation amongst animals in the same genotype
**Because of their large values, these additive effects were verified and are correct

^{***}Kilogram live weight gained per one kilogram feed consumed

Table 6.4(b) Heterosis effects on carcass traits for crossbred steers

Effect	Breed	Live ADG (g)	Carcass ADG (g)	Feed conversion ratio (kg/kg)**
Individual	ВА	127.7 ± 79.3	29.3 ± 57.4	-0.8 ± 0.6
(direct)	CA	-419.8 ± 121.9	-297.1 ± 88.6	1.0 ± 0.9
	HA	225.0 ± 82.8	94.8 ± 59.9	-0.9 ± 0.6
	SA	183.7 ± 76.5	51.0 ± 55.5	-0.7 ± 0.6
	ВС	-47.4 ± 107.9	-163.2 ± 78.4	0.0 ± 0.8
	ВН	261.5 ± 83.9	123.2 ± 60.8	-1.6 ± 0.6
	BS	142.6 ± 79.0	-44.0 ± 57.2	-0.7 ± 0.6
	СН	-329.9 ± 111.7	-235.8 ± 81.2	1.2 ± 0.9
	CS	-369.6 ± 106.7	-225.8 ± 77.6	1.0 ± 0.8
	HS	54.0 ± 81.6	23.0 ± 59.3	-0.3 ± 0.6
Maternal	ВА	-115.1 ± 48.9	-229.2 ± 37.5	0.6 ± 0.4
	CA	316.4 ± 90.1	212.1 ± 65.6	-1.1 ± 0.7
	HA	-163.1 ± 53.8	-105.9 ± 38.9	0.7 ± 0.4
	SA	-81.2 ± 45.8	-24.3 ± 33.3	0.1 ± 0.3

^{*}All standard errors are expressed in measured units and represent a lack of fit to the genetic model, rather than variation amongst animals in the same genotype **Kilogram live weight gained per one kilogram feed consumed

6.3.1 Feedlot gain (FG)

From Table 6.4(a) it is evident that that Bos taurus (S, C, and H) breeds had positive individual (direct) additive (breed) effects of +335.4, +1335.9 and +122.4 g respectively for FG over that of the A breed (+809.0 g/day, Table 6.1), but the B breed (-18.9 g/day) had a negative effect. The maternal additive effect of the B was however desirable (+58.9 g/day). C was the only breed with an undesirable maternal additive effect (-764.9 g/day). Since the semen of the exotic bulls used was imported, the large additive effects of the C breed can be explained in that the French had at that stage selected the C breed for rapid growth, size and muscling (Els, 1988). Garrick (1990) suggested that genes that partition nutrients for growth in beef cattle are partly antagonistic with genes that partition for lactation. This study confirmed the tendency for post-weaning live weight gain and carcass growth. All breeds had desirable combined (direct and maternal) additive effects on FG; +363.0, +40.0, +571.0 and +392 g/day for S, B, C, and H respectively.

Table 6.4(b) shows that the individual heterosis contributions of all two-breed genotypes on the FG were desirable, except in heterozygotic genotypes which had 50% C in their composition. The contributions were +127.7, +225.0, +183.7, +261.5, +142.6 and +54.0 g/day respectively for BA, HA, SA, BH, BS and HS respectively, but -419.8, -47.4, -329.9 and -369.6 g/day respectively for CA, BC, CH, and CS respectively. The aforementioned genotypes could thus be used as sire lines on purebred A dams to improve feedlot traits. The maternal heterosis contribution of the CA dam line was desirable; +316.4 g/day, but the BA, HA and SA dams had undesirable effects; -115.1, -163.1 and -81.2 g/day respectively. The combined (individual plus maternal) heterosis effect of the respective dam lines BA, CA, HA and SA were +12.6, -90.8, +61.9 and +102.5 g/day.

6.3.2 Carcass gain (CG)

For CG all breeds complimented the A (497 g/day, Table 6.2); +223.1, +62.3, +839.0 and 83.9 g/day respectively for S, B, C and H breeds (Table 6.4(a)). The maternal contributions of S and C were however undesirable; -105.1 and -606.0 g/day respectively. The B dam outperformed the H dam (+289.7 versus +121.1 g/day respectively). The combined additive effects for the S, B, C and H breeds were +118.0, +352.0, +233.0 and +205.0 g/day respectively.

Out of the ten two-breed genotypes in Table 6.4(b), only five genotypes had desirable individual heterosis effects of +29.3, +94.8, +51.0, +123.2 and +23.0 g/day for BA, HA, SA, BH and HS respectively on CG. The remaining genotypes, CA, BC, BS, CH and CS had negative values of -297.1, -163.2, -44.0, 235.8 and -225.8 g/day respectively. The CA dam line was the only A crossbred dam line with a positive maternal heterosis value (+ 212.1 g/day), while the other crossbred dam lines (BA, HA and SA) showed negative values (-229.2, -105.9 and -24.3 g/day respectively), with that of BA being the highest. The SA genotype was the only one with a desirable combined heterosis effects for CG of +26.7 g/day, the BA, CA, and HA had negative combined heterosis effects of -199.9, -85.0, and -11.1 g/day respectively.

6.3.3 Feed conversion ratio (FCR)

All breeds except the B (+0.8 kg/kg) had desirable negative contributions for FCR (7.9 kg/kg, Table 6.3) in the A breed; -1.0, -4.3 and -0.2 kg/kg for the S, C, and H breeds respectively (Table 6.4(a)). The B and H dam had an equal small desirable maternal effect (-1.1 kg/kg)

on FCR, but the S (+0.4 kg/kg) and C (+2.6 kg/kg) undesirable maternal additive effects on FCR.

The combined additive effects for the S, B, C and H breeds were -0.6, -0.3, -1.7 and -1.3 kg/kg respectively.

Table 6.4(b) shows that six two-breed genotypes had desirable individual heterosis effects on the FCR of their parent breeds. They were BA, HA, SA, BH, BS and HS with -0.8, -0.9, -0.7, -1.6, -0.7 and -0.3 kg/kg respectively. While the BC genotype had no effect, the CA, CH and CS genotypes showed poorer FCR of +1.0, +1.12 and +1.0 kg/kg respectively.

The C crossbred genotype however had a desirable maternal heterosis effect of -1.1 kg/kg, whilst the other two-breed dams, BA, HA and SA had positive values of +0.6, +0.7 and +0.1 kg/kg respectively. The combined heterosis effect for the BA, CA, HA and SA genotypes were -0.2, -0.1, -0.2 and -0.6 kg/kg respectively. However, these differences are small.

6.4 PREDICTION OF PERFORMANCE IN CROSSBRED GENOTYPES

The expected phenotypic means for carcass traits in two- and three-breed genotypes were subsequently calculated and are presented in Tables 6.5 to 6.7.

6.4.1 Feedlot gain (FG)

The expected phenotypic values (Table 6.5) of all genotypes of two- and three-breed crosses of the A dam line showed increased FG compared to the A (809.0 g/day), the only exception being the recombination loss in ACA (708.8 g/day). All two-breed genotypes had higher FG than their backcrosses in either direction, except for CCA with FG of 1376.8 g/day. The latter genotype had the highest FG of all genotypes involved in the study. While the C sire and dam lines had the highest (1158.0 and 1086.1 g/day respectively), the A sire and B dam lines had the lowest average expected FG (878.0 and 1000.3 g/day respectively). It was evident that the A dam line outperformed the BA, HA and SA dam lines and that the A should not constitute more than 50 percent of the genetic make up of steers in order to maximize FG.

Table 6.5 Expected phenotypic values for feedlot gain (g/day) for steers in the different sire and dam groups

	Sire breed					
Dam	Afrikaner	Brahman	Charolais	Hereford	Simmentaler	
breed	(A)	(B)	(C)	(H)	(S)	Average
Α	(809.0)	927.3	1057.2	1095.2	1160.4	1060.0
ВА	840.0	830.6	1153.0	1128.4	1049.5	1000.3
CA	708.8	1107.6	1376.8	1085.7	1151.6	1086.1
НА	1005.4	996.5	1104.4	1066.6	1097.9	1054.2
SA	957.9	951.2	1098.7	1070.5	1125.6	1040.8
Average	878.0	962.6	1158.0	1089.3	1117.0	

() Not included in the average

The purebred comparison in Table 6.1 indicates that the A and B gained much slower than the *Bos taurus* (C, H and S) genotypes.

6.4.2 Carcass gain (CG)

Table 6.6 indicates that the A breeds had lowest CG of all purebred genotypes (497.0 g/day). The results indicate that the C sire line and A dam line had the highest average expected phenotypic values for CG (655.8 and 617.6 g/day respectively).

Table 6.6 Expected phenotypic values for carcass gain (g/day) for steers in different sire and dam groups

	Sire breed					
Dam breed	Afrikaner (A)	Brahman (B)	Charolais (C)	Hereford (H)	Simmentaler (S)	Average
A	(497.0)	557.5	619.5	633.8	659.6	617.6
ВА	557.5	588.7	617.6	579.2	543.2	577.2
CA	361.3	580.1	781.2	587.3	640.0	590.0
НА	573.0	580.0	626.7	615.0	621.2	603.3
SA	537.9	499.7	634.0	680.3	649.5	600.3
Average	507.4	561.2	655.8	619.1	622.7	

() Not included in the average

Backcrossing two-breed genotypes to the A dam line decreased CG in all three-way genotypes, especially in the ACA genotype (361.3 g/day). Backcrossing the two-breed genotypes to their respective sire lines increased CG in the BBA (588 g/day) and CCA (781.2 g/day) genotypes. This suggests that the H and S genotypes used in the study should not constitute more than 50% of the A crossbred genotype. While the C sire and A dam lines had the highest expected CG (655.9 and 617.6 g/day respectively), the A sire and BA dam lines had the lowest average expected CG (507.4 and 577.2 g/day respectively).

6.4.3 Feed conversion ratio (FCR)

Table 6.7 Expected phenotypic values for feed conversion ratio (kg weight gain/kg feed consumed) for steers in different sire and dam groups

Sire breed						
Dam	Afrikaner	Brahman	Charolais	Hereford	Simmentaler	
breed	(A)	(B)	(C)	(H)	(S)	Average
Α	(7.9)	7.5	6.8	6.9	6.6	7.0
ВА	7.5	7.9	6.5	6.8	7.0	7.1
CA	8.1	7.0	6.0	7.1	6.7	7.0
НА	7.2	7.2	7.0	7.1	6.7	7.0
SA	7.6	7.6	6.8	7.3	7.1	7.3
Average	7.6	7.4	6.6	7.0	6.8	

() Not included in the average

The A and B genotypes had the less favourable FCR (7.6 and 7.6 kg/kg respectively; Table 6.3). The expected phenotypic values (Table 6.7) indicate that all sire and dam lines had improved FCR, the only exception being BBA (7.9 kg/kg) and ACA (8.1 kg/kg). Backcrossing two-breed genotypes in both directions had either no effect or had decreased expected FCR in the progeny, except for the CCA genotype which had the most favourable FCR of all genotypes involved in the study (6.0 kg/kg). The A, CA and HA dam line had similar average expected FCR of 7.0 kg/kg. The C sire line was the most efficient with an average FCR of 6.6 kg/kg.

6.5 THE CORRELATION BETWEEN THE ESTIMATED PHENOTYPIC VALUES AND THE LEAST SQUARES MEANS

In order to validate the predicted breed additive and heterosis effects, Pearson's correlations (r) were calculated between the estimated phenotypic values and least squares means for all the weight traits and are presented in Table 6.8. A shortcoming was that biological replicates were averaged before correlations were calculated due to a lack of the raw data of the experiment.

Table 6.8 Pearson's correlation between expected phenotypic values and least squares means for growth traits

Carcass traits	Correlation		
Feedlot average daily gain (FG)	0.88		
Carcass average daily gain (CG)	0.76		
Feed conversion ratio (FCR)	0.84		

The Pearson's correlations between the estimated phenotypic value and the least squares means for the feedlot and carcass traits vary between 0.76 and 0.88 (Table 6.8). Possible explanations for the < 1 correlations have already been discussed in Chapter 4.

6.6 NON-ADDITIVE EFFECTS

The results of the average percentage heterosis effects were calculated from Table 6.4(b) and are indicated in Table 6.9.

The individual and maternal heterosis effects on carcass traits (Table 6.9) in the different cattle types contradicted each another. This study found positive heterosis effect in the CG trait in the Bos indicus x Sanga and British x Sanga with improved FCR. It is evident that Bos indicus x Bos taurus also had improved FCR, but CG was negatively affected.

Only the Continental crossbred dams had desirable maternal heterosis contributions for the feedlot and carcass traits that were measured. It is difficult to explain the reasons for the maternal heterosis. A possible explanation could be on the mitochondrial level. About 90% of cellular energy is produced by the mitochondria, which are numerous and contribute as much as 10% of the body weight of an adult male (Ojano-Dirain *et al.*, 2007). However,

these crosses all have Sanga mitochondria. A possibility may be that there are specific autosomal genes in the continental breeds that modify the functions of the mitochondria.

Table 6.9 The average percentage heterosis effects for carcass traits in two- and three-breed crosses

	Feedlot gain (g/day)	Carcass gain (g/day)	Feed conversion ratio (kg/kg)****
Individual heterosis			_
Bos indicus** x Sanga*	+15.8%	+5.9%	-10.1%
Continental** x Sanga*	-14.6%	-24.8%	+1.9%
British** x Sanga*	+27.8%	+19.1%	-11.4%
Bos indicus*** x Bos taurus***	+14.7%	-5.6%	-9.7%
Bos taurus*** x Bos taurus***	-26.6%	-29.4%	+8.0%
Maternal heterosis			
Bos indicus** x Sanga*	-14.2%	-46.1%	+7.6%
Continental** x Sanga*	+14.5%	+18.9%	-6.7%
British** x Sanga*	-20.2%	-21.3%	+8.9%

^{*} Sanga was represented by the Afrikaner breed

6.7 CONCLUSIONS

Although most of the average heterosis effects in the current study suggest that feedlot traits do not benefit from crossbreeding, selected genotypes offer opportunity to increase production efficiency.

As purebred the A breed compared less favourably in feedlot traits with *Bos taurus* breeds. However, it was evident that the A dam in two-breed crossbreeding could outperform the purebred S and *Bos taurus* crossbred dam lines in most of the these traits.

Crossbreeding with the B genotype also enhanced feedlot traits in two-way crosses. Three-way crossbreeding systems suggested that the A should not constitute more than 50 percent of the genetic make up of steers in order to maximize feedlot traits. Thus in order for A cattle to be competitive in feedlots, the former should be utilized in two-way crossbreeding systems with a terminal sire such as the C. Alternatively, the BH crossbred sire offers highest

^{**} Continental breeds were represented by the Simmentaler and Charolais breeds, British was represented by the Hereford breed and *Bos indicus* was represented by the Brahman breed

^{***} Bos indicus x Bos taurus and Bos taurus x Bos taurus values were derived, because these progenies were not produced (Afrikaner was not included as a Bos taurus in this calculation)

^{****} A negative value indicates better feed conversion

desirable paternal heterosis effects for all three feedlot traits when mated to purebred A cows. Other crossbred sires that had positive contributions towards feedlot traits in the A breed were BA, HA, SA, BS and HS.

Chapter 7

GENERAL CONCLUSIONS AND RECOMMENDATIONS

The efficiency of beef production can be increased when economic important traits are maximized through heterosis. Crossbreeding systems are generally employed for this purpose and/or to improve adaptation. The development and/or improvement of beef breeding strategies are therefore the main aim of crossbreeding research that analyse heterosis effects. The results can serve to increase the accuracy of predicting phenotypic values for traits that increase the profitability of beef production.

The primary producer benefits the most from hybrid vigour, mainly because the reproductive traits responded the most to crossbreeding and carcass traits the least. Therefore, it is anticipated that crossbreeding systems that would maximize fitness traits would be most profitable.

Although the crossbreeding programs raised the traits for beef production levels, the increased cow weights of crossbred dams can have increased nutritional requirements. However, all crossbred genotypes, except for the BA genotype, increased the calf/cow weight ratio. In backcrossing systems BA and CA genotypes mated to the A dam line increased cow/calf ratios from 0.446 to 0.464 and 0.448 to 0.467 respectively. These results suggest that the A breed should constitute 75% of the genetic make up of B and C crossbred genotypes. Backcrossing HA and SA genotypes to their respective sire lines changed the cow/calf ratios from 0.459 to 0.462 and 0.452 to 0.476 respectively. The A breed should therefore only constitute 25% of the genetic make up of H and S crossbred genotypes. The three-breed HSA, HBA and BSA genotypes had the highest calf/cow weight ratios of 0.509, 0.506 and 0.495 respectively. Since the B breed had a true ability to increase the expected BW in the A dam, it might be suggested that a specific or rotational crossbreeding which involves the S and A breeds can be complimented with either the H or B (on mature cows only) as terminal sire breeds for the production of weaner calves. Backcrossing the SA genotype to either one of the parent breeds has also increased cow calf/ratios.

Alternatively, since HS and BS genotypes had maximum direct heterosis effect for WW, it is also suggested that these crossbred sires could be mated to purebred A dams in a specific crossbreeding system in which the problem with dystocia is not anticipated. It should,

however, be noted that the data did not take cognianzes of the genetic trends in the growth traits and the effects on heterosis parameters in any of the breeds since the conduction of the crossbreeding experiments.

Maximum expected calf/cow weight ratios in a weaner calf production system were obtained with HA and CA two-breed genotypes and HSA, BHA and BSA three-breed genotypes which had ratios of 0.448 and 0.441 and 0.509, 0,506 and 0.495 respectively. Maximum expected WR was also obtained with HA and CA two-breed genotypes and ACA, AHA and BHA three-breed genotypes with 83.1 and 80.3 and 86.9, 86.8 and 83.0% respectively. The CA genotype had a high WR (80.3%), but a possibility of dystocia problems was suggested. The management of the cow herd will thus dictate if such a specific cross could be feasible. For the A to be competitive in the feedlot, the breed should be used in two-way crossing systems with a terminal sire. The C terminal bull maximized feedlot traits in the CCA genotype with expected phenotypic FG and CG of 1376 and 781 g/day respectively. The CCA genotype also had the most favourable FCR of 6.0 kg/kg.

One form of measuring cow efficiency is to measure the calf/cow weight ratio. Results in this study showed that weaning weight in calves can be increased in two ways: Firstly, crossbred SA dams can be bred to a terminal H or B sire or BA dams can be bred to a terminal H bull. These genotypes had the largest calf/cow weight ratios, irrespective of the increase in cow weights. Since B bulls proved to have large heterosis contributions to birth weight, the use of B sires will not be feasible under all management programs. Secondly, HS, HB and SB two-breed bulls can be bred to purebred A, since these bulls had the largest paternal heterosis effects on WW.

Fertility traits displayed the largest heterosis effects. Weaning rate (the number of calves weaned as ratio to the number of dams mated) is a cumulative trait that measures fertility in the cow herd and survival of the calves. Crossbred female genotypes, combined with specific terminal sire genotypes can increase fertility in relation to the pure A cow. Theoretically, WR can be maximized when HA dams are mated either to an A or a B sire. CA dams mated to an A sire will also have a desirable effect on WR.

Rotational crossbreeding systems are not recommended, since backcrossing these dam lines to their respective sire lines decreased the WR. Alternatively, HA, CH or CA crossbred sires could be used on purebred A dams in a specific crossbreeding system. These genotypes will have the largest paternal heterosis effect on WR of all ten two-breed genotypes. In a specific two-breed system the HA dams maximized WR.

In all abovementioned genotypes, purebred bulls were used. However, the study also predicted direct heterosis effects for crosses that were not made. This brought the value of hybrid bulls to the forth. Thus, the same three-breed genotypes could also be bred when F1 crossbred sires were mated to purebred A dams. HS, HB and BS sires could theoretically increase calf/cow weight ratios in matings with purebred A dams. Similarly CA, HA and CH sires could increase WR in the A breed and the BA, HA, SA, BH, BS and HS had desirable heterosis contributions to feedlot traits.

The A breed may be classified as a dam line, as it is small framed with good maternal abilities and has low birth weights and mortality at birth. The meat quality of the A is also very good (Strydom, 2008). Results obtained confirmed the breed's potential as a dam line and almost all the growth, fitness, feedlot and carcass traits were improved through crossbreeding.

The genotype with 75% C and 25% A maximized all feedlot traits. However, this can only be accomplished in a specific combination through a terminal sire crossbreeding system. Paternal heterosis contributions to feedlot traits for the BA, HA, SA, BH, BS and HS sire lines were all small, but favourable.

This analyses of the experimental results of Els (1988) and De Bruyn (1991) to characterize the heterosis effects of beef breeds could have changed the face of the South African beef industry, had the data been properly analysed twenty years ago when most of the field work was completed.

Most South African beef cattle producers believe that profitability can only be increased through upgrading and selection and are thus mainly afflicted with stud breeding and in some instances performance values are ignored.

Crossbreeding in commercial beef production is happening, but is not well planned and is often hap hazard. Furthermore, producers are not accustomed to the use of crossbred sires in the planning of their breeding objectives. The seed stock industry will also respond very negatively to such systems. Concerning the use of crossbred sires, it is recommended that producers must be cautioned about the fact that these sires must have high additive genetic merit for important traits, as well as the potential to demonstrate heterosis, in order to increase production efficiency. It is therefore of the utmost importance that both parents of the crossbred sire must have the desired genetic merit for the traits concerned.

The breeding of high quality crossbred bulls may not find acceptance among farmers. Proper systems to evaluate and regulate the use of such bulls will have to be put in place. It is therefore recommended that the procedure for the use of such bulls in the USA should be investigated. In Brazil there is also a beef programme where a special identification and production certificate is issued to commercial bulls giving them the same status as stud bulls. It is certainly worthwhile to also look at this programme. South Africa has a number of genetically improved composite breeds. These sires have EBV for traits and could also be used in crossbreeding systems on purebred or crossbreed Afrikaner dams.

It is recommended that future research should focus on the following:

- The heterosis values (South African conditions) obtained from this study should be used to simulate breeding objectives for crossbreeding systems in South Africa. Previous simulations were based on values from the USA.
- These crossbreeding parameters should be used to develop new models to predict performance of specific crosses to maximize hybrid vigor in effective crossbreeding systems.
- 3. The existing breeding values in South Africa should be used to model the expected impact on total herd productivity. For crossbreeding, information on cow breed composition and heterosis need to be incorporated into the model to predict phenotypic performance, which can be used to derive monetary values for production efficiency
- 4. The information from this study should be used to initiate multi-breed genetic evaluations for South Africa and/or to develop breed conversion factors, which will make it possible that different breeds/genotypes can be compared directly. The motivation for the development of multi-breed genetic evaluations is according to Pollak (2006):
 - the need to better evaluate established composite breeds
 - the need to accommodate in evaluations the growing number of F1 bulls being developed internationally
 - to provide the platform for a national evaluation where different breeds are evaluated together and for whom EBV's are directly comparable

- A simulation study is needed to quantify the relative biological and economic differences in which straight breeding and different crossbreeding options are compared.
- 6. Economically important traits must be prioritized and biological and economic models that can generate index values from predicted phenotypes must be developed in order to optimize production efficiency.
- 7. Although the results of the study allow for customizing the use of heterosis in beef production units in sweet veld areas of the Northern Cape Province, changes in the genetic trends of the different breeds were not considered for the different traits. It is recommended that these trends be used to calculate the genetic change (positive or negative) that may influence heterosis effects.

If these recommendations can be implemented in South Africa it will create an equitable and enabling environment that allows all cattle producers to improve their livelihoods in an industry that is market responsive.

The results of this study stimulated the interest for future crossbreeding and evaluation. The aim of this will be to evaluate the indigenous Nguni breed and the locally developed Bonsmara breed in crossbreeding systems with British and European breeds.

CHARACTERIZATION OF BREED ADDITIVE AND HETEROSIS EFFECTS IN BEEF CATTLE USING EXPERIMENTAL RESULTS

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ABSTRACT

The objective of this study was to infer direct and maternal additive effects and direct and maternal heterosis effects for growth, fitness and carcass traits in beef cattle using least squares means estimated from crossbreeding studies by Els (1988) and De Bruyn (1991). The dataset was formed by recording each least squares mean along with the breed composition, maternal breed composition and direct and maternal heterozygosity. Each trait was analyzed using a single trait fixed effect model which included source of data as a fixed effect and breed composition and heterozygosity as covariates. Breed solutions were relative to the Afrikaner breed. Heterosis results were also obtained for crosses not made. Among breed groups, crossbred calves showed higher average values for almost all traits than purebred calves.

The average direct heterosis contributions to weight traits in ten two-breed genotypes, which involved the Afrikaner (A) as dam line and the Simmentaler (S), Brahman (B), Charolais (C) and Herefords (H) as sire lines were 3.5, 7.9, 8.2 and 4.3% for birth weight (BW), weaning weight (WW), 19-month heifer weight (HW) and cow weight at partus (CW) respectively. Similarly, the average maternal heterosis effects for the weight traits in the four A crossbred dam genotypes (BA, CA, HA and SA) were 1.5, 8.8, 4.9 and 2.9% for the growth traits respectively. Due to additive and non-additive effects of C and B purebreds on BW these sires should only be bred to mature cows. For a weaner calf production system, the C genotype had the highest direct breed effect of +64.1 kg or 34.8% for WW. The combined additive effect of the C dam line was however, exceeded by the S dam line (+38.4 kg or +20.9% versus +50.0 kg or +27.2%). The total combined heterosis effect of the CA dam line was +32.5 kg *versus* the +19.2 kg effect of the SA dam line. The average expected phenotypic values for WW for the SA dam line was thus larger than the CA dam line (233.3 *versus* 230.7 kg). The maternal heterosis effect of the HA dam was the second largest (+22.1 kg) of the four two-breed combinations of A.

The B genotype used in the study did not have a true superior ability to increase the expected WW in the A breed. The direct and maternal heterosis effects of the breed were - 0.5 kg or -0.3% and +22.1 kg or 12.0% respectively. The H breed had the lowest direct breed effects of +24.7 kg or +13.4% on WW out of the four purebred sire lines that were bred to the A dam line and a small negative direct heterosis effect (-0.5 kg or -0.3%). Furthermore, the maternal additive effect was negative (-29.6 kg or -16.1%). The maternal heterosis effect however, was positive (+22.1 kg or +12.0%).

The A sire line had the lowest expected phenotypic values for HW and CW (323.9 and 434.3 kg respectively), indicating that these heifers would probably reach puberty earlier and that these cows would be smaller compared to genotypes from S, B, C and H genotypes. On average two-breed genotypes had 48.9 and 40.6 kg expected increase in HW and CW respectively, and an additional 21.9 kg and 20.4 kg for the two traits respectively in three-breed genotypes (backcrossing excluded). The H sire line did not have a true ability to increase expected CW in the A breed. The C genotypes had the lowest average individual heterosis effect of -17.6 kg (-4.0%) on CW of all four sire lines which were involved in the ten different two-breed combinations of the study. However, the CA dam line was responsible for the highest maternal heterosis effect of +54.8 kg or +12.6% out of the four crossbred A dam lines.

By utilizing genotypic differences the opportunity for high productivity and profitability can be maximized, especially through cumulative traits such as the calf/cow weight ratio. All crossbred genotypes, except the BA genotype, increased the calf/cow weight ratio. Results indicated that the A breed should constitute 75% of the genetic make up of B and C crossbred genotypes and 25% of H and S crossbred genotypes to maximize calf/cow weight ratios. The HSA, HBA and BSA, genotypes had the largest calf/cow weight ratios of 0.509, 0.506 and 0.495 respectively, mainly due to the large direct heterosis effects of +22.7 (+12.3%), +28.0 (+15.2%) and +36.7 kg (+19.9%) of the HS, HB and BS genotypes for WW respectively. This gives opportunity for direct paternal heterosis to be used in crossbreeding systems with purebred A dams. Alternatively, since the B breed had a true ability to increase the expected BW in the A dam, it is suggested that a specific or rotational crossbreeding system which involves S and A dams that are mated with either H or B (only on mature dams) sires for the production of weaner calves under sweet veld conditions, be used.

The data were also used to estimate the additive and non-additive effects for fitness traits in the two- and three-breed crosses. The average direct heterosis contributions were +14.9, +109.1, -162.7, +21.0 and 15.4% respectively for CR, MB, MP, WP and WR for ten two-

breed genotypes. Similarly, the average maternal heterosis effects in four A crossbred dam genotypes were 0.0, -87.5, +97.7, -1.9 and -7.4% for the fitness traits respectively. The HA genotype had the highest expected F of 83.1% in two-breed genotypes. The direct heterosis contributions in the HA genotype were +21.7, -2.3, -5.8, +28.3 and +30.1% percentage units respectively and the maternal contributions were -8.2, -2.4, +1.6, -6.4 and -11.6 for the traits respectively. The expected phenotypic values for improved traits in the HA and AHA genotypes were 94.9 versus 96.4% for CR, 92.2 versus 96.3% for WP and 83.1 versus 86.8% for WR (MB and MW remained unchanged). Crossbreeding the A dam line with the B sire line resulted in improved expected WR: 66.7 versus 80.2% in BA. Backcrossing the BA genotype decreased WR. This could mainly be explained by the increased expected MW; 3.3% in the A versus 6.0 and 15.6% in the BA and ABA genotypes respectively and the lower expected WR of 72.8 and 74.5% in the ABA and BBA genotypes respectively. While the SA genotype had an improved expected WR of 78.4% compared to the A genotype (66.7%), the WR in the ASA progeny was the lowest of all genotypes (60.4%). The low expected WR of the SA genotype could be explained by the increased expected MB of 5.3 versus 2.2% and MW 5.7 versus 3.3% of the A breed. The poor performance of the SSA genotype could be ascribed to an increase in MB and MW which was 7.3 and 4.3% respectively. The ACA, AHA and BHA genotypes had the highest expected WR of 86.9, 86.8 and 83.0% respectively. A specific crossbreeding combined with a terminal sire system is suggested to increase fertility in the A breed. Rotational systems will not have the same advantage since backcrossing the CA or HA dams to their respective sire lines would decrease the WR to 64.2 and 73.1% respectively. Alternatively, CA, HA or CH crossbred sires could be used on purebred A dams in a specific crossbreeding system. These genotypes had the largest direct heterosis effect on WR of all ten two-breed genotypes (36.5, 30.1 and 30.8% percentage units respectively). In a specific two-breed system the HA genotype would maximize WR.

Although the average direct heterosis effects were unfavourable (-2.1 and -13.0 g/day respectively) for feedlot gain (FG) and carcass gain CG), feed conversion ratio (FCR) was -2.3% (a desirable effect). The average maternal heterosis effects for the feedlot traits were undesirable in the four A crossbred dam genotypes (-1.3, -7.4, and +0.9% respectively) for all the traits. Although these average heterosis effects suggest that feedlot traits do not benefit from crossbreeding, selected genotypes offer opportunity to increase feedlot production efficiency.

As purebred the A compared less favourably in feedlot traits with *Bos taurus* breeds. However, it was evident that the A dam in two-breed crossbreeding could outperform the

purebred S and *Bos taurus* crossbred dam lines in most of the these traits. The average direct heterosis contributions to feedlot traits in ten two-breed genotypes for the S, B, C and H as sire lines were -2.1, -13.0 (undesirable) and -2.3% (desirable) for feedlot gain (FG), carcass gain (CG) and feed conversion rate (FCR) respectively. Similarly, the average maternal heterosis effects for the feedlot traits in the four A crossbred dam genotypes were -1.3, -7.4, and +0.9% (undesirable) for FG, CG and FCR respectively. However, the A dam could be utilized in two-way crossbreeding systems with a terminal sire such as the C. The CCA genotype had expected average FG, CG and FCR of 1376.8 g/day, 781.2 g/day and 6.0 kg/kg respectively. Alternatively, the paternal heterosis contributions from BA, HA, SA, BH, BS and HS sire lines were also favourable. The aforementioned genotypes could thus be used as sire lines on purebred A dams to improve feedlot traits.

It should however be noted that the data did not take cogniance of the genetic trends in the traits and the effects on heterosis parameters in any of the breeds since the conduction of the crossbreeding experiments. Heterosis units are therefore not directly applicable.

Keywords: Afrikaner cattle, calf/cow weight ratio, carcass traits, crossbreeding parameters, growth traits, weaning rate, feed conversion ratio, fitness traits, paternal heterosis, specific two- and three-breed crossing systems, terminal sire

KARAKTERISERING VAN RAS ADDITIEWE EN HETEROSE EFFEKTE IN VLEISBEESTE DEUR GEBRUIK TE MAAK VAN EKSPERIMENTELE RESULTATE

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OPSOMMING

Die doel van die studie was om direkte- en maternaal-additiewe en direkte- en maternaal-heterose effekte vir groei-, fiksheid- en karkaseienskappe van vleisbeeste te bepaal deur gebruik te maak van die kleinste kwadraat gemiddeldes wat bereken is deur Els (1988) en De Bruyn (1991). Die datastel was saamgestel deur elke kleinste kwadraat gemiddelde met sy ooreenkomsige rassamestelling, maternale-rassamestelling en direkte- en maternaleheterosigositeit aan te teken. Elke eienskap was ontleed deur gebuik te maak van 'n enkeleienskap vaste-effek model met bron van data as 'n vaste-effek en rassamestelling en heterosigositeit as kovariante. Rasoplossings was relatief tot die Afrikanerras. Heterose-effekte was ook verkry vir kruisings wat nie gedoen was nie. Tussen rassegroepe het kruisgeteelde kalwers gemiddeld hoër waardes getoon as suiwergeteelde kalwers vir byna alle eienskappe.

Die gemiddelde direkte heterose bydraes tot speengewig in tien twee-ras genotipes wat die Afrikaner (A) as moederlyn en die Simmentaler (S), Brahman (B), Charolais (C) en Hereford (H) as vaarlyne, was 3.5, 7.9, 8.2 en 4.3% vir geboortegewig (BW), speengewig (WW), 19-maande versgewig (HW) en koeigewig by partus (CW) respektiewelik. Dienooreenkomstig was die gemiddelde maternale heterose-effekte in vier A kruisgeteeltde genotipes (BA, CA, HA en SA) 1.5, 8.8, 4.9 en 2.9% vir groei-eienskappe respektiewelik. As gevolg van die additiewe en nie-additiewe effekte van die C en B suiwerrasse op BW moet hierdie rasse net met volwasse koeie gepaar word. Vir 'n speenkalfproduksiestelsel het die C genotiepe die hoogste direkte raseffek van +64.1 kg of 34.8% vir WW gehad. Die gekombineerde additiewe effek van die C moederlyn was egter deur die S moederlyn oortref (+38.4 kg of 20.9% *versus* +50.0 of +27.2%).

Die totale gekombineerde heterose effek van die CA moederlyn was +32 kg versus die +19.2 kg effek van die SA moederlyn. Die gemiddelde verwagte fenotipiese waarde vir WW in die SA moederlyn was dus groter as vir die CA moederlyn (233.3 versus 230.7 kg). Die B genotipe in die studie het nie 'n ware meerderwaardige vermoë gehad om die verwagte WW in die A ras te verhoog nie. Die H genotype het 'n positiewe raseffek (+2.4 kg of 13.4%), maar 'n groot negatiewe (-29.6 kg of 16.1%) maternale additiewe effek op WW. Die direkte maternale heterose effek van die ras was -0.5 kg of -0.3% en +22.1 kg of 12.0% respektiewelik. Die A vaarlyn het die laagste verwagte fenotipiese waarde vir HW en CW (323.9 en 434.3 kg, respektiewelik) gehad, wat daarop kon dui dat hierdie verse waarskynlik vroëer puberteit kan bereik en dat die koeie kleiner sou wees as die S, B, C en H genotipes. Deur genotipiese verskille te gebruik kan die geleentheid vir hoë produktiwiteit en wins gemaksimaliseer word, veral met 'n kumulatiewe eienskap soos kalf/koei-gewig verhouding. Alle kruisgeteelde genotipes, behalwe die BA genotipe, het die kalf/koei-gewig verhouding verhoog. Resultate het getoon dat die A ras 75% van die genetiese samestelling van die B en C kruisgeteelde genotipes en 25% van die H en S kruisgeteelde genotiepes moet lewer om kalf/koei-gewig verhoudings te maksimaliseer. Die HSA, HBA en BSA genotipes het die hoogste kalf/koei- gewig vehoudings van 0.509, 0.506 en 0.495, respektiewelik gehad, hoofsaaklik vanweë die direkte heterose effekte van +22,7 (12.3%), +28.0 (+15.2%) en 36.7 kg (19.9%) van die HS, HB en BS genotiepes vir WW respektiewelik. Dit gee die geleentheid vir direkte paternale heterose om in kruisteeltstelsels met suiwer A koeie gebruik te word. Alternatiewelik, omdat die B ras wat 'n ware meerderwaardige vermoë getoon het om BW in die A moederlyn te verhoog, word voorgestel dat 'n spesifieke of roterende kruisteeltstelsel met S en A koeie gebruik word met H of B (laasgenoemde slegs op volwasse koeie) vaars vir die produksie van speenkalwers in 'n soetveld omgewing.

Die data was ook gebruik om die additiewe en nie-additiewe effekte vir fiksheidseienskappe in twee-en drie-ras kruisings te bepaal. Die gemiddelde direkte heterose bydraes was +14.9, +109.1, -162.7, +21.0 en 15.4% respektiewelik vir besettingstempo (CR), geboorteprobleme (MB), voorspeense mortaliteit (MW), speenpersentasie (WP) en speentempo (WR) vir tien twee-ras genotipes. Dienooreenkomstig was die gemiddelde maternale heterose effekte in vier A kruisgeteelde genotipes 0.0, -87.5, +97.7, -1.9 en -7.4% vir die fiksheidseienskappe respektiewelik.

Die HA genotipe het die hoogste verwagte WR van 83.1% in twee-ras genotipes gehad. Die ACA, AHA en BHA genotipes het die hoogste verwagte WR van 86.9, 86.8 en 83.0% respektiewelik gehad. 'n Spesifieke kruisteelt-gekombineerde terminale-vaar stelsel word voorgestel om die vrugbaarheid in die A ras te verhoog. Roterende stelsels sal nie dieselfde voordeel inhou nie omdat terugkruising van die CA of HA moeders na hulle respektiewelike vaarlyne WR sal verlaag na 64.2 en 73.1%. Alternatiewelik kan CA, HA of CH kruisgeteeltde vaars op suiwergeteelde A moeders in a spesifieke kruisteeltstelsel gebruik word. Hierdie genotipes het die grootste direkte heterose effek op WR uit al die tien twee-ras genotiepes (36.5, 30.1 en 30.8% eenhede, respektiewelik) gehad. In 'n spesifieke twee-rasstelsel sal die HA genotipe WR maksimaal verhoog.

Alhoewel die gemiddelde direkte heterose effeke ongunstig (-2.1, en -13.0 g/dag, respektiewelik) vir voerkraaltoename (FG) en karkastoename (CG) was, het voeromsetting (FCR) 'n -2.3% (gunstige) effek getoon. Die gemiddelde maternale heterose effekte vir voerkraaleienskappe in die vier A kruisgeteelde moedergenotipes was -1.3, -7.4, en +0.9% (ongunstig) vir al die eienskappe respektiewelik. Alhoewel hierdie gemiddelde heteroseeffekte sugireer dat voerkraaleienskappe nie deur kruisteling bevoordeel word nie, kan geselekteerde genotipes effektiwiteit in voerkraalproduksie verbeter.

As 'n suiwergeteelde ras het A ongunstig vergelyk met *Bos taurus* rasse in voerkraaleienskappe. Dit het egter geblyk dat die A-moederlyn in twee-ras kruise beter presteer het as die suiwer S en *Bos taurus* kruisgeteelde moederlyne in meeste van die eienskappe. Eersgenoemde moet in twee-ras kruisteeltstelsels met 'n terminale vaar soos die C gebruik word. Die CCA genotipe het verwagte gemiddelde FG, CG en FCR van 1376.8 g/dag, 781.2 g/dag and 6.0 kg/kg, respektiewelik gehad. Alternatiewelik was die paternaleheterose bydraes van BA, HA, SA, BH, BS en HS vaarlyne ook gunstig. Laasgenoemde genotipes kan dus as vaarlyne op suiwergeteelde A-moeders gebruik word om voerkraaleienskappe te verbeter.

References

- Acocks, J.P.H.,1975. Veldtypes of South Africa. Memoirs of the Botanical Survey of South Africa no. 40. Botanical Research Institute, Pretoria. Government Printer.
- Alenda., Martin, T.G., Lasey, J.F. & Ellersieck, M.R.,1980. Estimation of genetic and maternal effects in crossbred cattle of Angus, Charolais and Hereford parentage. I.
 Birth and weaing weights. J. Anim. Sci. 50: 226 234.
- Anderson, P., 1990. Crossbreeding systems for beef cattle. Available at: http://www.ansci.umn.edu/beef/beefupdates.htm
- Anderson, H. & Plum, M., 1965. Gestation period and birth weight in cattle and buffalo.

 J. Dairy Sci. 48: 1224 1235.
- Anitei, S., 2006. The effects of global warming in Africa. Available at: http://news.softpedis.com
- Appel, A., 2006. Global warming may dry up Africa's rivers, study suggests. Available at: http://news.nationalgeographic.com/news/2006/03/03033_060303_africa.html
- Arthur, P.F., Hearnshaw, H. & Stephenson, P.D., 1999. Direct and maternal additive and heterosis effects from crossing Bos indicus and Bos taurus cattle: cow and calf production in two environments. Livest. Prod. Sci. 57: 231 241.
- Baker, J.F., Bryson, W.L. & Knutson, R., 1987. Feed intake and growth during finishing of Angus-, Charolais- and Piedmontese-sired calves when slaughtered at similar measurements of subcutaneous fat. J. Anim. Sci. 65: 10 12.
- Barkhouse, K.L., Van Vleck, L.D., Buchanan, D.S. & Marshall, D.M., 1998. Comparison of sire breed solutions for growth traits adjusted by mean expected progeny differences to a 1993 base. J. Anim. Sci.76: 2287 2293.
- Barwick, S. A. & Yeats, A. P., 1998. Using BREEDOBJECT in industry to help breed more profitable cattle. Anim. Breed. Abstr. 66: 388 -389.
- Bennett, G.L., 1987a. Periodic rotational crosses. I. Optimizing breed and heterosis use. J. Anim. Sci. 65: 1471.

- Bennett, G.L., 1987b. Periodic rotational crosses. II. Optimizing breed and heterosis use.

 J. Anim. Sci. 65: 1477 1486
- Bonsma, J.C., 1980. Livestock production: a global approach. Tafelberg Publishers, Cape Town.
- Bonsma, J.C., 1983. Man must measure: livestock production, Agri Books, Cody, WY.
- Bradley, D.G. & Cunningham, E.P., 1999. Genetic aspects in domestication. In: Fries, R. & Ruvinsky, A. (Ed.). The Genetics of Cattle, 15 31. CABI Publishing.
- Burrow, H.M., 2006. Utilization of diverse breed resources for tropical beef production. 8th World Congress on Genetics Applied to Livestock production, Belo Horizonte, MG, Brasil.
- Calegare, L., Alencar, M.M., Packer, I.U., & Lanna, D.P.D., 2007. Energy requirements and cow/calf efficiency of Nellore and Continental and British *Bos taurus* X Nellore crosses. J. Anim. Sci. 85: 2413 2422.
- Cardoso, F.F. & Templeton, (2004). The value of hierarchical Bayes models on genetic evaluation of multiple-breed beef cattle populations. J. Anim. Sci. 83: 62 72.
- Cartwright, T.C., 1973. Comparison of F1 cows with purebred and other crosses. Crossbreeding Beef Cattle, Series 2: 49. Univ. of Fla. Press. Gainesville, Fla. Ed. by M. Koger, T.J., Cunha & A.C. Warnick.
- Casas, E., Thallman, R.M., Kuehn, L.A. & Cundiff, L.V., 2010. Post-weaning growth and carcass traits in crossbred cattle from Hereford, Angus, Brangus, Beefmaster, Bonsmara, and Romosinuano maternal grandsires. J. Anim. Sci. 88: 102 108.
- Craig, R., 2011. Crossbreeding and rotational systems for beef production. Available at: http://informedfarmers.com
- Crook, B.J., Neser, F.W.C. & Bradfield, M.J., 2010. Genetic parameters for cow weight at calving and at calf weaning in South African Simmental cattle. Available at: http://www.scielo.org.za/scielo.php?script=sci
- Cundiff, L.V., 1970. Experimental results on crossbreeding cattle for beef production.

 J. Anim. Sci. 30: 694 705.

- Cundiff, L.V., Gregory. K.E., Schwulst, F.J. & Koch, R.M., 1974. Effects of heterosis on maternal performance and milk production in Hereford, Angus and Shorthorn cattle. J. Anim. Sci. 38: 728 – 745.
- Cundiff, L.V., Koch, R.M., Gregory. K.E. & Smith, G.M., 1981. Charaterization of biological types of cattle-Cycle II. IV. Post weaning growth and feed efficiency of steers. J. Anim. Sci. 53: 332 346.
- Cundiff, L,V., Greory, K.E., & Kock, R.M., 1982. Selection for increased survival from birth to weaning. Proc. 2nd Wrld. Congr. on Genet. Apl. Livest. Prod. 5: 310 337.
- Cundiff, L.V., Gregory, K.E., Koch, R.M. & Dickerson, G.E., 1986. Genetic diversity among cattle breeds in its use to increase beef production efficiency in a temperate environment. Proc. 3rd World Cong. Genet. Appl. Livest. Prod. IX, 271.
- Dadi, H., Jordaan, G.F., Schoeman, S.J. & Van der Westhuizen, J., 2002. The effect of Charolais and Hereford sires and straightbred and crossbred dams on pre-weaning growth of calves. S. Afr. J. Anim. Sci. 32 (1): 38 42.
- Daley, D., 2006. Crossbreeding still untapped. Available at: http://beefmagazine.com/mag/beef_crossbreeding_untapped
- De Bruyn, J.F., 1991. Production and product characteristics of different cattle genotypes under feedlot conditions. PhD. Thesis, University of Pretoria.
- DeRouen, T.M., Reynolds, W.L. & Meyerhoeffer, D.C., 1967. Mortality of beef calves in the Gulf Coast area. J. Anim. Sci. 26: 202 (Abstr.).
- Dickerson, G.E., 1969. Experimental approaches in utilizing breed resources. Anim. Breed. Abstr. 37: 191 202.
- Dickerson, G.E., 1973. Inbreeding and heterosis in animals. In: Proc. of Anim. Breed & Genet. Symposium in honor of Dr. J.L. Lush, Chapaign. Illinois. Amer. Soc. Anim. Sci. 54 77.
- Els, D.L., 1988. Kruisteling vir vleisproduksie. PhD Thesis, University of the Free State.
- Franke, D.E., 1994. Genetic effects of beef cattle preweaning traits. Proc. 5th World Cong. Gen. Appl. Livestock Prod. 17, 296. (Guelph, Canada).

- Franke. D.E., Habet, O., Tawah, L.C. Williams, A.R. & DeRouen, S.M., 2001. Direct and maternal genetic effects on birth and weaning traits in mutibreed cattle data and predicted performance of breed crosses. J. Anim. Sci. 79: 1713 1722.
- Frisch, J. E. & O'Neill, C. J., 1998. Comparatative evaluation of beef cattle breeds of African, European and Indian origins. 2. Resistance to cattle ticks and gastrointestinal nematodes. Anim. Sci. 67: 27 38.
- Garrick. D.J., 1990. Maternal effects on growth in beef cattle. In: Proc. 8th Conf. Aust. Ass. of Anim. Breed. and Genet., Hamilton and Palmerston North, New Zealand: 397 400.
- Garrrick, D.J., 2006. Genetic improvement of beef cattle assessing the ramifications of genetic change. 8th World Congress on Genetics Applied to Livestock production, Belo Horizonte, MG, Brasil.
- Graham, J., Hygate, L., Cummins, L., Ponzoni, R., Goddard, M., Dealand, M., & Carrick, M., 1998. Developing multi-breed estimated breeding values for beef cattle. Anim. Breed. Abstracts 66: 389.
- Green, R.D., 2009. ASAS Centennial paper: Future needs in animal breeding and genetics.

 J. Anim. Sci. 87: 793 800.
- Gregory, K.E. & Cundiff, L.V., 1980. Crossbreeding in beef cattle: Evaluation of systems.

 J. Anim. Sci. 51: 1224 1242.
- Gregory, K.E., Cundiff, L.V. & Koch, R.M., 1991. Breed effects and heterosis in advanced generations of composite populations for birth weight, birth date, dystocia, and survival as traits of dam in beef cattle. J. Anim. Sci. 69: 3574 3589.
- Gregory, K.E., Smith, G.M., Cundiff, L.V., Koch, R M. & Laster, D.B., 1979. Characterization of biological types of cattle cycle III: Birth and weaning traits. J. Anim. Sci. 48: 271 279.
- Gregory, K.E., Dearborn, D.D., Cundiff, L.V. & Koch, R.M., 1987. Maternal heterosis and grand maternal effects in beef cattle: post weaning and carcass traits. J. Anim. Sci. 65: 1180 1194.
- Greiner, S.P., 2009. Beef cattle breeds and biological types. Available at: http://pubs.ext.vt.edu/400/400-803/400-803.html

- Hall, J.B., Seay, W.W. & Baker, S.M., 2009. Nutrition and feeding of the cow-calf herd: Production cycle nutrition and nutrient requirements of cows, pregnant heifers and bulls. Available at: http://pubs.ext.vt.edu/400/400-012/400-012.html
- Harvey, W.R., 1972. Instructions of use of least squares maximum likelihood model general purpose program (LSMLMM); 252k Version. Ohio State Univ.
- Harvey, W.R., 1976. Instructions for use of revised least squares and maximum likelihood mixed model general purpose program (LSMLMM), Ohio State Univ.
- Harvey, W.R., 1988. User's guide for LSMLMV. PC-1 version. January 1988.
- Johnson, M.H. & Notter, D.R., 1987. Simulation of genetic control of reproduction in beef cows. III. Derived genetic parameters. J. Anim. Sci. 65: 76 87.
- Kahi, A.K., Thrope, W., Nitter, G. & Baker, R.L., 2000. Crossbreeding for dairy production in the lowland tropics of Kenya. I. Estimation of individual crossbreeding effects on milk production and reproductive traits and on cow live weight. Livest. Prod. Sci. 63: 55 63.
- Kinghorn, B.P., 1882. Genetic effects in crossbreeding. II. Multibreed selection indices. Z. Tierz. Züchtungsbiol. 99: 315 320.
- Koger, M., Mitchell, J.S., Kidder, R.W., Burns, W.C., Hentges, J.F. (Jr.) & Warnick, A.C., 1967. Factors influencing survival in beef calves. J. Anim. Sci. 26: 205 (Abstr.).
- Koger, M., Peacock, F.M., Kirk, W.G., & Crockett, J.R., 1975. Heterosis effects on weaning performance of Brahman-Shorthorn calves. J. Anim. Sci. 40: 826 822.
- Laker, M.C., 2003. Soil classification. A global desk reference. Print ISBN: 978-0-8493-1339-4. CRC Press.
- Lamb, M.A., Tess, M.W., Robinson, O.W., 1982. Evaluation of mating systems involving five breeds for intergrated beef production systems: I. Cow-calf segment. J. Anim. Sci. 70: 689 - 699.
- Lamberson, B., Massey, J. & Whittier, J.C., 1993. Crossbreeding systems for small herds of beef cattle. Available at:

 http://extension.missouri.edu/publications/DisplayPub.aspx?P=G2040
- Laster, D.B. & Gregory, K.E., 1973. Factors affecting pelvic size and dystocia in beef cattle.

- J. Anim. Sci. 37: 1092 1097.
- Long, C. R., 1980. Crossbreeding for beef production: Experimental results. J. Anim. Sci. 51: 1197 -1223.
- MacNeil, M.D., 1987. Formation of optimal composite populations. Theor. Appl. Genet. 74: 837 840.
- MacNeil, M.D., 2005. Beef Cattle Management: Crossbreeding. In: Encyclopedia of Animal Science. Marcel Dekker, New York, NY.
- MacNeil, M.D., Dinkel, C.A. & Van Fleck, L.D., 1982. Individual and maternal additive and heterotic effects on 205-day weight in beef cattle. J. Anim. Sci. 54: 951 956.
- MacNeil, M.D., Cundiff, L.V., Dinkel, C.A. and Koch, R.M., 1984. Genetics correlations among sex-limited traits in beef cattle. J. Anim. Sci. 58: 1171 -1180.
- MacNeil, M.D., Cundiff, L.V. & Gregory, K.E., 1988. Crossbreeding systems for beef production. Appl. Agric. Res. 3: 44 54.
- MacNeil, M.D. & Newman, S., 1991. Using heterosis to increase profit. Proc. Int. Beef Symp. Great Falls, Montana, 129 -134.
- MacNeil, M. D. & Matjuda, L.E., 2007. Breeding objectives for Angus and Charolais specialized sire lines for use in the emerging sector of South African beef production. S.A. J. Anim. Sci. 37: 1 7.
- McDonald. R.P. & Turner, J.W., 1972. Estimation of maternal heterosis in pre-weaning traits of beef cattle. J. Anim. Sci. 35: 1146 1154.
- McElhenny,W.H., Long, C.R., Baker, J.F. & Cartwright, T.C., 1986. Production characters of first generation cows of five-breed diallel: Reproduction of mature cows and preweaning performance of calves by two third-breed sires. J. Anim. Sci. 63: 59 57.
- McManus, C., Abreu, U.G.P., Lara, M.A.C., & Sereno, J.R.B., 2002. Genetic and environmental factors which influence weight and reproduction parameters in Pantaneiro cattle. In: Brazil Arch. Zootec. 51: 91 97.
- Mentz, A.H., 1977. Produksiepotensiaal van verskillende eerstekruising Afrikanerbeeste. Ph.D. Thesis, University of the Free State.

- Miller, S.P., 2010. Fact sheet: Crossbreeding systems for beef production. Available at: http://www.omafra.gov.on.ca/enghlish/livestock/beef/crossbreeding
- Mirkena, T., Duguma, G., Haile, A., Tibbo, M., Okeyo, A.M., Wuringer, M., & Sölkner, J., 2010. Genetics of adaptation in farm animals: A Review. Livest. Sci. 132: 1 12.
- Mpofu, N., 2002. Comparison of indigenous and foreign cattle for beef production at Matopos Research Station in Zimbabwe. Available at: http://agtr.ilri.cgiar.org/casestudy/case-mpofy-1.
- Moyo, S., Swanepoel, F.J.C. & Rege, J.E.O., 1996. Evaluation of indigenous, exotic and crossbred cattle for beef production in a semi-arid environment: reproductive performance and cow productivity. Proc. Austr. Soc. Anim. Prod. 21: 204 206.
- NDA, 2001. The Strategic Plan for South African Agriculture. Directorate Agricultural Information Services. Private bag X144, Pretoria, 0001.
- Neser, F.W.C., van Wyk, J.B. & Erasmus, G.J., 2003. Performance of Simmentaler cattle in South Africa: a scientific review. Available at: http://www.wsff.info/files/congress
- Neville, W.E. (Jr.), Mullin, B.G., & McCormick, W.C., 1984. Grading and rotational crossbreeding of beef cattle. Reproductive performance. J. Anim. Sci. 58: 25 37.
- Newman, S. & Reverter, A., (2000). Practical aspects of crossbred genetic evaluation.

 Available at: http://www.lifestockgenomics.csiro.au/courses/TR_publication/
- Ntombizakhe, M., 2002. The multiplication of Africa's indigenous cattle breeds internationally: the story of the Tuli and Boran breeds. Available at: http://agtr.ilri.cgiar.org/Casestudy/case-mpofu-1-TuliBoran-31.htm
- Ojano-Dirain, C, Tinsley, N.B., Wing, T., Cooper, M, & Bottje, W.G., 2007. Membrane potential and H2O2 production in duodenal mitochondria from broiler chickens (*Gallus gallus domesticus*) with low and high feed efficiency. Comparative biochemistry and physiology. Part A, Molecular & integrative physiology 147(4): 934-41.
- Olsen, T.A., 2002. Crossbreeding programs for beef cattle in Florida. BUL 326/AN055. Available at: http://edis.ifas.ufl.edu/an055

- Peacock, F.M., Kirk, M., Koger, J.W., Carpenter, J.W. & Crockett, J.R., 1999. Evaluation of the Brahman breed as straightbred and crossbred for beef production in South Central Florida. Available at: http://www.brahman.co.za. Reviewed.
- Pico, B.A., Neser, F.W.C. & van Wyk, J.B., 2004. Genetic parameters for growth in South African Brahman cattle. S.A. J. Anim. Sci. 34: 44 46.
- Pichner, F. & Mergl, R., 1977. Overdomoninance as cause for heterosis in poultry. Zeitschrift für Tierzüchtung und Züchtungsbiologie 94: 151 158.
- Pollak, E.J., 2006. Multibreed genetic evaluations of beef cattle in the United States. 8th World Congress on Genetics Applied to Livestock production, Belo Horizonte, MG, Brasil.
- Prayaga, K.C., 2003a. Evaluation of beef cattle genotypes and estimation of direct and maternal genetic effects in a tropical environment. 1. Growth traits. Aust. J. Agric. Res. 54: 1013 -1025.
- Prayaga, K.C., 2003b. Evaluation of beef cattle genotypes and estimation of direct and maternal genetic effects in a tropical environment. 2. Adaptive and temperament traits. Aust. J. Agric. Res. 54: 1027 1038.
- Prayaga, K. C. 2004. Evaluation of beef cattle genotypes and estimation of direct and maternal genetic effects in a tropical environment. 3. Fertility and calf survival traits. Aust. J. Agric. Res. 55: 811 824.
- Prayaga. K. C., Barendse, W. & Burrow, H.M., 2006. Genetics of tropical adaptation. 8th World Congress on Genetics Applied to Livestock production, August 13 18, 2006, Belo Horizonte, MG, Brazil.
- Reynolds, W.L., DeRouen, T.M., Moiu, S. & Koonce, K.L., 1980. Factors influencing gestation length, birth weight and calf survival of Angus, Zebu and Zebu cross beef cattle. J. Anim. Sci. 51: 860 867.
- Ritchie, H.D. & Coran, L.R., 1996. Beef cattle research: Where have we been and where are we headed? Available at:

 https://www.msu.edu/~ritchieh/historical/wherehavewebeen.html

- Roughsedge, T., Thompson, R., Villanueva, B. & Simm, G., 2001. Synthesis of direct and maternal genetic components of economically important traits from beef breed-cross evaluations. J. Anim. Sci. 79: 2307 2319.
- Roberson, R.L., Sanders, J.O. & Cartwright, T. C., 1986. Direct and maternal genetic effects on pre-weaning characters of Brahman, Hereford and Brahman-Hereford crossbreed cattle. J.Anim. Sci.: 63: 438 446.
- Romanini, C.E.B., Nääs. I.D.A., D'Alessandro Salgado. D Lima, K.A.O., do Valle, M.M., Labigalini, M.R., de Souza, S.R.L., Menezes, A.G., & de Moura, D.J., 2008. Impact of Global Warming on Brazilian Beef Production, Livest. Environ. VIII, 31 August 4 September 2008, Iguassu Falls, Brazil 701P0408.
- RMRD SA, 2010. Research and development plan for the large stock and small stock meat industries in South Africa. Pretoria. http://www.samic.co.za/samic/rd.htm#rdRMRDT
- Said, R., Bryant, M.J. & Msechu, J.K.K., 2003. The survival, growth and carcass characteristics of crossbred beef cattle in Tanzania. Tropical Animal Health and Production, 35 (5): 441-454.
- SAS, 2010. SAS/STAT User Guide. Cary, NC: SAS Institute Inc.
- Schoeman, S. J., 1989. Recent research into production potential of indigenous cattle with special reference to Sanga (Review). S.A. J. Anim. Sci. 19: 55 61.
- Schoeman, S.J., 1999. Cross breeding in beef cattle: In: M.M. Scholtz, L.Berg & D.J. Bosman, eds. Beef breeding in South Africa. Irene, South Africa, Agricultural Research Council, Animal Improvement Institute.
- Schoeman, S.J., Van Zyl, J.G.E & De Wet, R., 1993. Direct and maternal additive and heterotic effects in crossbreeding Hereford, Simmentaler and Afrikaner cattle. S.A. J. Anim. Sci. 23: 61 71.
- Scholtz, M.M., 1988. Selection possibilities for hardy beef breeds in Africa: The Nguni example. Proc. 3rd World cong. Sheep and Beef Cattle Breed. 2: 303 319.
- Scholtz, M.M., Bester, J., Mamabolo, J.M. & Ramsay, K.A., 2008. Results of the national cattle survey undertaken in South Africa, with the emphasis on beef. Appl. Anim. Hus. & Rur. Dev. (1): 1-9.
- Scholtz, M.M. & Bester, J., 2010. Off-take and production statistics in the different South African cattle sectors: Results of a structured survey. S.A. J. Anim. Sci. 3: 19 23.

- Scholtz, M.M., Roux, C.Z. & Lombard, P.E., 1990. Breeding strategies for beef cattle in the subtropics and tropics: terminal crossbreeding. Proc. 4th Wrld. Cong. Genet. Appl. Livest. Prod., Edinburg, Scotland XV, 361 – 364.
- Scholtz, M.M. & Lombard, P.E., 1992. Prospects and potential of Southern African cattle breeds: The Nguni example. Proc. Aust. Assoc. Anim. Breed. Genet. 10: 47 50.
- Scholtz, M.M., 2010. Beef breeding in South Africa. 2nd Edition. ARC, Pretoria. ISBN-13 978-1-86849-391-3.
- Scholtz, M.M. & Theunissen, A., 2010. The use of indigenous cattle in terminal crossbreeding to improve beef cattle production in Sub-Saharan Africa. Animal Genetic Resources Information 46: 33.
- Skrypzeck, H., Schoeman, S.J., Jordaan, G.F. & Neser, F.W.C., 2000. Estimates of crossbreeding parameters in a mutibreed beef cattle crossbreeding project. S.A. J. Anim. Sci. 3: 193 - 204.
- Smith, J.W., 2005. Correlation of pelvic shape and birth weight EPDs in reducing dystocia in beef cattle. M.Sc. study. Univ. of Tennessee.
- Spangler, M.L., 2007. The value of heterosis in cow herd: lessons from the past that apply to today. Range Beef Cow Symposium, Univ. Nebraska, Lincoln. Available at: http://Fdigitalcommons.unl.edu/rangebeefsowsyp/21
- Sprinkle, J., 2001. Crossbreeding systems for Arizona rangelands. Arizona Rancher's Management Guide. Arizona Cooperative Extension.
- Sprott, L.R., & Troxel, T.R., 2008. Management of replacement heifers for high eproduction and calving rate. Available at: http://animalscience.tamu.edu
- Strydom, P.E., 2008. Do indigenous South African cattle breeds have the right genetics for commercial production of quality meat? Meat Sci. 80: 86 93.
- Strydom, P.E., Naude, R.T., Smith, M.F., Scholtz, M.M. & Van Wyk, J.B., 2000. Characterization of indigenous African cattle in relation to meat quality traits. Meat Sci. 55: 79 88.
- Van der Merwe, C.R., 1962. Soil groups and subgroups of South Africa. Third Ed. Science Bulletin 356. Pretoria: Government Printer.
- Van der Westhuizen, R.R., Schoeman, S.J., Jordaan, G.F. & van Wyk, J.B., 2001. Heritability estimates derived from threshold analysis for reproduction and stayability traits in a beef cattle herd. J. Anim. Sci. 31: 25 32.

- Vercoe, J.E. & Frisch J.E., 1992. Genotype (breed) and environment interaction with particular reference to cattle in the tropics. A review. Aust. J. Anim. Sci. 5: 401 409.
- Weaber, R.L., 2009. Cattle breeds: Considering crossbreeding? Available at: http://www.cattlenetwork.com/
- Weaber, B., 2010. Crossbreeding for commercial beef production. In: Beef sire selection manual. Available at: http://www.ca.uky.edu/agcomm/PUBS/ASC/asc169 2nd Edition.
- Williams, A.R., Franke, D.E., Saxton A.M. & Turner, J.W., 1990. Two-, three- and four-breed rotational crossbreeding of beef cattle: reproductive traits. J. Anim. Sci. 68: 1536 1546.
- Williams, A.R., Franke, D.E. & Saxton, A.M., 1991. Genetic effects for reproductive traits in beef cattle and predicted performance. J. Anim. Sci. 69: 531 542.
- Williams, J.L., Aguilar, I., Rekaya, R. & Bertrand, J.K., 2010. Estimation of breed and heterosis effects for growth and carcass traits in cattle using published crossbreeding studies. J. Anim. Sci. 88: 460 466.
- Wilson, L.L., Rishel, W.H. & Harvey, W.R., 1972. Influence of herd, sire and herd x sire interactions on live and carcass characters of beef cattle. J. Anim. Sci. 35: 502 506.