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GENETIC FACTORS AFFECTING MILK PRODUCTION, GROWTH AND REPRODUCTION TRAITS IN *BOS indicus* X *BOS taurus* CROSSES IN ETHIOPIA

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Genetic factors affecting milk production, growth and reproduction traits in *Bos indicus x Bos taurus* crosses in Ethiopia

By

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Preface

It is the wish of the author that this thesis will serve as a useful source of information for the design of crossbreeding strategies for dairy cattle improvement in Ethiopia as well as in other similar tropical environments. The thesis is prepared in the form of five separate papers, of which one is accepted for publication (Demeke *et al.*, 2002), while the other four are submitted. The papers are augmented by a general introduction and a general conclusion and recommendations in an effort to create a single unit. The general introduction provides a brief review on the need for crossbreeding *Bos indicus* breeds with the improved European breeds in the tropics, the genetic basis of crossbreeding in relation to the major results of *Bos taurus* x *Bos taurus* crosses and background information on cattle production and crossbreeding programs in Ethiopia. Since the data used in this study were obtained from the major dairy breeds and their crosses that were collected over several years in Ethiopia, the chapter on conclusions and recommendations discusses the implications of the major findings of this study and its contributions towards future crossbreeding/breeding programs for dairy cattle improvement in Ethiopia. In the chapters compiled in this thesis, possible care has been taken to avoid unnecessary repetitions. However, some repetitions in background information and reference citations were necessary to explain individual parts of the study,.and were thus unavoidable.

This study was completed with the material, intellectual and moral support of several individuals and institutions that the author morally obliged to acknowledge.

The financial support, study leave and permission granted to use the crossbreeding data by the Ethiopian Agricultural Research Organization for this study is highly acknowledged. Dr. Emuru Zewede at the Ministry of Agriculture, the National Artificial Insemination Centre and Mr. Tesfaye Hailue at Holetta farm deserve special thanks for making the data of the purebred Friesian herd available. Dr. Alemu G/Wold, Dr. Beyene Kebede, Mrs. Roman H/silassie and other several staff members at the four research stations of the Ethiopian agricultural Research Organization are also thanked for the part they played in the execution of the long-term crossbreeding project and collecting the data.

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Finally, I wish to express my sincere appreciation to my wife, Asselef Teshome and to our son Berekete and our daughter Belene, for their love, patience and constant encouragement throughout the period of my study, whom were a source of inspiration and motivation to me to complete this study.

Above all, thanks to Almighty God, for granting me the patience, ability and means to complete this study.

Dedication

I dedicate this work to my wife Asselef Teshome, and to our children, Berekete and Belene, for their unreserved love, patient and encouragement during our long separation period for this work.

They are my life.

Chapter 1

General introduction

1.1 General

It is generally known that in tropical and sub-tropical areas the stress, produced by heat and solar radiation, external parasites, disease, highly fibrous roughages and other concurrent difficulties, impede the introduction of selected, high-producing European breeds, unless a high level of management and feeding can be provided to ameliorate the environment (e.g. McDowell, 1985; Cunningham and Syrstad, 1987; McDowell *et al.*, 1996). In general, in the extensive areas of the tropics where the improvement of managerial and nutritional conditions is either not feasible, or practical, the development of milk and meat production can only be attempted either by selecting the best available local breeds, or by crossing them with improved cattle of European origin. Increasing the productivity of the indigenous tropical cattle through selection, particularly for dairy traits, is expected to be slow because of the low level of genetic variance for milk yield in the population (McDowell, 1996). Crossbreeding with adapted indigenous breeds, however, allows for the effective use of the imported high producing *Bos taurus* germplasms within the constraints of the slowly changing local farming conditions and results in superior overall performance (Madalena, 1990; Kahi *et al.*, 2000).

Systematically designed crossbreeding programs allow for the utilization of breed additive differences and heterosis in production performance. It also synchronizes more effectively the performance characteristics and adaptability of genetic resources to the climatic and nutritive environments, as well as other resources that are more economical to provide (Dickerson, 1969; Gregory and Cundiff, 1980). Information on performance of breeds and crosses, including estimates within and inter-population genetic parameters, is needed to design breeding programs aimed at the economic utilization of genetic resources (Dickerson, 1969). Several crossbreeding (breed additive and non-additive) and within population (heritability and genetic correlations) genetic parameter estimates for production, reproduction and viability traits can be found in the literature for *Bos taurus*, *Bos indicus* as well as their crosses. However, these estimates vary widely across production systems, breeds, method of estimation etc. (e.g. Long, 1980; McDowell, 1985; Cunningham and Syrstad, 1987; Madalena, 1990; Koots *et al.*, 1994a,b; Rege *et al.*, 1994; McDowell *et al.*, 1996; Rege, 1998; Kahi *et al.*, 2000; Lôbo *et al.*, 2000). Since there is a marked difference in production inputs, management level, climatic factors and breeds, both within and amongst tropical countries, crossbreeding and within population genetic parameters are needed for each specific condition to design effective breeding programs.

The crossbred animal's performance is affected by breed additive and non-additive genetic effects. The breed additive effect can be defined as the average of the two parental breed gene contributions. For two breeds that have the same gene frequencies for the traits of interest, the breed additive effect is the simple average of the two. If two traits are negatively correlated across breeds, for example productivity traits in *Bos taurus* and adaptability (stress and disease resistance) in *Bos indicus*, the crossbred progeny of the two are expected to receive multiplicatively acting genes in the expression of economic values (Swan and Kinghorn, 1992). This is possibly one of the reasons for the extraordinary superiority in both production and adaptability of the F_1 *Bos taurus* x *Bos indicus* crosses in the tropics (e.g. McDowell, 1985; Syrstad, 1989, 1990; McDowell *et al.*, 1996). The non-additive effect of crossbreeding is heterosis. This is the amount by which the merit in crossbreds deviates from the additive component, on mid-parent value. Heterosis is usually attributed to genetic interactions within loci (dominance) and interactions between loci (epistasis). When an individual's parents come from two different breeds, an increased level of allelic heterozygosity is expected (Falconer and Mackay, 1996), because the individual's genes are sampled from the two different breeds. The dominance effect is therefore expected to endow the individual to perform well, especially under a varying or stressful environment, and its influence on production and adaptability traits is usually favourable (Falconer and Mackay, 1996). On the other hand, epistasis, the interaction between genes at different loci, is expected to be positive and high in the purebred populations. Due to many generations of both natural and artificial selection, purebreds are expected to accumulate genes at different loci that cooperate well in carrying out their tasks. When breeds are crossed, genes derived from different breeds are recombined in the crossbred progeny resulting in a breakdown of parental epistatic genes. Epistatic effects on performance of crossbred animals are, therefore, hypothesized to be negative (e.g. Dickerson, 1969; Kinghorn, 1987; Rutledge, 2001), particularly in the crosses of highly divergent breeds of *Bos taurus* and *Bos indicus* origin (Rutledge, 2001). Epistatic effects have been implicated as a possible reason for low milk production and reproduction in the F_2 and latter generation of *Bos taurus* x *Bos indicus* crosses in the tropics (e.g. McDowell, 1985; Syrstad, 1989; McDowell *et al.,* 1996; Rutledge, 2001).

In several past crossbreeding studies between *Bos taurus* x *Bos taurus* crosses, heterosis for growth traits was mainly attributed to the dominance effect and heterosis retention in the advanced generations of crosses was also predicted to be a linear function of a reduction in heterozygosity (Long, 1980). The importance of epistasis as a component of heterosis was only recognized later on, especially for *Bos taurus* x *Bos indicus* crosses. For instance, Arthur et al. (1999) reported a significant improvement in accuracy of prediction of the growth performances of genotypes produced from *Bos taurus* x *Bos indicus* crosses, when epistatic effects were included in the model.

Epistatic effects are difficult to measure and are often ignored in designing crossbreeding programs. However, ignoring epistatic effects may lead to the use of wrong models for the prediction of the performance of crossbred genotypes (Kinghorn and Vercoe, 1989). This could mean that the prediction performances of particularly the untested later generations of crossbreds based on a simple dominance model of heterosis may then be strongly biased upwards. Swan and Kinghorn (1992) listed the following important points about epistatic effects on production performance of crossbred populations: 1) crosses involving more breeds may suffer more loss, because there is less interaction between genes from the same breed; 2) crosses that include one purebred parent, such as rotational crosses, may tend to show less loss. This is because at least one gene from the purebred parent breed is represented on all loci, giving a total complement of genes that were derived from a single breed. 3) Crosses developed over a number of generations, such as new composite breeds, may suffer more loss, because recombination effects take longer to break down between closely linked and functionally related genes. Rutledge (2001) hypothesised that epistatic loss might be one of the reasons for the failure to develop a superior dairy breed in a century of crossbreeding efforts in the tropics. There were several attempts to breed a composite dairy breed using *Bos taurus* x *Bos indicus* crosses in different countries in the tropics (e.g. the Jamaican, Jamaica Hope, the Brazilian Pitanqueries, the Indian Karan Swiss and Karan Fries; the Australian milking Zebu; and the Cuban Siboney and Mambi); however, non of these composite breeds yet recognized as an outstanding tropical dairy breed(s) and except for a few, their performance is usually lower than those of the F_1 crossbreds (McDowell, 1985; McDowell *et al.,* 1996).

Though experimental evidence are limited as relating to production traits, because of a potential bias on heterotic estimates, it is important to check for epistatic effects in the evaluation of crossbred data, particularly in *Bos taurus* x *Bos indicus* crosses (e.g. Mackinnon *et al.,* 1996; Arthur *et al.*, 1999; Kahi *et al.*, 2000; Rutledge, 2001). Several crossbreeding models have been proposed for the estimation of crossbreeding parameters in livestock experiments (e.g. Dickerson, 1969,1973; Hill, 1982; Koch *et al.,* 1985; Kinghorn, 1987). These models have a similar definition and expectations in modelling the additive components of crossbreeding. The major difference between them is the modelling of the dominance and epistatic components. In spite of the differences in the hypothesis of the non-additive components, the models have a linear relationship and their parameter estimates are also linearly transformable from one model into the other (Koch *et al.,* 1985; Wolf *et al.*, 1995). However, the difficult aspect of crossbreeding parameter estimation is that the number of parameters to be estimated in most cases are more than the number of crossbred genotypes available. The option proposed to overcome such problem is to select a reduced model that gives the highest fit to the observed genotypic differences (Wolf *et al.*, 1995).

For estimating individual breeding values, mixed model methodology has become the standard procedure world-wide. However, crossbreeding data are commonly analysed, using least-squares fixed-model procedures. Komender and Hoeschele (1989) showed that standard errors of crossbreeding parameters are underestimated when fixed models are used, instead of a mixed model that takes all relationships between animals via an animal model into account. The application of mixed models for crossbred data also allows for the simultaneous estimation of crossbreeding and within population genetic parameters (e.g. Van Der Werf and De Boer, 1989; Akbas *et al.*, 1993).

1.2 Background of cattle production and the crossbreeding experiment in Ethiopia

Ethiopia is a tropical country with a landmass of about 1.1 million km^2. It is situated between 3° and 18° northern latitude. The topography of the country ranges from the coastal southern and southeastern lowlands to the dominant highlands of the northern and central part, as well as the rift valley, which divides the country from the northeast to the south. The agro-ecology of the country is quite diverse and ranges from the arid tropics, where the rainfall is erratic and under 300 mm per annum, to the humid tropics, where the annual rainfall exceeds 1400 mm with a short dry period. As a result of this wide variation in climatic conditions, vegetation, feed supply, water availability and human and livestock density are extremely variable from one region to the other.

The diversity of the topography and climatic conditions resulted in the evolution of different agricultural and livestock production systems in the country. Accordingly, two major livestock production systems, with some intermediate types, can be identified. These are the highlands smallholder mixed farming systems, covering about 55% of the total land area, 92% of the total human population and 78% of the cattle population; and the lowlands pastoral systems, which covers the rest of the land, human and cattle populations (MOA, 1984). In the highland mixed farming system, livestock especially cattle, plays a major role in providing draft power, as well as milk, meat and manure for fuel and fertilizer. Due to the importance of draft animals in this area, 50 to 55% of the cattle population are draft oxen, while only 15 to 20% are breeding cows. In the lowlands, on the other hand, where about 8% of the human population and 22% of cattle population reside, cattle are kept primarily for milk and milk products and the herd is dominated by female animals (80-85%). People living in lowlands lead a nomadic and semi-nomadic life.

The cattle population of Ethiopia is estimated at 35 million, which is the largest in Africa and among the top ten in the world (FAO, 2000). Albero and Haile-Mariam (1982a,b) identified several indigenous cattle breeds (types) in Ethiopia that could be classified into four major types: the humpless Hametic Long horn and Short horn (*Bos taurus*), the Zebu, the Sanga, which is a result of interbreeding between the Hametic Long horn and the Zebu, and the intermediate Sanga /Zebu types. The Zebu is the predominant type, followed by the Sanga. The productivity of the indigenous cattle breeds is generally low. The average annual milk yield for the estimated 4.5 million cows milked is estimated to be 204 kg per cow per year. The average cattle off-take is 7.4% per annum, with an average dressed carcass weight of 108.4 kg (FAO, 2000). Cows usually calve for the first time at around four years of age, and the calving interval is about two years. The major factors contributing to low animal productivity in Ethiopia are unfavourable climatic conditions (including frequent droughts), large animal population causing overgrazing and scarcity of feed, and a high incidence of animal diseases.

Trials conducted to evaluate the production performance of some of the indigenous *Bos indicus* breeds under station 'improved' management conditions yielded results of performance not far from that reported for the national average. For instance, Schaar *et al.* (1981) reported a milk yield of 224 kg in 148 days for Arsi type cattle. In a similar study evaluating the Boran, Barca and Horro breeds, lactation milk yield and lactation length was estimated at 682 kg and 164 days, 675 kg and 184 days and 559 kg and 285 days, respectively (IAR, 1976). For the three breeds, the average weight ranged from 18 to 23 kg at birth and 90 to 100 kg at 180 days (IAR, 1976). It was within these production conditions that the long-term cattle crossbreeding projects of the Institute of Agricultural Research (IAR) was started in 1974.

The overall objective of the project was to compare different combinations of indigenous Zebu and European breeds, primarily for growth rate, milk production, reproductive efficiency and draft power. Further comparisons were also to be made for viability and diseases resistance in regimes with contrasting environmental and farming conditions in order to determine the best performing crossbred group(s) for each region (Wiener, 1972). This long-term crossbreeding program was conducted in three phases. In the first phase F_1 crosses were produced alongside their contemporary purebred Zebus. In the second phase animals of different genetic levels such as F_2 and 3/4*Bos taurus* crosses were produced, while still maintaining the contemporary production of F_1 crosses and purebred Zebus. In the third and last phase, 5/8 and 7/8*Bos taurus* and three-breed crosses were produced alongside contemporary genotypes from phase one and two. Though the crossbreeding experiment was designed to be carried out in phases, there was a significant overlap between the different phases. The experiment was conducted at four stations representing different agro-ecological and farming systems in the country. Each station had two indigenous breeds (dam lines). One indigenous breed was common to all stations and served as the connecting breed between the four stations. The same sires, representing the three *Bos taurus* breeds, were used at all four stations.

The three *Bos taurus* breeds used in the crossbreeding project were Friesian, Jersey and Simmental. The majority of the bulls representing the three *Bos taurus* breeds were imported from Europe (Denmark, Germany and Switzerland) and were progeny tested in the 1970s. Since 1990 Friesian semen, obtained from the National AI Centre was also used. The indigenous breeds used were Boran, Barca and Horro. Both *Bos taurus* and *Bos indicus* breeds involved in the crossbreeding program were chosen for the following reasons or advantages.

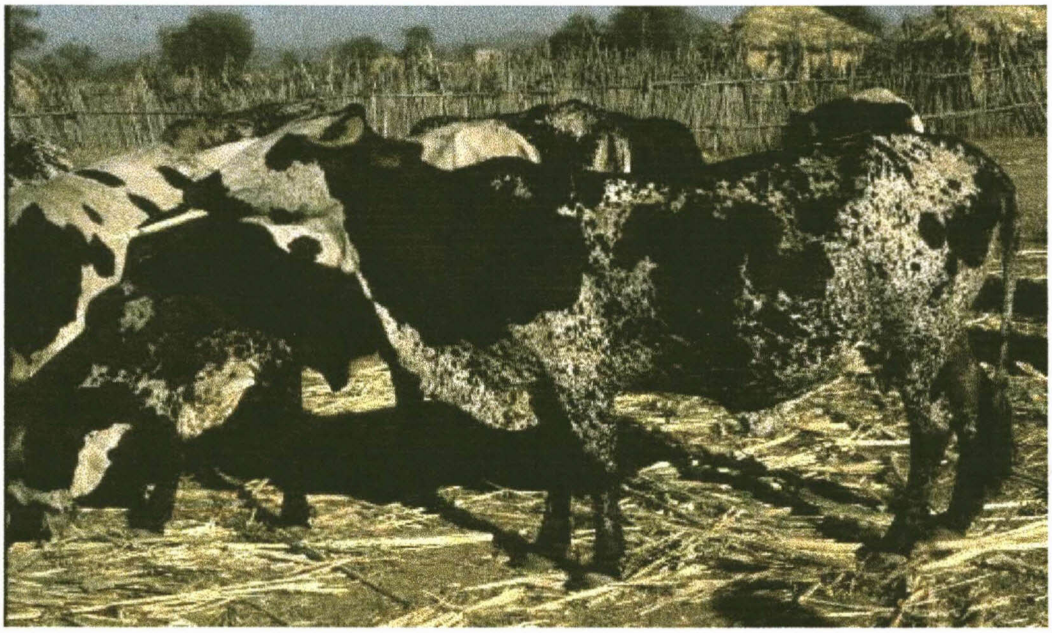
The Friesian has long been introduced and was wildly accepted as a dairy breed in the country, as is also the case elsewhere in the world. The crosses of this breed were expected to adapt well to the temperate-like climate of the Ethiopia highlands. The Jersey, because of its smaller body size, was expected to have a relative advantage over the larger breeds where nutrition is a limiting factor. In addition, it is also believed to be more heat tolerant, and therefore, its crosses may also adapt better to the warmer regions. The Simmental was considered as an alternative 'large' breed to the Friesian in terms of meat and milk production. Furthermore, since it was an important draft animal in Europe, it may also provide better draft ability to their crossbred progeny.

The three indigenous breeds chosen are widely distributed and represented in different agro-ecological zones and production systems in Ethiopia. Hence, their crossbred progenies were expected to show similar adaptations to the different production systems.

The Boran (the large east African Zebu) is found in the lower altitudes (arid) of the southern rangelands of the country known as the Borena region, from which the name 'Boran' was derived. The Boran has spread throughout the southern part of Ethiopia and northern regions of Kenya and Somalia, and is known for its good performance under arid conditions. It is tolerant to heat and can withstand lack of water for a couple of days. In this habitat, where it is owned by pastoralist people, the Boran is kept mainly for milk production. It has, however, shown to have an excellent beef production performance when sold to feedlots in the highlands and mid-altitudes of Ethiopia. The population size of the Boran is estimated to be about 1 million (Albero, 1986). A mature Boran bull weighs about 450 to 550 kg and cows weigh 350 to 400 kg with an average daily milk yield of 3 to 5 kg and lactation milk yield of 500 to 800 kg under good management conditions (Albero and Haile-Mariam, 1982b; ILCA, 1993). The Boran is the only indigenous breed under selection for beef performance in Ethiopia (Haile-Marim and Kassa-Mersha, 1995) (Picture 1).

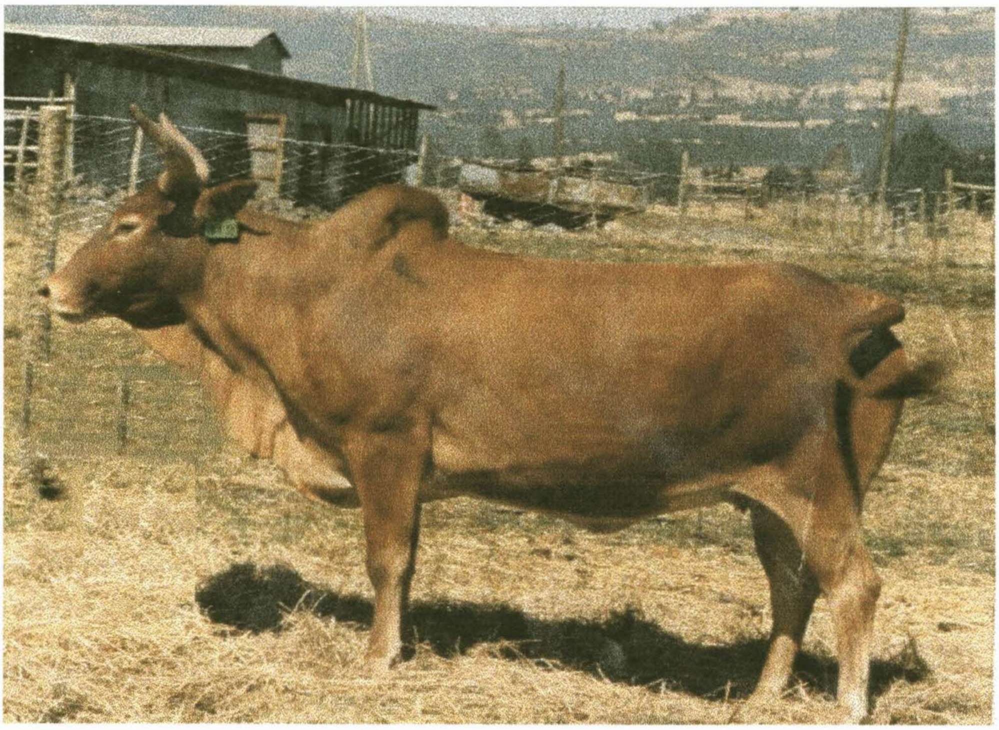
Picture 1. Boran heifers

The Barca is mainly found in the lowlands of Eritrea and smaller numbers in the northern lowlands of Ethiopia. The Barca is also classified as Zebu and it is considered to have higher milk potential relative to the other indigenous breeds. It has also an advantage of being well adapted to a hot climates. The Barca is a tall animal with long, straight legs, its average height being 125cm in cows and 130-135cm in bulls. The population size of this breed is estimated to be about 850,000. The cows weigh about 280 kg and the bulls about 380 kg (Albero and Haile-Mariam, 1982b) (Picture 2).



Picture 2. Barca cows (Source: Indigenous Animal Genetic Resource, ILRI)

The Horro is classified as a Sanga type (Albero and Haile-Mariam, 1982a). It is found in the vast areas of the highlands of the central and western parts of the country, and is not considered to be a very good milk producer, yet it plays an important role for draft and beef production in the highland mixed farming systems. The population size of this breed is not known, because of the significant inter-mixing with other highland indigenous animals in the area of its distribution. A mature Horro bull weighs about 300 to 400 kg and cows weigh 200 to 330 kg. The cows have notably short lactations, usually less than six months, with an average milk yield of about 1 to 4 kg per day (Albero and Haile-Mariam, 1982a) (Picture 3).



Picture 3. A Horro cow

The data collected from the purebred *Bos indicus* breeds and their crosses in the project described were used in the study. The objectives of this study were to:

- compare different genetic models for the estimation of crossbreeding parameters for the crossbred population under investigation;
- estimate crossbreeding effects on early growth traits;
- estimate variance components and genetic parameters for early growth traits;
- quantify crossbreeding and genetic parameters for milk production, cow weight and reproduction traits.

Early growth performance of *Bos taurus* x *Bos indicus* cattle crosses: I. Evaluation of different crossbreeding models

2.1 Introduction

The use of *Bos indicus* x *Bos taurus* crosses, particularly for dairy purposes is widespread in tropical and sub-tropical climates, because of their higher production in these environments than the corresponding purebreds (e.g. Cunningham and Syrstad, 1987; Madalena *et al.*, 1990b).

Reliable crossbreeding parameter estimates are required to design a sound crossbreeding program. By extrapolating the estimates obtained from the best fitting model, the merit of untested crossbred genotypes can be predicted. Therefore, the choice of an appropriate genetic model is important for the analysis of a crossbred population (Kinghorn and Vercoe, 1989).

The most commonly applied model in crossbreeding studies was derived by Dickerson (1969, 1973). This model accounts for heterosis and recombination loss, which expresses the loss of favourable genetic interactions within gametes. However, heterosis in his model includes a part of the additive x additive epistasis in addition to dominance. Other authors, such as Kinghorn (1980, 1982, 1987), Hill (1982), Koch *et al.* (1985), Grosshans *et al.* (1994) and Wolf *et al.* (1995) developed alternative genetic models that allow a separate estimation of heterotic (dominance) and epistatic effects.

In *Bos taurus* x *Bos indicus* crossbreeding studies in the tropics (e.g. Thorpe *et al.*, 1993; Rege *et al.*, 1994; Kahi *et al.*, 1995), models with simple additive and dominance effects, ignoring epistasis, were often used for the estimation of crossbreeding parameters. However, studies which evaluated the performances of different generations of crosses revealed the insufficiency of models which include only additive and dominance effects to explain the observed variability between the different crossbred groups (Syrstad, 1989; Kahi *et al.*, 2000). On the other hand, studies comparing models with epistatic effects indicated the difficulty of estimating all kinds of expected epistatic interactions simultaneously from field data (e.g. Kinghorn, 1982, 1987; Grosshans *et al.*, 1994; Wolf *et al.*, 1995). The suggested approach to overcome such problem is to make some assumptions about the biological nature of the epistatic interactions (Kinghorn, 1987) and/or to use some form of restriction to limit the number of parameters to be estimated (Grosshans *et al.*, 1994; Wolf *et al.*, 1995).

Despite the problem of fitting all genetic effects involved in a model for crossbred animals, ignoring epistatic effects might lead to the selection of a wrong model for the estimation of parameters and prediction of the performance of untested genotypes (Kinghorn and Vercoe, 1989). This study evaluates the goodness of fit of five genetic models in estimating crossbreeding parameters for early growth traits for *Bos taurus* x indigenous *Bos indicus* crosses in Ethiopia.

2.2 Material and methods

2.2.1 Breeding plan and data source

The data were obtained from a comprehensive crossbreeding project conducted from 1974 to 1999 in four experimental herds of the Ethiopian Agricultural Research Organization. The herds are located at four stations, namely Holetta, Bako, Adamitulu and Werrer. These stations represent the different agro-ecological zones in the country. The project involved three *Bos indicus* Ethiopian breeds, namely the Boran (Bo), Barca (Ba) and Horro (Ho) and three *Bos taurus* European breeds, namely the Friesian (F), Jersey (J) and Simmental (S).

The crossbreeding program was designed in such a way that the Boran breed and its crosses were common to all stations, whereas the Barca breed and its crosses were common only to the Adamitulu and Werrer stations and the Horro breed and its crosses were common only to the Holetta and Bako stations. This mating design allowed the production of purebred and crossbred calves from two dam breeds per station. An overview of the distribution of records by genotype and station is shown in Table 2.1.

Semen from the three *Bos taurus* breeds was used to produce the crossbred calves. For the production of purebred calves and advanced generations of crosses, natural mating was practiced with indigenous and crossbred bulls recruited from the available bulls. Selection between bulls was only based on physical appearance. A total of 61 Friesian, 51 Jersey, 43 Simmental purebreds and 131 crossbred bulls (58 F, 43 J and 30 S crossbreds, see Table 2.1 for details on mating design) were used over the years in the four stations. Likewise, 36, 17 and 24 bulls representing straightbred Boran, Barca and Horro breeds were used to produce purebred calves. In mate assignments, pedigree information of both males and females was thoroughly checked to avoid mating of close relatives. Cows were mated and calved all year round. In order to avoid sire by station confounding within each *Bos taurus* breed, the same sires semen were used across the four stations.

All calves were weighed at birth and allowed to suckle their dams for the first 24-h in order to obtain colostrum, after which they were moved to individual calf pens for bucket feeding until weaning. Each calf was fed a fixed total of 260 kg of whole milk during the preweaning period. All calves were weaned at 90 days and kept indoors until the age of 6 months. During the indoor rearing period all calves were fed *ad lib* on natural pasture hay and supplemented with approximately 1 kg of concentrate composed of 30% wheat bran, 32% wheat middling, 37% Noug seedcake (*Guzeta Absynica*) and 1% salt per animal per day. The weight taken at the end of the indoor rearing period for each calf was considered to be the weaning weight in this study. After six months of age, all animals were grazed in a group on natural pastures for about 8-h per day and supplemented with conserved hay at night.

Table 2.1 Mating design used and distribution of progeny records by station

Genotype[1]			Number of records				
Sire	Dam	Progeny	Holetta	Bako	Werrer	Adami-tulu	Total
***Bos indicus* –pure breeds**							
Bo	Bo	Bo	70	84	44	59	257
Ba	Ba	Ba			53	77	130
Ho	Ho	Ho	68	136			204
Two-breed crosses							
F	Ba	1/2F:1/2Ba (F1)			44	70	114
F	Bo	1/2F:1/2Bo (F1)	260	61	57	59	437
F	Ho	1/2F:1/2Ho (F1)	53	73			126
J	Ba	1/2J:1/2Ba (F1)			38	55	93
J	Bo	1/2J:1/2Bo (F1)	101	64	45	52	262
J	Ho	1/2J:1/2Ho (F1)	47	72			119
S	Ba	1/2S:1/2Ba (F1)			39	41	80
S	Bo	1/2S:1/2Bo (F1)	74	64	52	46	236
S	Ho	1/2S:1/2Ho (F1)	60	72			132
1/2F:1/2Ba (F1)	1/2F:1/2Ba (F1))	1/2F:1/2Ba (F2			42	54	96
1/2F:1/2Bo (F1)	1/2F:1/2Bo (F1)	1/2F:1/2Bo (F2)	189	48	55	33	125
1/2F:1/2Ho (F1)	1/2F:1/2Ho (F1)	1/2F:1/2Ho (F2)	58	35			93
1/2J:1/2Ba (F1)	1/2J:1/2Ba (F1)	1/2J:1/2Ba (F2)			49	41	90
1/2J:1/2Bo (F1)	1/2J:1/2Bo (F1)	1/2J:1/2Bo (F2)	162	46	39	31	278
1/2J:1/2Ho (F1)	1/2J:1/2Ho (F1)	1/2J:1/2Ho (F2)	17	63			80
1/2S:1/2Ba (F1)	1/2S:1/2Ba (F1)	1/2S:1/2Ba (F2)			42	24	66
1/2S:1/2Bo (F1)	1/2S:1/2Bo (F1)	1/2S:1/2Bo (F2)	41	38	35	46	160
1/2S:1/2Ho (F1)	1/2S:1/2Ho (F1)	1/2S:1/2Ho (F2)	37	45			82
1/2F:1/2Bo (F1)	3/4F:1/4Bo (BC)	5/8F:3/8Bo (SC)	81				81
1/2J:1/2Bo (F1)	3/4J:1/4Bo (BC)	5/8J:3/8Bo (SC)	33				33
1/2S:1/2Bo (F1)	3/4S:1/4Bo (BC)	5/8S:3/8Bo (SC)	25				25
3/4F:1/4Bo (BC)	3/4F:1/4Bo (BC)	3/4F:1/4Bo (SC)	6		8		14
F	1/2F:1/2Ba (F1)	3/4F:1/4Ba (BC)			31	39	70
F	1/2F:1/2Bo (F1)	3/4F:1/2Bo (BC)	53	51	44	40	188
F	1/2F:1/2Ho (F1)	3/4F:1/2Ho (BC)	58	58			116
J	1/2J:1/2Ba (F1)	3/4J:1/4Ba (BC)			40	40	80
J	1/2J:1/2Bo (F1)	3/4J:1/2Bo (BC)	50	34	33	35	152
J	1/2J:1/2Ho (F1)	3/4J:1/2Ho (BC)	32	58			90
S	1/2S:1/2Ba (F1)	3/4S:1/4Ba (BC)			38	18	56
S	1/2S:1/2Bo (F1)	3/4S:1/2Bo (BC)	56	39	24	37	156
S	1/2S:1/2Ho (F1)	3/4S:1/2Ho (BC)	42	74			116
Three-breed crosses							
1/2F:1/2Bo (F1)	1/2J:1/2Bo (F1)	1/4F:1/4J:2/4Bo[3]	136				136
1/2F:1/2Bo (F1)	1/4F:1/4J:2/4Bo	3/8F:1/8J:4/8Bo	47				47
1/2F:1/2Bo (F1)	3/4J:1/4Bo (BC)	2/8F:3/8J3/8Bo[3]	41				41
3/4F:1/4Bo (BC)	1/2J:1/2Bo (F1)	3/8F:2/8J:3/8Bo[3]	15				15
3/4F:1/4Bo (BC)	1/4F:1/4J:2/4Bo	4/8F:1/8J:3/8Bo	26				26
3/4F:1/4Bo (BC)	5/8J:3/8Bo (SC)	6/16F:5/16J:5/16	15				15
1/2J:1/2Bo (F1)	1/4F:1/4J:2/4Bo	1/8F:3/8J:4/8Bo	40				40
Total			1993	1215	852	897	4957

[1] Bo, Boran; Ba, Barca, Ho, Horro, F, Friesian; J, Jersey; S, Simmental; the fraction values are breed contribution to the genotype class.

F1, first filial generation; F2, second filial generation; BC, first backcrosses; SC, second generation crosses

[3] include progeny records from the reciprocal matings

Birth weight (BWT), weaning weight (WWT), preweaning average daily gain (ADG) and yearling weight (YWT) recorded on 4969 calves were available, after editing 4957 BWT, 4245 WWT and ADG and 3330 YWT records were used from the three purebred and 38 crossbred groups.

2.2.2 Statistical methods

Least-squares means of the genotypes to be used in the final regression analyses were estimated in two preliminary steps. First, using the SAS-GLM procedure (SAS, 1999), environmental effects to be fitted in the second step were identified. The fixed effects fitted in the analysis of all traits included genotype (41 groups), sex (male & female), contemporary group of station-birth year-season (195, 189 and 184 levels for BWT, WWT and YWT, respectively) and parity (1, 2, 3 and 4+), while weaning and yearling ages were fitted as covariates for WWT and YWT, respectively. All main effects had a significant ($P<0.01$) influence on all the traits and were kept for subsequent analyses, whereas, no interactions were significant ($P>0.05$).

In the second step, the least-squares means of the 41 genotypes were estimated using the ASREML program of Gilmour *et al.* (2000). In this step, an animal model was fitted with the fixed effects (including genotypes) selected from step one, plus animal and maternal associated effects as random effects. The covariance between animal and dam additive effects was also included. Analysis in this step is expected to minimize the underestimation of the standard error of the parameters through the consideration of the animal relationships (Komender and Hoeschele, 1989) and to correct possible influences of maternal effects on early growth traits (Meyer, 1992).

In the third step, using SAS-REG procedures (SAS, 1999), crossbreeding parameters were estimated. Least-squares means of genotypes for each trait were regressed on crossbreeding coefficients as defined by the five genetic models (to be described). A weighted multiple regression analysis was conducted, where the reciprocal of the variances of genotype class means (V^{-1}) was used as a weighting factor to account for the differences in the number of observations as was used by

Grosshans *et al.* (1994), Wolf *et al.* (1995) and Kahi *et al.* (2000). The variances used are the diagonal elements from the animal model corresponding to the genotype classes (Komender and Hoeschele, 1989). However, the most appropriate weighting factor would be the use of the full variance and covariance matrix associated with genotype means derived from the animal model. This was, however, not possible to obtain from the software used in this analysis. On the other hand, comparison of estimates and their standard errors obtained from the two-step analysis were approximately the same to those obtained from the direct fitting of crossbreeding effects as covariates in the animal model. This might indicate that the residual covariance between the genotypes might not be important in influencing the crossbreeding parameters as well as the comparison of different genetic models in this study.

A general model used for the estimation of crossbreeding parameters from each model can be written in the following form:

$$f = Kp + e$$

$$\hat{p} = (K'V^{-1}K)^{-1}K'V^{-1}f$$

$$\mathrm{var}(\hat{p}) = (K'V^{-1}K)^{-1}$$

where f is the vector of least-squares mean values of genotypes, K is the matrix of crossbreeding coefficients of the genotype classes as defined by each genetic model, $\hat{p}$ is the vector of weighted least-squares estimators of crossbreeding parameters and V^{-1} is the variance of genotype class means.

The test for significance between each epistatic model and the dominance model was done by considering the reduction in error variance due to the addition of epistatic parameter(s), using the F statistic as in Kinghorn (1983). In addition to this, a comparison of the goodness of fit across traits between the best fitting epistatic model and others was also done. This comparison was made by carrying out a single factor analysis of variance, where models were considered as effects and traits as replications, on the arcsine transformed square root values of the adjusted R^2 (as variable), following the procedure of Kinghorn (1987). Also, sampling correlations between parameters for each model were calculated and compared.

2.2.3 Genetic models

The five genetic models tested differ from each other by their definition of epistasis or in terms of the restrictions applied. The first model used is the dominance model (M1), which includes only parameters of additive breed differences (g) and dominance effects (d/h). This model is used as a base for testing the significance of the models with epistatic effects. The second model (M2) tested is the Dickerson model (Dickerson, 1969, 1973), which additionally includes epistasis or recombination loss(r) for each combination of crosses. The recombination loss of the Dickerson's model measures the epistatic loss already confounded in the F_1 heterosis.

The third (M3) and fourth (M4) models are derived from a general crossbreeding model for two source populations described by Grosshans *et al.* (1994) and Wolf *et al.* (1995). In these models, only one form of interaction between two loci in two breeds were assumed to cause the epistatic effects. In the two models epistatic effects are assumed to be caused by additive x dominance and dominance x dominance gene interactions only.

The fifth model (M5) is based on the hypothesis 'x 'of Kinghorn (1980), where a single epistatic (e_x) parameter is defined for all crossbreeding groups. The epistatic effects in this model are based on the assumption of additive x additive gene interactions.

For a detailed discussion on the hypothesis and re-parameterisation procedures used to derive the five genetic models, see Dickerson (1969, 1973), Kinghorn (1980, 1982, 1987), Grosshans *et al.* (1994) and Wolf *et al.* (1995). After applications of the assumptions and hypothesis described above, the regression equation used for the estimation of crossbreeding parameters from each model can be written as follow:

1) $Gm_i = m + \alpha_i g_i + \delta_{ij} h_{ij} + \varepsilon$ M1

2) $Gm_i = m + \alpha_i g_i + \delta_{ij} h_{ij} + (4\alpha_i \alpha_j - \delta_{ij}) r_{ij} + \varepsilon$ M2

3) $Gm_i = m + \alpha_i g_i + \delta_{ij} d_{ij} + (\alpha_i - \alpha_j)\delta_{ij} ad_{ij} + \varepsilon$ M3

4) $Gm_i = m + \alpha_i g_i + \delta_{ij} d_{ij} + \delta_{ij}{}^2 dd_{ij} + \varepsilon$ M4

5) $Gm_i = m + \alpha_i g_i + \delta_{ij} d_{ij} + [\sum 2(\alpha_i \alpha_j)] e_x + \varepsilon$, M5

where, Gm_i is the i^th^ genotype mean for the trait of interest. m is an intercept. h_{ij} or d_{ij} is heterotic or dominance effect due to crossing the i^th^ with j^th^ breed. r_{ij} is the recombination loss as defined by Dickerson (1969, 1973). aa_{ij}, ad_{ij} and dd_{ij} are epistatic effects due to additive x additive, additive x dominance and dominance x dominance interactions, respectively, involving two loci genes of an individual coming from two breeds (Wolf *et al.*, 1995). e_x is the epistatic loss as defined by Kinghorn (1980, 1982). ε is random vector of residuals. α_i is the proportion of breed i's contribution to the calf, which was calculated as $\alpha_i = (1/2\alpha_i^S + 1/2\alpha_i^D)$. δ_{ij} designates the probability that at a randomly chosen locus of an individual, one allele comes from the i^th^ breed and the other from the j^th^ breed, which was derived as $\delta_{ij} = \alpha_i^S \alpha_j^D + \alpha_j^S \alpha_i^D$, where α_i^S and α_i^D are the contributions of breed i in the sire and dam of an individual, respectively (Wolf *et al.*, 1995). The coefficients for g and h or d are equal in all models and the difference between the models is in the epistatic coefficients as shown in the equations.

The additive breed effects of Ba, Ho, F, J and S were fitted as a deviation from the Bo breed in all models. The Bo effect was included in the intercept (m). The dominance and epistatic effects fitted in each model refer to the crosses of F x Ba, F x Bo, F x Ho, J x Ba, J x Bo, J x Ho, S x Ba, S x Bo and S x Ho. In the three-breed crosses, dominance and epistatic effects due to the interactions of genes from two *Bos taurus* breeds, were assumed negligible. This was done because the proportional contribution of *Bos taurus* breeds to the individual in this class is very low. In general, for each model effects that were not described were assumed to be negligible or set to be zero.

2.3 Results

2.3.1 Least-squares means for genotypes

Least-squares means and standard errors for traits used for the evaluation of the different genetic models are presented in Table 2.2. The overall means and coefficients of variation were 24.8±0.5 kg and 21% for BWT, 98.0±0.3 kg and 30% for WWT, 409.0±1.4 g and 39% for ADG, 138.1±0.3 kg and 24% for YWT, respectively. Differences between genotypic means were significant ($P<0.01$) in all traits. The differences between minimum and maximum genotypic mean values were 10.5 kg in BWT, 27.2 kg in WWT, 134.9 g in ADG and 33.7 kg in YWT. These differences were further partitioned into different genetic components using the different genetic models, with the assumption of a linear relationship between performance and the underlying genetic effects.

2.3.2 Goodness of fit and comparison of dominance and epistatic models

The adjusted R-squared values for all models and the F-statistics for testing the significance of the epistatic models are shown in Table 2.3. All models tested had high R-squared values in all traits, averaging 93% over traits. Fitting the epistatic effects in addition to additive and dominance effects improved the R^2 values in all epistatic models. The significant improvement in the R^2 values was also reflected in the F values calculated (Table 2.3). Except for M3 in BWT, all models fitted the observed genotypic means significantly better than M1 for all traits. The R^2 values from M2 were higher than estimates from other models for almost all traits.

Further, the analysis of variance conducted on the R^2 values of the epistatic models across traits indicated that the mean differences in R^2 between models M2 and M3 (4.3%) and M5 (2.7%) were significant ($P<0.05$); but the difference between M2 and M5 (1.5%) was not significant.

Table 2.2 Least-squares means and standard errors for birth (BWT), weaning (WWT) and yearling (WWT) weights and preweaning average daily gain (ADG) for the different genotypes

Genotypes[1][2]	Traits						
Pure breeds	n	BWT (kg)	n[3]	WWT (kg)	ADG (g)	n	YWT (kg)
Boran (Bo)	257	22.9±0.3	209	95.2±1.3	401.4±7.1	185	129.3±1.8
Barca (Ba)	130	22.6±0.5	109	92.0±1.9	385.3±10.0	98	124.5±2.5
Horro (Ho)	204	19.9±0.4	176	88.0±1.6	377.6±8.4	152	123.0±2.2
Two- breed crosses							
F x Ba	114	25.5±0.4	103	114.7±1.8	492.9±9.6	91	155.8±2.3
F x Bo	437	25.7±0.3	374	111.9±1.0	479.6±5.6	256	156.7±1.5
F x Ho	126	22.9±0.4	114	104.5±1.7	453.7±9.2	105	148.2±2.2
J x Ba	93	21.6+0.5	88	99.2±1.9	430.6±10.3	75	141.7±2.5
J x Bo	262	21.5±0.3	248	102.6±1.2	452.3±6.3	205	146.9±1.6
J x Ho	119	19.9±0.4	107	94.3±1.8	413.1±9.6	94	134.3±2.3
S x Ba	80	24.8±0.5	76	110.4±2.0	478.9±11.1	60	148.6±2.8
S x Bo	236	26.2±0.3	223	113.5±1.3	485.3±6.7	184	155.4±1.7
S x Ho	132	23.9±0.4	119	105.0±1.7	452.4±9.0	97	147.6±2.2
FBa x FBa	96	28.2±0.6	77	95.7±2.2	375.4±11.7	56	132.8±3.0
FBo x FBo	325	27.9±0.4	257	101.7±1.3	411.3±6.9	196	138.3±1.8
FHo x FHo	93	26.1±0.6	75	96.2±2.2	391.5±11.7	62	135.7±2.9
JBa x JBa	90	23.3±0.5	77	87.5±2.2	358.0±11.7	60	130.0±3.0
JBo x JBo	278	22.8±0.4	227	94.5±1.4	398.3±7.3	166	134.2±1.9
JHo x JHo	80	22.0±0.6	68	89.8±2.4	376.1±12.6	53	131.4±3.3
SBa x SBa	66	27.6±0.6	49	92.2±2.7	364.2±14.2	43	129.1±3.4
SBo x SBo	160	28.8±0.4	124	98.0±1.7	385.7±9.1	94	136.4±2.4
SHo x SHo	82	25.9±0.6	67	94.0±2.3	375.3±12.1	55	128.7±3.1
FBo x FFBo	81	28.9±0.7	65	106.5±2.6	429.5±13.8	45	148.7±3.8
JBo x JJBo	33	21.9±0.9	30	91.9±3.4	388.2±18.0	21	137.2±4.8
SBo x SSBo	25	27.0±1.1	25	97.4±4.1	385.8±21.8	18	137.0±6.2
FFBo x FFBo	14	28.6±1.2	8	108.3±6.0	444.4±32.1	7	136.3±7.6
F x FBa	70	29.3±0.6	68	105.7±2.2	423.5±12.0	59	143.9±2.9
F x FBo	188	29.7±0.4	170	109.6±1.5	444.3±7.9	138	146.3±2.0
F x FHo	116	28.4±0.5	103	103.0±1.9	416.3±9.9	80	141.2±2.5
J x JBa	80	21.3±0.6	68	89.2±2.3	377.4±12.0	58	130.3±2.9
J x JBo	152	21.1±0.5	129	91.2±1.7	390.3±8.9	99	131.5±2.3
J x JHo	90	21.0±0.5	79	89.3±2.1	379.5±11.1	58	128.6±2.9
S x SBa	56	30.1±0.7	46	99.8±2.7	391.4±14.3	36	136.9±3.6
S x SBo	156	30.4±0.4	129	103.1±1.7	403.7±8.7	89	140.7±2.3
S x SHo	116	28.8±0.5	93	100.2±2.0	397.0±10.4	70	137.9±2.6
Three- breed crosses							
FBo x JBo	136	25.4±0.5	127	95.7±2.0	390.5±10.5	91	138.7±2.7
FBo x JBoFBo	47	26.1±0.7	37	102.7±3.0	424.7±16.2	13	142.3±5.7
FBo x JJBo	41	24.7±0.8	29	96.4±3.4	398.0±18.4	20	138.2±4.9
FFBo x JBo	15	26.2±1.1	15	106.5±4.6	449.6±24.5	15	147.8±5.5
FFBo x JBoFBo	26	25.6±0.9	19	101.9±4.1	427.2±21.7	11	139.1±6.1
FFBo x JJBoJBo	15	25.7±1.1	13	100.5±4.8	418.7±25.8	7	139.8±7.6
JBo x JBoFBo	40	22.6±0.8	25	98.8±3.6	425.2±19.3	8	123.9±6.9
Overall mean	4957	24.8±0.1	4245	98±0.3	409±1.4	3330	138±0.3
CV%		21.3		29.9	38.9		24.1
R^2		45		72	72		73

[1] Bo, Boran; Ba, Barca, Ho, Horro, F, Friesian; J, Jersey; S, Simmental and the sire breeds given before the dam breeds.

[2] Number of records for WWT and ADG

Table 2.3 Adjusted R-squared values and F-statistics for different genetic models (M1-M5)

Traits[1]		M1	M2	M3	M4	M5
BWT	R^2	0.95	0.98	0.96	0.97	0.98
	F	-	4.3**	1.40	2.8*	35.7**
WWT	R^2	0.86	0.97	0.93	0.96	0.93
	F	-	13.3**	3.44*	8.64**	28.5**
ADG	R^2	0.77	0.96	0.88	0.94	0.91
	F	-	15.4**	3.4*	9.0**	43.8**
YWT	R^2	0.89	0.95	0.93	0.93	0.93
	F	-	4.4**	2.5*	2.7*	15.5**

[1] BWT, birth weight; WWT, weaning weight; ADG, average daily gain; YWT, yearling weight.

*, $P< 0.05$; **, $P<0.01$

2.3.3 Sampling correlations between parameters

Sampling correlations between parameters were also calculated to assess the level of multicollinearity of estimates. The results from this analysis showed that all models produced a similar pattern of correlations between parameters in all traits. In addition, the correlations between parameters containing the three *Bos taurus* breeds and their crosses with the three *Bos indicus* breeds were similar in all trait and the correlations between parameters containing different breeds and breed crosses were negligible in all models. Therefore, the selected correlation estimates between parameters involving Ba, Ho and F breeds for weaning weight for models M1, M2 and M4 are only presented as an example (Tables 2.4 and 2.5).

In general, the sampling correlations between some crossbreeding parameters increased as the number of parameters increased in the model (See Table 2.4 vs 2.5). Since the coefficients of the crossbreeding parameters were linearly related in one way or the other, complete independency was not expected. However, different model assumptions cause different levels of sampling correlations between parameters for each model. For instance, in comparison with M1 estimates from M2 and M4 had higher sampling correlations. Though M4 gave nearly a similar fit to that of M2, the sampling correlations between parameters were much higher in M4 (Table 2.5).

Table 2.4 **Sampling correlations between crossbreeding parameters for weaning weight under model M1.**

Genetic effects	g_{Ba}	g_{Ho}	g_F	h_{FxBa}	h_{FxBo}
g_{Ba}^1	-				
g_{Ho}^1	0.35	-			
g_F^1	0.31	0.35	-		
h_{FxBa}^2	-0.38	-0.02	-0.50	-	
h_{FxBo}^2	0.21	0.23	-0.43	0.43	
h_{FxHo}^2	-0.02	-0.33	-0.54	0.35	0.47

[1] g_{Ba}, g_{Ho} and g_F are breed additive differences as a deviation from Boran (Bo) for Barca (Ba), Horro (Ho) and Friesian (F)

[2] h_{FxBa}, h_{FxBo},h_{FxHo} are heterotic effects for crossbred types shown by the subscript letters.

Table 2.5 **Sampling correlations between crossbreeding parameters for weaning weight under model M2 (above diagonal) and M4 (below diagonal)**

Genetic effects	g_{Ba}	g_{Ho}	g_F	h_{FxBa}	h_{FxBo}	h_{FxHo}	r_{FxBa}	r_{FxBo}	r_{FxHo}
g_{Ba}^1	-	0.37	0.22	-0.27	0.19	0.01	-0.12	0.11	0.01
g_{Ho}^1	0.37	-	0.24	0.01	0.21	-0.22	0.01	0.12	-0.09
g_F^1	0.12	0.13	-	-0.60	-0.62	-0.63	-0.41	-0.55	-0.46
h_{FxBa}^2	-0.11	0.02	-0.81	-	0.54	0.45	0.07	0.44	0.33
h_{FxBo}^2	0.09	0.11	-0.87	0.78	-	0.56	0.37	0.43	0.41
h_{FxHo}^2	0.02	-0.07	-0.84	0.73	0.81	-	0.31	0.47	0.11
r_{FxBa}^2	0.06	-0.02	0.71	-0.97	-0.68	-0.63	-	0.31	0.23
r_{FxBo}^2	-0.07	-0.08	0.83	-0.73	-0.98	-0.76	0.64	-	0.34
r_{FxHo}^2	-0.02	0.03	0.75	-0.65	-0.73	-0.97	0.57	0.68	-

[1] g_{Ba}, g_{Ho} and g_F are breed additive differences as a deviation from Boran for Barca (Ba), Horro (Ho) and Friesian (F)

[2] h_{FxBa}, h_{FxBo},h_{FxHo} and r_{FxBa}, r_{FxBo} r_{FxHo} are heterosis and recombination effects for cross types indicated by the subscript letters and read 'd' and 'dd' instead of 'h' and 'r' for M4

The correlations between the breed additive effects of *Bos indicus* breeds with both dominance and epistatic parameters were low in all models, whereas the correlations between the breed additive effects of *Bos taurus* breeds, shown here for Friesian, with the dominance and epistatic parameters ranged from intermediate to high. Since all *Bos taurus* breeds were represented as only crossbred in the data used, higher sampling correlations and lower efficiency in the estimation of breed additive effects for these groups was expected. In general, high correlation values between parameters for some models indicate that the genotypes used to derive both breed additive and non-additive coefficients are not sufficient to disentangle effectively the parameters according to the model assumptions. In other words, the linear dependences between parameters are high, therefore, estimates would be unstable and have high standard errors (Sölkner and James, 1990).

2.3.4 Trend in parameter estimation

All five genetic models showed a similar trend in parameter estimation for all traits; therefore, only estimates for weaning weight are presented for illustrative purposes (Table 2.6).

The intercept and the breed additive estimates for the two *Bos indicus* breeds showed relatively small changes in the five models (Table 2.6). On the other hand, the three *Bos taurus* breeds additive (g_F, g_J and g_S) estimates obtained from the five models showed large fluctuations both in magnitude and for some estimates also change in sign. As discussed earlier in association with the sampling correlations between parameters, the available genotypes were not sufficient to provide accurate estimates on breed additive differences for *Bos taurus* breeds compared to models that contained purebred information (Sölkner and James, 1990).

Dominance (heterosis) and epistatic estimates obtained from the five models were all different. Despite differences in magnitude, the dominance estimates from the four models (M1, M2, M3 and M5) are all positive and significant. Model 4 showed a unique behaviour in its parameter estimation. The estimates from this model showed differences both in sign of values and magnitude compared to the other genetic models. All crossbreeding parameters estimated from M2 had smaller values and lower standard errors than the other epistatic models (Table 2.6).

Table 2.6 Crossbreeding parameter estimates for weaning weight (kg) using different genetic models

	Models				
Effects[2]	M1	M2	M3	M4	M5
Bo	93.6±1.9	95.2±0.9	95.4±1.5	95.2±1.0	95.7±1.4
g_{Ba}	-4.5±3.3	-3.1±1.5*	-5.4±2.5*	-3.8±1.8	-5.2±2.3*
g_{Ho}	-6.2±3.0*	-7.1±1.4**	-7.1±2.2**	-7.0±1.6**	-7.2±2.1**
g_F	6.6±3.7	15.8±2.2**	-7.9±4.7	25.3±4.2**	13.1±2.9**
g_J	-13.7±4.0**	-12.0±2.4**	-15.9±5.0**	-8.7±4.6	-7.1±*
g_S	-4.3±-4.1	5.4±2.5*	-26.4±6.3**	20.8±5.4**	1.3±3.0
$h_{F \times Ba}$[3]	17.4±3.5**	13.1±1.8**	24.2±3.2**	-44.3±10.0**	23.6±2.7**
$h_{F \times Bo}$[3]	15.0±2.7**	9.0±1.4**	20.9±2.7**	-22.9±8.3*	21.2±2.2**
$h_{F \times Ho}$[3]	10.3±3.3**	4.7±1.7*	16.6±3.1**	-35.7±10.0**	16.4±2.6**
$h_{J \times Ba}$[3]	13.4±3.8**	11.8±1.9**	13.0±3.4**	-10.3±10.6	19.6±2.9**
$h_{J \times Bo}$[3]	15.6±2.9**	13.3±1.5**	15.4±3.0**	2.3±8.8	21.8±2.3**
$h_{J \times Ho}$[3]	11.5±3.6**	8.8±1.8**	10.6±3.3**	2.5±10.8	17.6±2.7**
$h_{S \times Ba}$[3]	19.4±3.9**	14.1±2.0**	30.2±4.1**	-49.7±12.7**	26.2±3.0**
$h_{S \times Bo}$[3]	21.3±3.1**	15.6±1.6**	31.2±3.6**	-39.4±11.7**	27.7±2.4
$h_{F \times Ho}$[3]	16.9±3.5**	10.7±1.8**	26.8±3.8**	-36.8±12.4**	23.7±2.4**
$r_{F \times Ba}$[4]		-25.4±3.4**	-21.7±13.4	53.1±8.6**	
$r_{F \times Bo}$[4]		-10.5±2.2**	-38.9±10.1**	26.9±6.4**	
$r_{F \times Ho}$[4]		-13.2±3.4**	-27.8±12.2*	35.9±8.5**	
$r_{J \times Ba}$[4]		-11.1±3.5**	-2.2±13.8	20.6±9.0*	
$r_{J \times Bo}$[4]		-3.4±2.4	1.8±10.8	9.4±6.8	
$r_{J \times Ho}$[4]		0.1±3.7	-9.1±13.3	4.5±9.2	
$r_{S \times Ba}$[4]		-22.3±4.0**	-41.7±16.9*	56.4±10.7**	
$r_{S \times Bo}$[4]		-15.9±2.9**	-46.3±13.8**	47.3±9.3**	
$r_{F \times Ho}$[4]		-11.1±3.6**	-51.9±14.6**	39.7±10.2**	
e_X					-21.6±4.0

* significant at: *, $P<0.05$; **, $P<0.01$

[2] g_{Ba}, g_{Ho}, g_F, g_J, and g_S are breed additive differences as a deviation from the Boran (Bo) breed for Barca (Ba), Horro (Ho), Friesian (F) and Jersey (J) and Simmental (S). h, r and e refer to heterosis, recombination and epistasis loss for cross types indicated by the subscript letters.

[3] read 'd' instead of 'h' for model 3 to 5.

[4] read 'ad' or 'dd' instead of 'r' for models 3 and 4 respectively.

2.4 Discussion

The models that include epistasis fit significantly ($P<0.01$) better than the dominance models for all traits (Table 2.3). This implies that breed additive and dominance effects are not sufficient to describe the observed genetic differences between different generations of crosses involved in this study.

Comparisons among different epistatic models across traits also showed significant differences. The differences between M2 and M3 or M5 were significant. Further examination of the correlation coefficients generated by the different models revealed that models are different in their efficiency of parameter estimation. For example, M4 was not significantly different in model fit compared to M2, but its parameter estimates showed high correlations and correspondingly high standard errors on estimates. It could, therefore, not be considered the best model, particularly for parameter estimation. Among the four epistatic models tested, model M2 have the lowest correlations between parameters and correspondingly low standard errors on estimates. Even estimates from this model could not be considered of high accuracy. As demonstrated by Sölkner and James (1990) the genetic groups without all purebreds involved in the crossing are not efficient for the estimation of the crossbreeding parameters with high accuracy. Other models, such as M3 and M4, which generated high correlations between parameters, require much more diverse genotypes for accurate estimation of parameters. Sölkner (1991) has shown that over 15 genotypes, including the purebred parents from two breed crosses, were needed for efficient estimation of parameters with a complex epistasis structures.

Among the epistatic models tested, the two models, M2 and M5, are interrelated. Their epistatic effects are based on the assumption of additive x additive gene interactions. Except for model M5, which is based on single epistatic parameters for all types of crosses, M2 gave the highest fit and lower estimates with relatively better accuracy. This result seems to support the hypothesis that additive x additive interaction is the main cause for epistatic loss of performance in crossbred animals (Kinghorn, 1983, 1987). However, since all models were derived through the application of some form of restriction, as indicated by Wolf *et al.* (1995), it is difficult to provide a unique biological interpretation for the epistatic parameters from different models. Wolf *et al.* (1995) demonstrated how to derive additive x additive epistatic coefficients of Kinghorn's model, from assumed dominance x dominance interactions and restrictions applied to derive coefficients for these effects.

In general, accurate estimation of different crossbreeding parameters requires large numbers of crossbred groups and proper design in a crossbreeding experiment (Sölkner and James, 1990; Sölkner, 1991). Most often, the simultaneous estimation of all crossbreeding parameters from field data is practically impossible. The total number of parameters that could be estimated at any given analysis would be equal or less than the number of crossbred groups available for the study. As suggested by Wolf *et al.* (1995), the alternative option would be to choose a submodel with a moderate number of parameters, which give the best fit among all submodels with an equal number of parameters. This recommendation was followed in this study and model M2 or alternatively a model that provide separate dominance and additive x additive epistatic estimates (tested, but not shown here) could be considered a suitable model for the analysis of the data used in this study. As shown by Wolf *et al.* (1995), M2 and the additive x additive epistatic models could be considered equivalent. The difference is that M2 measures epistatic effects that are already confounded in heterosis (Dickerson, 1969, 1973), whereas the latter estimates both dominance and epistatic effects separately (Grosshans *et al.*, 1994; Wolf *et al.*, 1995). However, both model estimates can be linearly transformed into one another i.e. heterosis of Dickerson model is equal to dominance plus half the epistatic estimates of the additive x additive model (Wolf *et al.*, 1995).

2.5 Conclusions

It could be concluded that the model with only breed additive and dominance effects is not sufficient to describe the observed genotypic differences between the crosses involved in this study. Model M2 that gave the best-fit, intermediate correlations between parameters and estimates with lower standard errors on all traits, could be considered the most suitable model for the predictions of untested genotypes from the breeds involved in this and other similar studies.

The major implications of the findings of this study is that the breakdown of the positively associated epistatic genes of parental origin seems the main cause for the lower growth performance in the later generations of *Bos taurus* x *Bos indicus* crosses. Hence, epistasis appears to be an important genetic effect that should not be ignored in the evaluation of performances of *Bos taurus* x *Bos indicus* crosses, particularly when the aim of the exercise is the prediction of the performances of untested genotypes for the decision of future breeding programs.

Chapter 3

Early growth performance of *Bos taurus* x *Bos indicus* cattle crosses: II. Estimation of individual crossbreeding effects

3.1 Introduction

In order to plan a sound crossbreeding program, information on the relative performances of breeds and their crosses, especially under varying environmental conditions are needed. The first step in this process is to obtain a precise knowledge of the extent of variation attributed to additive and non-additive gene actions. In such a study, examining of the performance of purebreds, F_1, F_2 and other advanced generations of crosses allows a separate estimation of various genetic effects influencing performance (Dickerson, 1969,1973).

Studies that reported on growth performance of *Bos taurus* x *Bos indicus* crosses, particularly from tropical Africa are fairly limited (e.g. Kebede and Galal, 1982; Thorpe *et al.*, 1993; Banjaw and Haile-Mariam 1994; Rege *et al.*, 1994; Kahi *et al.*, 1995). A few of these studies have reported separate estimates for the effects of breeds and heterosis on the growth performance of crossbred animals (e.g. Thorpe *et al.*, 1993; Rege *et al.*, 1994; Kahi *et al.*, 1995). Furthermore, in most studies, the number of breeds and breed cross combinations evaluated is limited. They consequently lack the diversity to represent a large variety of breeds and environments encountered in tropical Africa. More information on various traits from different breeds and breed crosses is therefore needed to design an efficient breeding program for a specific environment.

This study reports the results of a crossbreeding experiment that was initiated in Ethiopia during the early 1970s. The program provided information on the relative performance of three indigenous *Bos indicus* breeds (Boran, Barca and Horro) and their crosses with three exotic *Bos taurus* breeds (Friesian, Jersey and Simmental) for low input dairy cattle production systems in Ethiopia. Early growth traits of calves from birth to one year of age are reported, and estimates are given for individual additive breed, heterotic and recombination effects.

3.2 Material and methods

3.2.1 Data source and cattle management

The data of this study were obtained from a long-term crossbreeding experiment conducted from 1974 to 2000 at the four experimental stations of the Ethiopian Agricultural Research Organization. The data used included contemporary information from 38 crossbred and three purebred genotypes produced from the mating of three European breeds (Friesian, Jersey and Simmental) with three *Bos indicus* breeds (Boran, Barca and Horro). A total of 61 Friesian (F), 51 Jersey (J) and 43 Simmental (S) bulls were used at the four stations for the duration (25 years) of the experimental period. Likewise, 36 Boran (Bo), 17 Barca (Ba) and 24 Horro (Ho) bulls were used to produce their respective purebreds. Bulls representing each of the *Bos taurus* breeds were distributed across the herds in a balanced manner, i.e for each breed, the same bull semen was used in all four herds to avoid possible confounding of the bulls with herd effects within the breed. A detailed description on experimental environments and cattle management has been given in Chapter 2.

3.2.2 Traits and statistical analyses

The traits studied were birth weight (BWT), weaning weight (WWT), preweaning average daily gain (ADG) and yearling weight (YWT). The total number of records used in the analysis of each trait was: 4957 for BWT, 4245 for WWT and ADG and 3330 for YWT.

In Chapter 2, the merit of the different crossbreeding models were investigated when using these data. Finally, the Dickerson's model fitting an additive breed effect, heterosis and recombination loss (Dickerson, 1969, 1973), which gave the best fit among others, was used for estimating the crossbreeding parameters reported in this study. The full mixed model applied for the analysis of each trait was as follows:

$$\mathbf{y} = \mathbf{X}_1\mathbf{b}_1 + \mathbf{X}_2\mathbf{b}_2 + \mathbf{Za} + \mathbf{Wd} + \mathbf{e},$$

where $\mathbf{y}$ is a vector of observations for the traits of interest (BWT or WWT or ADG or YWT), $\mathbf{b}_1$ is a vector of fixed effects (overall mean, sex, dam parity and herd-birth year-season effects and also weighing age for WWT and YWT), $\mathbf{a}$ is a vector of random animal effects, $\mathbf{d}$ is a vector of random maternal effects, $\mathbf{X}_1$, $\mathbf{Z}$ and $\mathbf{W}$ are incidence matrices relating records to fixed effects, random direct animal and maternal effects, respectively. $\mathbf{X}_2$ is a matrix of coefficients relating fixed breed additive, heterosis and recombination effects to the individual calf record. The analysis of each trait was carried out using the ASREML program of Gilmour *et al.* (2000).

The fixed breed additive effects (g_i) fitted were g_{Ba} g_{Ho} g_F g_J and g_S for proportions of the Ba, Ho, F, J and S breeds in the calf, while the effect of the Bo breed component, g_{Bo}, was included in the overall mean. Heterotic (h_{ij}) and recombination (r_{ij}) effects were fitted for the F x Bo, F x Ba, F x Ho, J x Bo, J x Ba, J x Ho, S x Bo, S x Ba and S x Ho crosses. The crossbreeding effects due to maternal or paternal genotypes were assumed negligible in this analysis. Because of the very small breed content of F and J in three-breed composites, heterotic and recombination effects for the F x J were also considered negligible. The coefficients of breed additive (g_i), heterosis (h_{ij}) and recombination loss (r_{ij}) for each calf were derived following the procedure of Wolf *et al.* (1995). The following equations were used: $g_i = 1/2(\alpha_i^s + \alpha_i^d)$, $h_{ij} = \alpha_i^s\alpha_j^d + \alpha_j^s\alpha_i^d$ and $r_{ij} = 4g_ig_j - h_{ij}$, where, α_i^s and α_i^d denote the gene proportion of breed i in the sire and dam of the animal, respectively.

One of the main reasons for estimating crossbreeding parameters is to predict the performance of untested genotypes, without actually producing the animals, in order to make a choice of breeding systems that would give maximum benefit to the producers (Dickerson, 1969, 1973; Kinghorn and Vercoe, 1989). To illustrate this, predictions were made for selected crosses of the Boran with the Friesian (F), Jersey (J) and Simmental (S) breeds and purebreds. The Boran was chosen because of its superior performance compared to the other two indigenous breeds in this study as well as in previous reports (Kebede and Galal, 1982). The genotypes for which growth performance were predicted, were: purebred Bo, 3/4Bo:1/4(F or J or S), F_1(1/2Bo:1/2F or J or S), F_2(1/2Bo:1/2F or J or S), 3/8Bo:5/8(F or J or S) synthetic, 3/8Bo:5/8(F or J or S) 1/4Bo:3/4(F or J or S), 1/4Bo:3/4(F or J or S) synthetic and purebred F, J and S. These genotypes were chosen because they are commonly produced types in several *Bos taurus* x *Bos indicus* crossbreeding programs in the tropics (e.g. McDowell *et al.*, 1996). Breeding strategy and genotypes for which growth performances were predicted are presented in Table 3.1.

Table 3.1 Breeding strategy and genotypes for which growth performances were predicted

		Expected breed additive contribution (%)[1]		Expected non-additive effects (%)[2]	
Genotype Abbreviations	Breeding strategy	F or J or S	Bo	Heterosis	Recombination loss
Bo	Purebred Boran[3]	0.0	100.0	0.0	0.0
3/4Bo	First backcross to Boran	25.0	75.0	50.0	25.0
F_2	F_2 inter se[3]	50.0	50.0	50.0	50.0
F_1	First cross [3]	50.0	50.0	100.0	0.0
5/8(syn)	5/8 synthetic	62.5	37.5	46.9	46.9
3/4F or J or S	First backcross to F or J or S[3]	75.0	25.0	50.0	25.0
3/4(syn)	3/4*Bos taurus* synthetic	75.0	25.0	37.5	37.5
F or J or S	Purebred *Bos taurus*	100.0	0.0	0.0	0.0

[1] F=Friesian, J=Jersey, S=Simmental, Bo=Boran

[2] Heterosis and recombination loss are calculated as described in the text.

[3] Genotypes actually produced in the experiment

The mean values and standard errors of prediction for each genotype for the traits of interest was computed using the following equations:

$\hat{y} = Ma$; $SE(\hat{y}) = \sqrt{diagonal(MV^{-1}M')}$, (Lynch and Walsh, 1998)

where, $\hat{y}$ is the predicted mean for the genotype under consideration, $SE(\hat{y})$ is the standard error of prediction, M is the matrix of expected genetic contribution (breed additive, heterosis and recombination loss) including a column of one for the mean, a is a vector of estimated crossbreeding parameters including the overall mean and V^{-1} is the inverse matrix of the variance-covariance corresponding to the crossbreeding parameters.

3.3 Results and discussion

3.3.1 Fixed effects

Results of the least-squares analysis of variance for the early growth traits are presented in Table 3.2. Calf sex, dam parity and herd-birth year-season effects were significant (P<0.01) sources of variation in all traits. Males were significantly heavier at all ages and grew faster than female calves during the preweaning period. Weight at all ages showed an increasing trend with dam parity. The difference was, however, only significant between first and second parity born calves. The regression of weight on weighing age was highly significant for WWT (0.19±0.02 kg) at 180 days and YWT (0.15±0.13) at 364 days.

Calf genotype had a significant effect (P<0.01) on all traits. Of the total genotypic variance, the variances accounted for by the decomposed genetic effects (direct breed additive, heterosis and recombination loss) were highly significant (P<0.01) in all traits (Table 3.2). Relative to the total genotypic variance, the direct breed additive variance accounted for the highest percentage in BWT (89.9%) and WWT (46.2%), while the variance due to heterosis was the highest in ADG (49.8%) and YWT (72%). The variance due to the recombination loss was the lowest in all traits.

Table 3.2 **Least-square analysis of variance for weight at birth (BWT), weaning (WWT), yearling (YWT) and preweaning average daily gain (ADG)**

		Means squares of traits			
Source	DF	BWT (kg^2)	WWT (kg^2)	ADG (g^2)	YWT (kg^2)
Sex	1	1868.56***	6547.04***	61766.84***	2995.40**
Parity	3	640.43***	3684.88***	51183.28***	2225.48***
Herd-birth year-season[1]		51.56**	7201.57***	211067.14***	8262.25***
Age		-	15961.70***	-	8756.89***
Direct additive	5	1908.95***	4312.90***	37475.11***	2103.27***
Direct heterosis	9	116.54***	3149.97***	112564.31***	7870.51***
Direct recombination	9	96.95***	1882.52***	76047.04***	947.44**
Residual[1]		15.58	263.28	7690.03	384.94
Overall mean		24.63	98.73	410.73	140.08
CV%		16	16	21	14
R^2		0.45	0.72	0.72	0.73

**, $P<0.01$; ***, $P<0.001$

[1] Herd-birth year-season effects and residual degrees of freedom are 194 and 4730 for BWT, 188 and 4023 for WWT and ADG and 183 and 3101 for YWT, respectively.

The least-squares means for the various genotypes have previously been reported in Chapter 2, Table 2.2. However, because of its relevance to the results discussed in this chapter it is referred again. Selected least-squares contrasts for the group of genotypes indicated that, on average the Bo progeny were significantly heavier at birth (3.0±0.5kg), weaning (7.2±2.1kg) and yearling ages (6.3±2.8kg) and gained more (23.8±10.5g) than the Ho progeny. The difference between Bo and Ba was not significant for all traits (Table 2.2). On the other hand, the F and S crosses (mean of F_1, F_2 and ¾F or S), were significantly ($P<0.01$) heavier at birth (5.3±0.3 and 5.9±0.2kg), weaning (13.1±1.1 and 10.1±1.0kg) and yearling (18.7±1.4 and 14.5±1.6kg) ages and gained (44.0±5.9 and 26.8±6.1g) more than the average performance of the purebred *Bos indicus* cattle, but the growth performance of the Jersey crosses was only significantly ($P<0.01$) different at yearling age (8.7±1.5kg). Comparing the *Bos taurus* breeds, the F and S crosses (average of F_1, F_2 and ¾ crosses), were significantly ($P<0.01$) heavier at birth (5.5±0.2 and 5.8±0.2kg), weaning (11.7±0.9 and 8.7±0.9kg) and yearling ages (10.1±1.2 and

5.8±1.3kg) and gained more (34.8±4.7 and 17.6±5.6g) than the J crosses (Table 2.2).

The overall growth performance of the calves observed in this study is within the range of values reported in the literature for *Bos taurus* x *Bos indicus* cattle, particularly for dairy production in the tropics (e.g. Kebede and Galal, 1982; Thorpe *et al.*, 1993; Rege *et al.*, 1994; Kahi *et al.*, 1995). The higher growth performance observed for the crossbred calves compared to the purebred *Bos indicus* cattle in this study is also consistent with several literature reports on *Bos taurus x Bos indicus* crossbreeding (e.g. Kebede and Galal, 1982; Thorpe *et al.*, 1993; Banjaw and Haile-Mariam, 1994; Rege *et al.*, 1994; Udo *et al.*, 1995).

Comparisons between different generations of crosses (pooled over three *Bos taurus* crosses) indicated that the F_1 crosses were significantly (P<0.01) lighter (2.3±0.4 and 3.1±0.4kg) for BWT, but heavier (P<0.01) (11.8±1.8 and 7.2±1.6kg) for WWT and (15.4±2.4 and 10.9±2.2kg) YWT and gained (P<0.01) more (78.1±9.5 and 57.3±8.8g) than the F_2 and 3/4 *Bos taurus* crosses, respectively. The observed ranking order differences of F_1 vs F_2 or 3/4*Bos taurus* crosses between BWT and the other traits were similar to those reported for other types of *Bos indicus x Bos taurus* crosses (e.g. Thorpe *et al.*, 1993; Rege *et al.*, 1994; Udo *et al.*, 1995).

3.3.2 Crossbreeding parameter estimates

3.3.2.1 Breed additive effects

The estimates of additive breed effects for BWT, WWT, ADG and YWT, expressed as a deviation from the Boran breed, are presented in Table 3.3. Among the *Bos indicus* breeds, the Ho had a significantly (P<0.05) lower breed additive contribution to the calf's performance for all traits as compared to the Bo breed. No significant differences were found between Ba and Bo. Relative to the mean values of Bo, the J additive contribution to the BWT, WWT, ADG, and

YWT of calves were 16 % (P<0.01), 13% (P<0.01), 11% (P<0.05) and 7.5% (P>0.05) lower, respectively. On the other hand, the F's breed additive contribution to the BWT, WWT, ADG, and YWT of calves were 39.3% (P<0.01), 16.5% (P<0.01), 9.3% (P<0.05) and 10.3% (P<0.05) higher, respectively. The S breed additive genetic contribution to calves was positive and significant (P<0.01) for BWT only.

The significant breed additive effects of the large *Bos taurus* breeds (F for all traits and S on birth weight over the Bo performance) is in line with the expectation derived from their mature weight differences and is in general agreement with the results reported for other *Bos taurus* x *Bos indicus* crosses in the tropics (e.g. Thorpe *et al.*, 1993; Udo *et al.*, 1995; Hirooka and Bhuiyan, 1995; Kahi *et al.*, 1995). The lower additive contribution of the S to WWT, ADG and YWT traits compared to the F breed is unexpected, when considering its higher additive effects on BWT and compared to other studies as well (e.g. Schoeman *et al.*, 1993). This might, however, show the failure of the S breed to express its potential under a low input system, as is the case in this study. The significant negative additive effects of the J breed on all traits indicate that there will be no weight advantage when crossing it with a larger Zebu breed, like the Boran. The additive breed contributions of the J breed for all traits were even lower than those of the Ho breed, the smallest *Bos indicus* breed used in this study. Rege *et al.* (1994) reported similar negative additive effects on growth traits for the J breed compared to the Ghanaian Gudali breed. In contrast, the same authors reported a positive contribution of the J breed when crossing it with a smaller African *Bos taurus* breed, the Ghanaian Shorthorn.

Table 3.3 **Crossbreeding parameter estimates for birth weight (BWT), weaning weight (WWT), preweaning average daily gain (ADG) and yearling weight (YWT)**

Effects[1]	Traits			
	BWT (kg)	WWT (kg)	ADG (g)	YWT (kg)
m	22.9±0.3	95.2±0.9	401.0±5.2	129.2±1.5
g_{Ba}	-0.3±0.6	-3.2±2.2	-15.8±11.7	-4.9±2.9
g_{Ho}	-3.0±0.5**	-7.0±2.0**	-23.0±10.3*	-6.1±2.6*
g_{F}	9.0±0.8**	15.7±3.1**	37.4±16.5*	13.4±4.2*
g_{J}	-3.6±0.8**	-12.1±3.4**	-46.1±18.0*	-9.7±4.6
g_{S}	10.4±0.8**	5.5±3.5	-25.8±18.6	6.0±4.9
$h_{F \times Ba}$	-1.8±0.5**	13.1±2.4**	80.2±12.9***	22.2±3.1**
$h_{F \times Bo}$	-1.7±0.5**	8.9±1.9**	59.5±10.4***	20.6±2.6**
$h_{F \times Ho}$	-3.0±0.5**	4.7±2.3*	43.9±12.5**	15.0±3.0**
$h_{F \times Z}$[2]	-2.1±0.6**	8.8±2.1*	60.4±11.3**	19.8±2.6**
$h_{J \times Ba}$	0.6±0.6	11.8±2.6**	61.3±14.2**	19.8±3.5**
$h_{J \times Bo}$	0.4±0.5	13.4±2.1**	73.6±11.4**	22.3±2.8**
$h_{J \times Ho}$	0.4±0.6	8.8±2.5**	46.8±13.6**	12.9±3.3**
$h_{J \times Z}$[2]	0.2±0.6	11.8±2.3**	64.8±12.3**	19.5±2.8**
$h_{S \times Ba}$	-3.0±0.6**	14.1±2.8**	98.1±14.9**	18.7±3.7**
$h_{S \times Bo}$	-1.8±0.5**	15.6±2.2**	96.9±11.8**	23.0±2.9**
$h_{S \times Ho}$	-2.6±0.6**	10.6±2.5**	76.1±13.3**	18.6±3.3**
$h_{S \times Z}$[2]	-2.3±0.6**	13.7±2.4**	90.6±12.7**	20.8±2.9**
$r_{F \times Ba}$	3.4±1.1**	-25.5±4.8**	-157.3±25.7**	-23.1±6.5**
$r_{F \times Bo}$	2.8±0.8**	-10.5±3.2*	-71.8±16.8**	-14.4±4.4**
$r_{F \times Ho}$	3.5±1.1**	-13.4±4.8*	-88.4±25.7**	-11.2±6.3
$r_{F \times Z}$[2]	2.6±0.8**	-13.6±3.2**	-88.0±17.1**	-14.4±4.0**
$r_{J \times Ba}$	4.0±1.2**	-11.2±4.9*	-81.8±26.4**	-3.1±6.6
$r_{J \times Bo}$	3.1±0.8**	-3.6±3.4	-37.1±18.4*	-3.5±4.7
$r_{J \times Ho}$	4.7±1.3**	0.1±5.2	-25.5±27.6	7.3±6.9
$r_{J \times Z}$[2]	2.9±0.9**	-4.2±3.4	-39.4±18.4*	-0.1±4.4
$r_{S \times Ba}$	2.8±1.3*	-22.5±5.8**	-133.3±30.9**	-20.1±7.4*
$r_{S \times Bo}$	2.8±0.9*	-15.9±4.0**	-103.3±21.6**	-15.9±5.7*
$r_{S \times Ho}$	1.3±1.2	-11.18±5.1*	-76.4±27.2*	-17.9±6.8*
$r_{S \times Z}$[2]	2.4±1.0*	-16.0±4.0**	-102.2±21.3*	-17.5±4.9**

[1] m=Boran mean; g_{Ba}, g_{Ho}, g_{F} and g_{S} are additive breed effects as a deviation from Boran for Barca, Horro, Friesian, Jersey and Simmental breeds, respectively; $h_{F \times Ba}$ to $h_{S \times Ho}$ and $r_{F \times Ba}$ to $r_{S \times Ho}$ are heterosis and recombination effects for crossing Friesian, Jersey and Simmental with Barca, Boran and Horro breeds, respectively.

[2] $h_{F \times Z}$, and $r_{F \times Z}$, $h_{J \times Z}$ and $r_{J \times Z}$ and $h_{S \times Z}$ and $r_{S \times Z}$ are the average heterosis and epistatic loss for F, J and S crosses, respectively.

*, P<0.05 and **, P<0.01

3.3.2.2 Heterozygosity effects

Estimated direct heterozygosity effects on BWT for all crosses involving the F and S breeds with *Bos indicus* breeds were significant (P<0.01) and negative, with values ranging from –3.0 to –1.7 kg. Estimates for the J crosses were, however, not significant (Table 3.3). The negative heterotic estimates for the F and S crosses for BWT are unexpected and are in contrast to most estimates reported in the literature (e.g. Long, 1980; Arthur *et al.*, 1999). Similar negative heterosis for BWT was, however, also reported in other crossbreeding studies that used *Bos indicus* breeds as a dam line (e.g. Rege *et al.*, 1994; Frisch and O'Neill, 1998). When the positive heterotic estimates obtained for the same crosses in post-weaning traits were taken into consideration, the estimate for BWT seems to be confounded with the maternal effects. Thus, the *Bos indicus* breeds used as a dam line might have a similar birth weight suppression effect as those reported for Brahman dams by Frisch and O'Neill (1998), Arthur *et al.* (1999) and Franke *et al.* (2001).

The heterozygosity influence on WWT, ADG and YWT were positive and significantly (P<0.01) different from zero for all types of crosses evaluated (Table 3.3). Relative to the mean of parental breed performance for each trait, the magnitude of the heterotic increase ranged from 5% for F x Ho to 15% for S x Ba or J x Bo in WWT, 11% for F x Ho to 26% for S x Ba in ADG, and from 10% for S x Ho to 18% for J x Bo in YWT. The ranking orders of breed crosses for the heterotic values between traits were, however, not the same, while the Ho crosses within each of the *Bos taurus* breeds had lower heterotic values for all traits. In general, the heterotic estimates obtained for WWT, ADG and YWT are on the upper ranges of the reported literature values for *Bos indicus* x *Bos taurus* crosses (e.g. Long, 1980; Thorpe *et al.*, 1993; Rege *et al.*, 1994; Frisch and O'Neill, 1998; Arthur *et al.*, 1999).

3.3.2.3 Recombination effects

Estimates for recombination effects on BWT, WWT, ADG and YWT are shown in Table 3.3. Except for the S x Ho crosses, the recombination effects for BWT were significant ($P<0.05$) and positive for all types of crosses. As in contrast to this, all estimates for WWT, ADG and YWT were significant ($P<0.05$) and negative for all F and S crosses. A significant recombination loss was also estimated for the J x Ba for WWT and the J x Ba and J x Bo for ADG. The significant recombination loss obtained for the majority of crosses in all post-weaning traits indicates that there would be a considerable deviation in heterosis as measured and expected in a particular cross. Thus, relative to the expected second generation crossbred performances (prediction based on additive and heterotic effects only), the decline in the observed performances due recombination effects ranged from 8% for F x Bo to 24% for F x Ba in WWT, 9% for J x Bo to 35% for F x Ba in ADG and from 8% for F x Ho to 16% in F x Ba for YWT (Table 3.3). These results seem to indicate that the F x Ba crosses suffered the greatest recombination loss in all the traits, while the other types of crosses did not show a similar pattern across traits.

There are only a few literature reports that provide evidence for the existence of epistatic gene action for early growth traits in cattle. Arthur *et al.* (1999) for example, recently reported a significant epistatic loss in weaning weight and preweaning average daily gain for the direct and maternal effects when crossing Brahman with Hereford in Australia. In contrast to this, Koch *et al.* (1985) reported no epistatic effects on growth traits of crossbred calves from Angus and Hereford matings in the USA. Gergory *et al.* (1991), in a study evaluating heterosis retention in F2, F3 and F4 generations of crossbreds formed from several *Bos taurus* breeds in USA also found a positive deviation of heterosis relative to the expected level of heterozygosity for several growth traits, which they attributed to a favourable epistatic recombination effects.

3.3.3 Predicted performances

The predicted early growth performance of genotypes for the breeding strategies compared is presented in Table 3.4. The predicted performance values shown for the breeding strategies indicate that crossbreeding parameters used have relatively high accuracy of prediction for the genotypes actually tested and those genotypes with lower *Bos taurus* gene proportions. The predicted mean values for purebred *Bos taurus* breeds had high standard errors in all traits. This is because of the fact that all crossbreeding parameters were estimated from crosses with 75% or less *Bos taurus* breed contributions. Sölkner and James (1990) demonstrated the inefficiency of a design without all purebreds in crossbreeding parameter estimation and consequently for performance prediction of untested genotypes. In addition, the crossbreeding parameters used for the prediction were estimated with an assumption of a negligible influence of several other genetic effects, such as, maternal breed and maternal non-additive effects. Both the crossbreeding parameter estimates as well as the predicted performances reported should, therefore, be interpreted cautiously.

The predicted performances shown in Table 3.4 indicates that for BWT, all tested and untested genotypes involving the S and F breeds had higher values than the Bo breed. All crosses and purebred J, except crosses with 3/4Bo, had lower predicted growth performances than the Bo. With the exception of the purebred J and its crosses, the predicted values for BWT increased with an increasing contribution of both the F and S breeds in the calf. The predicted BWT seems highly affected by the additive genetic differences. In comparing breeding strategies with equal F and S contributions for this trait, the purebred S and its crosses were found to be heavier than the F at all levels. This was, however, reversed in WWT and post-weaning performance. This could indicate a better expression of the growth potential of the purebred F and its crosses compared to the purebred S and its crosses under low input postnatal management conditions. In comparison with the purebred J and its crosses the purebred F, S and their crosses had higher predicted performances for both WWT and YWT, which to a large extent seems to be a reflection of the mature weight differences between the groups. However, the purebred F and its crosses also showed their superiority in rate of gain.

Table 3.4 Predicted mean and standard error values for birth weight (BWT), weaning weight (WWT), preweaning average daily gain (ADG) and yearling weight (YWT) for Friesian, Jersey and Simmental based crossbreeding strategies

Breeding strategy[1]	BWT (kg)	WWT (kg)	ADG (g)	YWT(Kg)
Bo	22.90±0.30	95.2±1.29	401.0±7.0	129.2±1.79
Friesian based crossbreeding				
3/4Bo	25.0±0.25	101.0±0.93	422.2±5.1	139.3±1.30
F_2	28.0±0.31	102.3±1.07	413.6±5.8	139.0±1.51
F_1	25.7±0.30	112.0±0.99	479.2±5.6	156.5±1.49
5/8(syn)	29.0±0.27	104.3±0.95	418.6±5.2	140.5±1.33
3/4F	29.5±0.29	108.8±1.09	440.9±5.8	146.0±1.45
¾(syn)	30.1±0.31	106.4±1.16	424.4±6.1	141.6±1.56
F	31.9±0.82	110.9±3.07	438.4±16.4	142.6±4.10
Jersey based crossbreeding				
3/4Bo	23.0±0.26	98.0±1.0	417.2±6.3	137.1±1.37
F_2	22.9±0.32	94.1±1.18	384.9±8.3	133.8±1.62
F_1	21.5±0.30	102.6±1.19	485.0±6.7	146.7±1.58
5/8(syn)	22.3±0.30	92.2±1.08	381.9±7.2	132.0±1.48
3/4J	21.2±0.33	91.9±1.24	404.3±6.7	132.2±1.67
3/4(syn)	21.5±0.36	89.8±1.32	379.3±7.5	129.0±1.79
J	19.3±0.90	83.1±3.41	375.2±18.7	119.5±4.58
Simmental based crossbreeding				
1/4Bo	25.30±0.28	100.4±1.16	417.2±6.3	138.2±1.62
F_2	28.60±0.37	97.8±1.54	384.9±8.3	135.8±2.18
F_1	26.30±0.30	113.6±1.29	485.0±6.7	155.2±1.62
5/8(syn)	29.87±0.32	98.5±1.36	381.9±7.2	136.3±1.92
3/4S	30.50±0.31	103.2±1.26	404.3±6.7	141.2±1.74
3/4(syn)	31.08±0.35	99.2±1.42	379.3±7.5	136.4±1.97
S	33.30±0.87	100.7±3.45	375.2±18.7	135.2±4.79

[1] Breeding strategies are defined in Table 3.1; Bo, Boran; F, Friesian; J, Jersey.

Comparing breeding strategies within each *Bos taurus* breed the F_1 had the highest predicted growth performance, except for BWT. The lower predicted ADG and YWT, particularly of the F and S purebreds compared to the F_1, might indicate the environmental suppression of the additive genetic effects of these breeds. Cunningham (1981) suggested that mainly additive breed effects and small heterotic effects influence production performance in a good environment, while heterosis plays a pronounced role under poor environmental conditions. The results obtained in this study seem to support his suggestion.

The weaning and yearling weights that were observed or predicted from this study are generally low compared to *Bos indicus* x *Bos taurus* crossbred animals raised through suckling in beef production systems in the tropics (e.g. Banjaw and Haile-Mariam, 1994; Frisch and O'Neill, 1998), but, these weights are also not uncommon for crossbred dairy animals reared artificially under low input systems in the tropics (e.g. Kebede and Galal, 1982; Thorpe *et al.*, 1993; Rege *et al.*, 1994; Hirooka and Bhuiyan, 1995; McDowell *et al.*, 1996).

3.4 Conclusions

It could be concluded that there was a significant additive breed influence on the growth performance of the crossbred calves, particularly of the F breed. The direct heterotic gain was large for all growth traits, except for BWT, but this gain does not seem to be retained in later generations of crosses because of the relevant recombination loss in *Bos taurus* x *Bos indicus* crosses. As a result of this, no other composite genotype could be found that out-performs the first generation crossbreds. Thus, among all the crosses the F_1 crosses involving the Friesian seem to be the better performing genotype under the low input management system, such as the case in this experiment.

Chapter 4

Variance components and genetic parameters for early growth traits in a mixed population of purebred *Bos indicus* and crossbred cattle

4.1 Introduction

Genetic parameter estimates are needed to implement sound breeding programs and to assess the progress of ongoing programs. For growth traits of European and some prominent tropical beef cattle breeds, numerous heritability and correlation estimates are available (Koots *et al.*, 1994a,b). However, there is a paucity of reported genetic parameter estimates for purebred indigenous tropical cattle and their crosses (Lôbo *et al.*, 2000).

Genetic parameters apply to a specific population. However, in practical breeding programs, estimates are used to improve not only purebreds but also animals of diverse genetic composition. Several studies have shown that, for the estimation of additive genetic variances and breeding values in crossbred populations, it is important to account for the breed additive and non-additive effects. Various methods of accounting for crossbreeding effects have been explored using mixed models either by fitting genetic groups (e.g. Mackinnon *et al.*, 1996; Ahunu *et al.*, 1997) or linear regression on breed composition, heterozygosity and recombination (Van der Werf and de Boer, 1989; Akbas *et al.*, 1993; Hirooka *et al.*, 1998; Tosh *et al.*, 1999). Application of the latter procedure provides breed additive and non-additive effects, corrected heritability and genetic correlation estimates for use in breeding value prediction within the target population.

Nearly, all genetic variance estimates for early growth traits were for animals that suckled by their dams. For such animals, studies established the importance of maternal effects, primarily on preweaning and in some cases on postweaning growth traits (e.g. Meyer, 1992; Meyer *et al.*, 1993; Meyer, 1994; Meyer *et al.*, 1994; Koots *et al.*, 1994a; Robinson, 1996; Tosh *et al.*, 1999). However, there is no information whether these estimates apply to calves reared artificially.

Since 1974 data have been collected from a comprehensive cattle crossbreeding project in Ethiopia, involving three European breeds, Friesian, Jersey and Simmental and three indigenous Zebu breeds, Boran, Barca and Horro. The three indigenous breeds are widely used for multipurpose production of milk, meat and draft in the traditional smallholder farming sector (Albero and Haile-Mariam, 1982a,b). The objectives of this study were: 1) to estimate variance-covariance components for early growth traits in a mixed population of purebred *Bos indicus* and crossbred cattle; 2) to evaluate the influence of prenatal dam effects on genetic variance for early growth traits of non-suckled calves.

4.2 Material and methods

4.2.1 Data source

Data were obtained from a mixed population of purebred and crossbred animals of the Ethiopian Agricultural Research Organization and consisted of 4957 birth weight (BWT), 4525 weaning weight (WWT) and pre-weaning average daily gain (ADG) and 3330 yearling weight (YWT) records collected from 1974 to 1999. Animals in this study were produced from the mating of three *Bos indicus* breeds, Boran (Bo), Barca (Ba), and Horro (Ho) within and by out-crossing each using imported semen of Friesian (F), Jersey (J) and Simmental (S) breeds in four herds located at different agro-ecological zones in Ethiopia. Semen from the imported breeds was only used for crossbred production, while the indigenous breeds were also used for the production of their respective purebred calves. The crossbred groups consisted of mainly F_1, F_2, 5/8 *Bos taurus* and 3/4*Bos taurus* crosses of Friesian, Jersey and Simmental with the three indigenous breeds, respectively. The number of calves produced from each mating type is shown in Table 4.1.

Table 4.1 **Mating design used in the crossbreeding program and progeny records available for birth weigh (BWT), weaning weight (WWT), preweaning average daily gain (ADG) and yearling weights (YWT)**

Genotype[1]			Number of records analysed		
Sire	Dam	Progeny	BWT	WWT or ADG	YWT
Bos indicus **-pure breeds**					
Bo	Bo	Bo	257	209	185
Ba	Ba	Ba	130	109	98
Ho	Ho	Ho	204	176	152
Two-breed crosses					
F	Ba	1/2F:1/2Ba (F1)	114	103	91
F	Bo	1/2F:1/2Bo (F1)	437	374	256
F	Ho	1/2F:1/2Ho (F1)	126	114	105
J	Ba	1/2J:1/2Ba (F1)	93	88	75
J	Bo	1/2J:1/2Bo (F1)	262	248	205
J	Ho	1/2J:1/2Ho (F1)	119	107	94
S	Ba	1/2S:1/2Ba (F1)	80	76	60
S	Bo	1/2S:1/2Bo (F1)	236	223	184
S	Ho	1/2S:1/2Ho (F1)	132	119	97
1/2F:1/2Ba (F1)	1/2F:1/2Ba (F1)	1/2F:1/2Ba (F2	96	77	56
1/2F:1/2Bo (F1)	1/2F:1/2Bo (F1)	1/2F:1/2Bo (F2)	325	257	196
1/2F:1/2Ho (F1)	1/2F:1/2Ho (F1)	1/2F:1/2Ho (F2)	93	75	62
1/2J:1/2Ba (F1)	1/2J:1/2Ba (F1)	1/2J:1/2Ba (F2)	90	77	60
1/2J:1/2Bo (F1)	1/2J:1/2Bo (F1)	1/2J:1/2Bo (F2)	278	227	166
1/2J:1/2Ho (F1)	1/2J:1/2Ho (F1)	1/2J:1/2Ho (F2)	80	68	53
1/2S:1/2Ba (F1)	1/2S:1/2Ba (F1)	1/2S:1/2Ba (F2)	66	49	43
1/2S:1/2Bo (F1)	1/2S:1/2Bo (F1)	1/2S:1/2Bo (F2)	160	124	94
1/2S:1/2Ho (F1)	1/2S:1/2Ho (F1)	1/2S:1/2Ho (F2)	82	67	55
1/2F:1/2Bo (F1)	3/4F:1/4Bo (BC)	5/8F:3/8Bo (SC)	81	65	45
1/2J:1/2Bo (F1)	3/4J:1/4Bo (BC)	5/8J:3/8Bo (SC)	33	30	21
1/2S:1/2Bo (F1)	3/4S:1/4Bo (BC)	5/8S:3/8Bo (SC)	25	25	18
3/4F:1/4Bo (BC)	3/4F:1/4Bo (BC)	3/4F:1/4Bo (SC)	14	8	7
F	1/2F:1/2Ba (F1)	3/4F:1/4Ba (BC)	70	68	59
F	1/2F:1/2Bo (F1)	3/4F:1/2Bo (BC)	188	170	138
F	1/2F:1/2Ho (F1)	3/4F:1/2Ho (BC)	116	103	80
J	1/2J:1/2Ba (F1)	3/4J:1/4Ba (BC)	80	68	58
J	1/2J:1/2Bo (F1)	3/4J:1/2Bo (BC)	152	129	99
J	1/2J:1/2Ho (F1)	3/4J:1/2Ho (BC)	90	79	58
S	1/2S:1/2Ba (F1)	3/4S:1/4Ba (BC)	56	46	36
S	1/2S:1/2Bo (F1)	3/4S:1/2Bo (BC)	156	129	89
S	1/2S:1/2Ho (F1)	3/4S:1/2Ho (BC)	116	93	70
Three-breed crosses					
1/2F:1/2Bo (F1)	1/2J:1/2Bo (F1)	1/4F:1/4J:2/4Bo[2]	136	127	91
1/2F:1/2Bo (F1)	1/4F:1/4J:2/4Bo	3/8F:1/8J:4/8Bo	47	37	13
1/2F:1/2Bo (F1)	3/4J:1/4Bo (BC)	2/8F:3/8J3/8Bo[2]	41	29	20
3/4F:1/4Bo (BC)	1/2J:1/2Bo (F1)	3/8F:2/8J:3/8Bo[2]	15	15	15
3/4F:1/4Bo (BC)	1/4F:1/4J:2/4Bo	4/8F:1/8J:3/8Bo	26	19	11
3/4F:1/4Bo (BC)	5/8J:3/8Bo (SC)	6/16F:5/16J:5/16Bo	15	13	7
1/2J:1/2Bo (F1)	1/4F:1/4J:2/4Bo	1/8F:3/8J:4/8Bo	40	25	8

[1] Bo, Boran; Ba, Barca, Ho, Horro, F, Friesian; J, Jersey; S, Simmental; the fraction values are breed contribution to the genotype class

[2] include progeny records produced from the reciprocal matings

F1, first filial generation; F2, second filial generation; BC, first backcrosses; SC, second generation crosses

All base dams were purebred *Bos indicus* representing Bo, Ba, and Ho breeds at equal proportions per herd. The allocation of the dam breeds to the four herds was done in such way that each herd had two dam breeds in common, the Bo being the second breed in each herd and the connecting breed across the four herds. A total of 363 bulls representing different purebred and crossbred groups were used (Table 4.2). The number of bulls from each breed was as follows: 36 Boran, 17 Barca, 24 Horro, 61 Friesian, 51 Jersey and 43 Simmental purebreds while the rest (131) were crossbred bulls.

4.2.2 Management of animals

Calves were born year round, weighed at birth and allowed to suckle their dams for the first 24 h, after which they were separated and placed in individual calf pens and bucket fed milk. A total 260 kg of milk was fed to each calf until weaning at the age of 90 days. Calves were kept indoors until the age of six months, while feeding *ad lib* natural hay and 1 kg of local concentrate per head per day, before they joined the mature herd on pasture.

4.2.3 Statistical procedure

Variance components were estimated for each trait separately and for all pairs of traits jointly, using the ASREML software package (Gilmour *et al.*, 2000). An animal model was used throughout, incorporating all pedigree information available. In addition to the direct genetic effects, maternal genetic and permanent environmental effects on the traits studied were tested by fitting six alternative models, as described by Meyer (1992).

Fixed effects fitted were sex, dam parity and herd-year-season subclasses. Also breed additive and non-additive effects for all traits and age at weighing for WWT and YWT were fitted as covariates. The data structure and effects fitted in the mixed models are presented in Table 4.2. For the data used in this study, the suitable crossbreeding model and the corresponding parameter estimates (breed additive, heterosis and recombination effects) have previously been reported in Chapter 3. For all traits, the crossbreeding effects fitted were related to the genotype of an individual animal.

Table 4.2 Data structure and effects fitted in mixed models

Item	BWT	WWT	ADG	YWT
Animals with record	4957	4245	4245	3330
Animals in the analysis	5916	5209	5207	4242
Sire (no.)	363	330	330	319
With progeny	334	315	315	293
With their own record	161	144	144	112
Average progeny/sire	12.91	11.43	11.43	9.9
Dam (no.)	1519	1351	1351	1174
With progeny	1366	1195	1195	1013
With their own record	859	738	738	598
Average progeny/dam	3.01	2.85	2.85	2.47
Performance				
Mean	24.6[a]	98.2[a]	408.6[b]	138.5[a]
SD	5.2	29.4	158.8	33.3
CV%	21.3	29.9	38.9	24.1
Age (days)	-	Covariate	-	Covariate
Mean	-	180.3	-	364
SD	-	10.2	-	10.9
CV(%)	-	5.6	-	3.0
Breed additive and non-additive fixed effects				
Direct additive [1]	Covariates	Covariates	Covariates	Covariates
Direct heterosis [2]	Covariates	Covariates	Covariates	Covariates
Direct recombination loss [2]	Covariates	Covariates	Covariates	Covariates
Herd-year-season classes	195	189	189	184
Parity classes	4	4	4	4
Sex classes	2	2	2	2

Unit of measurement: [a] kg; [b] g

[1] represents breed proportions in the individual animal fitted as a covariate for Ba, Ho, F, J and S breed additive effects as a deviation from Bo.

[2] represents nine-direct heterosis and nine-direct recombination effects fitted as covariates for crosses of F x Bo, F x Ba, F x Ho, J x Bo, J x Ba, J x Ho, S x Bo, S x Ba and S x Ho.

The basic univariate animal model used for the analysis of each trait was:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_{d}\mathbf{u}_{d} + \mathbf{Z}_{m}\mathbf{u}_{m} + \mathbf{Z}_{c}\mathbf{c} + \mathbf{e} \,,$$

where $\mathbf{y}$ is a vector of observations, $\mathbf{b}$ is a vector of fixed effects with incidence matrix $\mathbf{X}$, $\mathbf{u}_{d}$ and $\mathbf{u}_{m}$ are vectors of individual and maternal genetic effects with incidence matrices $\mathbf{Z}_{d}$ and $\mathbf{Z}_{m}$, respectively, $\mathbf{c}$ is a vector of random maternal permanent environmental effects with incidence matrix $\mathbf{Z}_{c}$, and $\mathbf{e}$ is a vector of random residual effects. This model was used with the assumption of a common additive variance for all groups and the differences between the breed groups were expected to be accounted for by the fixed breed additive effects. Thus, the total direct additive genetic value of an individual was composed of a fixed group and random animal effects as described by Quaas and Pollak (1981), with:

$$\mathbf{u} = \mathbf{Gg} + \mathbf{a},$$

where $\mathbf{g}$ is a vector of fixed genetic group effects, representing the six purebred groups (Bo, Ba, Ho, F, J, S) with an incidence matrix $\mathbf{G}$ containing the fractional contribution of the breeds to the individual animals (Arnold *et al.*, 1992) and $\mathbf{a}$ is a vector of random animal genetic effects. This model has the following variance-covariance expectation: $\mathrm{Var(y)} = \sigma^{2}_{a} + \sigma^{2}_{m} + \sigma^{2}_{c} + \sigma_{am} + \sigma^{2}_{e}$,

where $\mathrm{Var(a)=A}\sigma^{2}_{a}$; $\mathrm{Var(m)=A}\sigma^{2}_{m}$; $\mathrm{Var(c)=I}\sigma^{2}_{c}$; $\mathrm{Var(e)=I}\sigma^{2}_{e}$; $\mathrm{Cov(a,m)=A}\sigma_{am}$. A is the numerator relationship matrix and I is an identity matrix equal to the number of dams for Var(c) and number of animals for Var(e). σ_{am} is the matrix of direct and maternal genetic covariances.

In addition to the comprehensive model (designated as model 6) described above, five reduced models, which ignored one or two of the maternal effects and/ or assumed no covariance between the direct and maternal genetic effects, were fitted to each trait. These models were numbered as follows: Model 1: h^{2}_{a}; Model 2: h^{2}_{a} and h^{2}_{m}; Model 3: h^{2}_{a} and c^{2}; Model 4: h^{2}_{a}, h^{2}_{m} and r_{am}; Model 5: h^{2}_{a}, h^{2}_{m} and c^{2}; and Model 6: h^{2}_{a}, h^{2}_{m}, r_{am} and c^{2}, where h^{2}_{a}, h^{2}_{m}, c^{2} are the direct individual, direct maternal and permanent maternal variance as a proportion of phenotypic variance, respectively, and r_{am} is a correlation between direct and maternal genetic effects.

Models with different random components were compared using the log likelihood ratio test (LR), which was calculated as minus two times the difference between the LogL of M1 and each other models. To declare the difference significant, the likelihood ratio was compared with the tabulated χ^2 statistics with the number of degrees of freedom taken as the difference in number of parameters fitted in the two models. Using the best model based on the LR for each trait in the unitrait analysis, genetic and phenotypic correlations between traits were computed using a bivariate analysis. In addition, after determining the best model for each trait, the influences of ignoring fixed heterotic and recombination loss effects on the variance components and heritability estimates were investigated.

4.3 Results

4.3.1 Univariate estimates

Estimates of variance components and genetic parameters for each trait from the six univariate analyses are presented in Table 4.3 and 4.4, respectively. For BWT, both the direct genetic variance and the corresponding direct heritability estimates were substantially reduced when maternal effects were included in the model. For this trait, fitting both direct genetic, maternal genetic and the covariance between direct and maternal genetic effects (Model 4) improved the LR significantly compared to a model fitting only direct genetic (Model 1) or one of the maternal component effects (Model 2 and 3). The inclusion of all maternal effects (Model 6), however, did not significantly improve the LR. Direct heritability estimates for BWT from the different models were significantly ($P<0.05$) different from zero and ranged from 14% in Model 4 to 34% in Model 1 (Table 4.4). The corresponding genetic maternal heritability ranged from 6% in Model 6 to 11% in Model 2. The permanent maternal environmental effect was only important when it was fitted as the only maternal effect (Model 3). For BWT the estimated correlation between the direct and maternal genetic effect was positive (Model 4), but because of large sampling errors the estimate was not significantly different from zero.

Table 4.3 **Estimates of variance and covariance components for birth weight (BWT), weaning weight (WWT), preweaning average daily gain (ADG) and yearling weight (YWT) using different univariate models**

			Models[1]			
Estimates	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
BWT (kg^2)						
σ^2_a	5.48	2.78	3.85	2.27	2.83	2.30
σ_{am}				0.76		0.74
σ^2_m		1.69		1.18	1.42	0.97
σ^2_c			1.28		0.28	0.24
σ^2_e	10.76	11.40	10.80	11.68	11.32	11.61
σ^2_p	16.24	15.87	15.93	15.89	15.85	15.87
WWT (kg^2)						
σ^2_a	28.14	18.76	21.83	18.32	18.96	18.37
σ_{am}				0.84		1.05
σ^2_m		9.68		8.96	6.73	5.83
σ^2_c			9.67		4.20	4.24
σ^2_e	236.90	236.00	233.00	236.40	234.50	234.90
σ^2_p	265.04	264.44	264.50	264.52	264.39	264.39
ADG (g^2)						
σ^2_a	613	449	459	436	403	433
σ_{am}				-76		-60
σ^2_m		270		337	175	231
σ^2_c			284		136	130
σ^2_e	6953	6840	6813	6862	6843	6822
σ^2_p	7566	7559	7556	7558	7556	7556
YWT (kg^2)						
σ^2_a	48.4	44.8	48.4	44.8	44.8	44.8
σ_{am}				0		0
σ^2_m		4.1		4.1	4.1	4.1
σ^2_c			0		0	0
σ^2_e	338.2	337.5	338.2	337.5	337.5	337.5
σ^2_p	386.6	386.4	386.6	386.4	386.4	386.4

σ^2_a, σ^2_m, σ^2_c, σ^2_e, σ^2_p and σ_{am} : genetic direct, genetic maternal, maternal permanent environmental, residual and phenotypic variances and direct and maternal genetic covariance, respectively.

[1] models are defined in inside the text.

Table 4.4 **Direct (h_a^2) and maternal (h_m^2) heritabilities, permanent maternal effect (c^2) and direct and material correlation (r_{am}) values for different growth traits**

	Models					
Traits[a]	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
BWT(-2logLR)[b]		37.7	26.1	42.6**[c]	38.3	43.1
h_a^2	0.34±0.03	0.18±0.03	0.24±0.03	0.14±0.03	0.18±0.03	0.15±0.03
h_m^2		0.11±0.02		0.07±0.02	0.09±0.03	0.06±0.03
r_{am}				0.47±0.25		0.49±0.27
c^2			0.08±0.02		0.02±0.02	0.02±0.02
h_T^2[d]	0.34±0.03	0.23±0.03	0.24±0.03	0.25±0.03	0.22±0.03	0.24±0.03
WWT(-2logLR)[b]		5.4*	4.6	5.4	5.8	5.8
h_a^2	0.11±0.03	0.08±0.03	0.08±0.03	0.07±0.03	0.07±0.03	0.07±0.03
h_m^2		0.04±0.02		0.03±0.02	0.03±0.02	0.02±0.03
r_{am}				0.07±0.49		0.10±0.61
c^2			0.04±0.02		0.02±0.02	0.02±0.02
h_T^2	0.11±0.03	0.09±0.02	0.08±0.03	0.09±0.03	0.08±0.02	0.09±0.03
ADG (-2logLR)[b]		5.6*	5.0	5.8	6.2	6.4
h_a^2	0.08±0.02	0.06±0.02	0.06±0.02	0.06±0.02	0.05±0.02	0.06±0.03
h_m^2		0.04±0.02		0.04±0.02	0.02±0.02	0.03±0.03
r_{am}				-0.20±0.39		-0.19±0.45
c^2			0.04±0.02		0.02±0.02	0.02±0.02
h_T^2	0.08±0.02	0.08±0.02	0.06±0.02	0.06±0.02	0.07±0.02	0.06±0.03
YWT(-2logLR)[b]		0.2	0	0.2	0.2	0.2
h_a^2	0.13±0.03	0.12±0.03	0.13±0.03	0.12±0.04	0.12±0.03	0.12±0.04
h_m^2		0.01±0.02		0.01±0.02	0.01±0.02	0.01±0.03
r_{am}						0
c^2			0	0	0	0
h_T^2	0.13±0.03	0.12±0.03	0.13±0.03	0.12±0.03	0.12±0.03	0.12±0.03

[a] traits are defined in Table 4.3

[b] log likelihood ratio values between Model 1 and each other model;

[c] **, P<0.01

[d] Total heritability, $h_T^2 = (\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am})/\sigma_p^2$, Willham (1972)

In the analysis for WWT and ADG the LR improved marginally ($P<0.05$) when additional maternal genetic effects (Model 2) or permanent maternal environmental effects (Model 3) was fitted, compared to Model 1. For YWT, however, none of the maternally associated effects showed any influence (see Table 4.4). For WWT and ADG, inclusion of additional maternal effects (Model 4, 5 or 6) did not improve the model fit. Since all the animals studied were artificially reared, maternal effects on WWT and ADG are not expected. The breed additive and non-additive genetic effects in the dam, which were not fitted in the genetic models, might have contributed to small, but significant maternal genetic effects.

Estimates in Table 4.5 show the potential bias that would have been incurred in the variance components and the corresponding heritability estimates by ignoring the non-additive effects on the individual animals. Compared to the correct model (A), ignoring heterosis and recombination effects (C) causes a substantial inflation of both direct and maternal genetic variances and the direct heritability estimates in all traits. However, the inflation was much higher in the maternal variance than on direct genetic variances. For instance, when compared to the full model (A), the variance inflation on direct and maternal genetic components due to ignoring non-additive effects (C) were 29 and 100% in BWT, 40 and 85% in WWT and 48 and 139% in ADG, respectively. The results in this table also show that including or excluding the recombination effects alone (sub-model A vs B) have a negligible influence on direct or maternal genetic variances. The possible reason for the large change in maternal variance when ignoring non-additive effects in the individual animal might be because both the maternal and non-additive effects measure the expected ancestral genetic effects on the progeny, i.e. heterosis and recombination effects measure the intra and inter locus interactions of the ancestral genes in the individual, while the maternal genetic effect measures the ancestral gene direct effects.

Table 4.5 Comparative estimates of variance components and heritabilities using the best model for birth weight (BWT), weaning weight (WWT), preweaning average daily gain (ADG) and yearling weight (YWT) by including or excluding part or whole of fixed non-additive effects[1]

Traits/ Effects	A	B	C
BWT, MODEL 4			
σ_a^2	2.27	2.64	2.79
σ_{am}	0.76	0.74	0.46
σ_m^2	1.18	1.20	1.75
σ_e^2	11.68	11.56	11.52
σ_P^2	15.89	16.14	16.51
h_a^2	0.14±0.03	0.16±0.03	0.17±0.04
h_m^2	0.07±0.02	0.07±0.03	0.11±0.02
r_{am}	0.47±0.25	0.42±0.24	0.21±0.20
h_T^2[a]	0.25±0.03	0.27±0.03	0.26±0.03
WWT. MODEL 2			
σ_a^2	18.8	22.2	26.3
σ_m^2	9.7	10.0	17.9
σ_e^2	236.0	236.0	237.8
σ_P^2	264.5	268.2	282.0
h_a^2	0.07±0.03	0.08±0.03	0.09±0.03
h_m^2	0.04±0.02	0.04±0.02	0.06±0.02
ADG. MODEL 2			
σ_a^2	449	580	690
σ_m^2	270	275	647
σ_e^2	6840	6915	6933
σ_P^2	7559	7769	8271
h_a^2	0.06±0.03	0.07±0.03	0.08±0.03
h_m^2	0.04±0.01	0.04±0.02	0.08±0.02
YWT. MDOEL 1			
σ_a^2	48.4	51.1	57.0
σ_e^2	338.2	336.6	368.0
σ_P^2	386.6	387.7	425.0
h_a^2	0.13±0.02	0.13±0.03	0.135±0.03

[1] A= fitted with breed additive differences, heterosis and recombination effects (full model) B= fitted with breed additive differences and heterosis effects and C= fitted with breed additive differences only

[a] Total heritability as in Table 4.4.

4.3.2 Bivariate estimates

The genetic and phenotypic correlation estimates between the growth traits obtained from the bivariate analyses are presented in Table 4.6. The within trait variance and covariance estimates obtained from biviariate analyses were virtually the same as those obtained in the univariate analysis (not shown). The estimated direct genetic correlations ranged from 0.50±0.12 between BWT and YWT to 0.96±0.01 between WWT and ADG. The phenotypic correlations ranged from 0.12±0.02 between BWT and ADG to 0.97±0.01 between WWT and ADG.

Table 4.6 Estimates of genetic (below diagonal) and phenotypic (above diagonal) correlations between different early growth traits

Traits	BWT	WWT	ADG	YWT
BWT	-	0.26±0.02	0.12±0.02	0.19±0.02
WWT	0.66±0.08	-	0.97±0.01	0.57±0.01
ADG	0.55±0.19	0.96±0.01	-	0.54±0.01
YWT	0.50±0.12	0.89±0.09	0.82±0.11	-

4.4 Discussion

The phenotypic variance estimated for BWT is higher than the estimate reported for purebred Boran cattle in Ethiopia by Haile-Marima and Kassa-Mersha (1995). However, much of this difference could be attributed to random environmental errors. Direct heritability estimates obtained were similar to what they reported using different genetic models (range: 0.16 to 0.24). Tawah *et al.* (1993) for Gudali and synthetic Wakwa cattle in Cameroon and Ahunu *et al.* (1997) for purebred Ndama and West African Shorthorn cattle and their in-between crosses and out-crosses with Red Poll and Santa Gertrudis in Ghana, reported lower phenotypic variances, but higher direct heritability estimates than the current study. The maternal genetic and maternal environmental variances and their ratio with the phenotypic variance for BWT were within the range of estimates reported in the literature (e.g. Meyer, 1992; Koots *et al.*, 1994a; Haile-Mariam and Kassa-Mersha, 1995). However, in the current estimates there might be some bias due to breed additive and non-additive effects in the dam not accounted for. Though not significant, the large positive correlation (0.47±0.25) between direct and maternal genetic effects using the best model (Model 4) might partly be the result of this confounding.

The estimates of direct heritabilities for WWT (7% to 11%), ADG (6% to 9%) and YWT (13%) are much lower than the corresponding estimates reported for crossbred (synthetic) or mixed populations elsewhere (e.g. Mackinnon *et al.*, 1991; Tawah *et al.*, 1993; Ahunu *et al.*, 1997; Tosh *et al.*, 1999; Schoeman and Jordaan, 1999; Lôbo *et al.*, 2000; Burrow, 2001). The current estimates are even lower than those reported by Haile-Mariam and Kassa-Mersha (1995) for suckled Boran calves in Ethiopia (24% for WWT and 34% for YWT). One of the major reasons for these low heritabilities could be the low standard of calf management followed in this experiment. Animal management levels as well as environmental stress highly affects the magnitude of additive genetic variance for different traits. For instance, Ojango and Pollott (2002) recently reported a higher additive genetic variance and hence a higher heritability for milk production in the UK (0.45±0.02) compared to that estimated under Kenyan (0.26±0.06) conditions for Holstein cows that were progeny of bulls commonly used in both countries. Literature reports are fairly limited on early growth traits of calves that were fed restricted milk and grazed on poor tropical pastures. In general agreement to the current results, Khan *et al.* (1999) found low heritability estimates of 17% to 19% for BWT, 8% for YWT and 12% to 13% for two year weight for Sahiwal calves that were separated from their dams at three days of age and raised artificially for dairy replacement in Pakistan.

Numerous estimates exist for both genetic and environmental maternal effects on birth to yearling weights in suckled beef cattle (e.g. Meyer, 1992; Meyer *et al.*, 1993; Meyer, 1994; Meyer *et al.*, 1994; Koots *et al.*, 1994a; Haile-Mariam and Kassa-Mersha 1995; Lôbo *et al.*, 2000; Burrow, 2001), but no reports for artificially reared animals are known to the authors. The maternal effects on growth traits of an animal originate from the care of the dam that starts during prenatal life and extends to the time until the young individual becomes independent. As indicated by Koch (1972) and Willham (1972), the causal components for the dam-progeny relationship are complex and are difficult to attribute to any single cause. Thus, the observed significant maternal genetic effect (Model 2) on WWT and ADG in this study could possibly be associated with carry over effects from the residual prenatal care of the dam or to the compound effects of the residual prenatal care plus additive and non-additive effects in the dam, which could not be accounted for in this analysis, because of the data structure. The dams milking ability, which is the major underlying cause of a direct maternal influence on weaning weight (e.g. r_g=0.80; Meyer *et al.*, 1994) could not be considered as a cause of the maternal genetic effect, because all the animals were reared artificially and fed an equal amount of milk until weaning.

Results in Table 4.5 clearly show potential bias in the estimates of direct and maternal variances when ignoring non-additive effects on the individual animals. Except for YWT, the change in variance components was substantial in all traits and indicates the importance of including non-additive effects in the genetic models when variance components and genetic parameters are estimated in a crossbred population. In general agreement to the patterns observed in this study, the influence of ignoring non-additive effects on additive genetic variances and consequently on heritability estimates, have previously been reported for carcass traits in crosses of dairy, dual purpose and beef cattle breeds (e.g. Hirooka *et al.*, 1998) and for milk production traits in a crossbred population of dairy cattle (e.g. Van der Werf and de Boer, 1989; Akbas *et al.*, 1993).

Even though the direct genetic correlation estimates among weaning and post-weaning traits were high, the values are within the ranges of average estimates summarized for temperate and tropical cattle (Koots *et al.*, 1994b; Lôbo *et al.*, 2000).

4.5 Conclusions

Genetic variances and associated parameters are characteristics of the population and their expression is affected by environmental conditions. The low genetic variances and consequently low heritability estimates obtained for all traits indicate the need for improved and uniform animal management over years to increase the precision of parameter estimates as well as animal performance. In spite of the low level, heritability and genetic correlation estimates obtained for early growth traits in this study show scope for improvement through selection in the mixed purebred and crossbred population. Furthermore, the combined analysis of data of different genetic groups also provide possibilities for selecting within and across genetic groups, by combining BLUE of breed additive estimates with individual breeding values (BLUP). Selection in such a population, ignoring the breed differences, would naturally results in a change of the composition of the population. Results from this study also indicated that direct genetic variance estimates for early growth traits of mixed purebred and crossbred populations are unbiased for models that accounted for maternal as well as breed additive and non-additive effects.

Genetic effects on milk production traits and cow weights in Boran, Friesian and crosses of Friesian and Jersey breeds with Boran breed

5.1 Introduction

Unimproved tropical environments are characteristically not suited to high producing European dairy cattle, while the indigenous cattle breeds, although adapted to the environment produce very little milk. To meet the increasing demand for dairy products in this region, crossbreeding has been widely proposed for genetic improvement of dairy cattle in the tropics (e.g. McDowell, 1985; Cunningham and Syrstad, 1987).

In crossbreeding *Bos indicus* with *Bos taurus* breeds, in addition to each breed's additive genetic contribution towards improved productivity of crossbred cows, there is also a substantial contribution of non-additive heterosis for milk yield and adaptive traits (e.g. McDowell, 1985; Cunningham and Syrstad, 1987; Thorpe *et al.*, 1993; Rege *et al.*, 1994; Mackinnon *et al.*, 1996; Rege, 1998; Kahi *et al.*, 2000). Rege (1998) reviewed results of 80 crossbreeding experiments involving European x indigenous breeds in the tropics. He estimated a high heterotic contributions to milk production traits in the F_1 cows, viz. a 17.3% increase in lactation milk yield, a 5.8% in lactation length, a 11% decrease in age at first calving, a 9% shorter calving interval and a 27.7% increase in annual milk yield. He also reported a significant deterioration in the performance of the F_2 generations in all traits compared to the F_1 generation. This finding was similar to the previous meta analysis of reported crossbreeding studies in the tropics by Syrstad (1989). Syrstad (1989) hypothesised that the recombination loss of the co-evolved epistatic parental genes is a contributing factor towards the higher than expected decline in milk production performance of the F_2 generations, but no statistical test of this hypothesis was made. Individual long term crossbreeding studies between *Bos taurus* x *Bos indicus* tested for the recombination effects on milk production traits failed to show this expectation (e.g. Mackinnon *et al.*, 1996; Kahi *et al.*, 2000). However, based on the results of crossbreeding data from the tropical countries reviewed by Rege (1998), Rutledge (2001) estimated a significant recombination loss for milk production traits.

Crossbreeding studies published for milk production traits between European dairy breeds and African indigenous cattle are fairly limited (e.g. Kiwuwa *et al.*, 1983; Rege *et al.*, 1994; Udo *et al.*, 1995; Tawah *et al.*, 1999) compared to similar studies reported from tropical Latin America and Asia (Syrstad, 1989, 1990). Only Rege *et al.* (1994) have reported separate estimates for breed differences and heterosis on milk production and reproductive traits for crosses of the Jersey with two indigenous African breeds. Thus, more results of crossbreeding studies from different tropical African breeds are needed to guide the breeding decisions for a specific production condition. A long-term crossbreeding program initiated in 1974 in Ethiopia has produced several generations of crosses between the indigenous Boran breed and the Friesian and Jersey breeds. Although the Boran is popular in beef production, the original owners in Ethiopia milk them, primarily for subsistence and also to sell surplus milk. The limited studies reported for Boran cattle showed that their milk production is low (500 to 1000 Kg) and the lactation length is less than 200 days (IAR, 1976; ILCA 1993). However, these studies were based on small samples and produced only indicative results. Limited studies compared Boran with other indigenous breed and their crosses for dairy performances in Ethiopia (e.g. Kiwuwa *et al.*, 1983; Albero, 1983; Haile-Mariam *et al.*, 1993; Negussie *et al.*, 1998). However, breed additive and non-additive effects for crossing Boran with Friesian and Jersey breeds for milk production traits have not been investigated. This study, therefore, has been undertaken with the following objectives: 1) to compare milk production performance and cow weight of different generations of crosses, 2) to estimate the relative contribution of breed additive, heterosis and recombination effects on milk yield per lactation

(LMY), daily milk yield (DMY), lactation length (LL), annual milk yield (AMY), annual milk yield per metabolic body weight (AMYBW) and cow weight (BW); 3) to estimate heritabilities and cow permanent environmental effects for milk production traits and cow weight.

5.2 Material and methods

5.2.1 Study location, genetic groups and herd management

A description of the study location is presented in detail in Chapter 1. In brief, the Holetta station, where the study animals were located is 45 km west of Addis Ababa at 38.5° E longitude and 9.8° S latitude and 2400 m above sea level. It is situated in the highlands in a mixed crop-livestock agro-ecological zone (MOA, 1984). The average annual rainfall is about 1200 mm, most of it occurring between June and October. The dry season lasts from November to February followed by light showers in March and April.

The genetic groups considered in this study included purebred Boran (B) and Friesian (F) and crosses between the Friesian and Jersey (J) breeds with the Boran. The information for Friesian cows was extracted from a farm that was managed similarly and is separated from the crossbred farm by only a fence. The Friesian cows were those that were born and calved during the period 1976 to 2000. This is the same period in which the crossbreeding experiment took place. The two herds were genetically linked by the use of common sires supplied by the Ethiopian national AI service from 1990 to 2000. The original design of the crossbreeding experiment did not include any Friesians or Jerseys as part of the breeding program. The crossbred groups consisted of eight genotypes, viz. four Friesian x Boran crosses: 1/2F:1/2B(F1), 1/2F:1/2B(F2), 5/8F:3/8B, 3/4F:1/4B; three Jersey x Boran crosses: 1/2J:1/2B(F1), 1/2J:1/2B(F2), 3/4J:1/4B; and a three-breed cross: 1/4F:1/4J:1/2B. The three-breed crosses were produced from mating F_1 Jersey x Boran bulls to F_1 Friesian x Boran cows or vice versa.

On both farms the cows were mated throughout the year using AI and natural service. Natural mating was used only for the production of purebred Boran calves and for the production of some crossbred calves from the matings of crossbred bulls with crossbred cows. The bulls used for natural services were all selected from the available males by visual appraisal. The pedigree information of bulls and cows were checked to avoid mating between close relatives on both farms, but no selective mating based on performance information was practiced. The cows used in this study were the progeny of 1804 dams and 205 sires. The number of sires used from the different genotypes involved in the crossbreeding program were 35 B, 40 J, 80 F, 30 F x B, and 25 J x B. Of the total number of Friesian bulls used, 10 sires had progenies in both the crossbred and purebred herds.

On both the crossbred and purebred Holstein-Friesian farms, the animals were grazed on natural pasture for about 8 hrs during daytime. At night all animals were housed and supplemented with natural pasture hay conserved from part of the grazing area during the rainy season. The stock density of grazing animals was not regulated, but the recommended practice was two tropical livestock units (250 kg) per hectare per year.

Except for the lactating cows, which were supplemented with approximately 3 to 4 kg of concentrate at each milking, no other animals received any regular concentrate supplement. Occasionally, during the long dry periods and based on the condition of the animals, dry and young stocks were supplemented with an unspecified amount of concentrate. All animals had free access to clean water.

Calves were separated from their dams soon after birth and bucket-fed twice daily, initially with colostrum and then on whole milk. Each calf received approximately 260 kg of milk up to the age of weaning (three months). All animals born on the crossbreeding farm were weighed at birth and monthly thereafter until they were culled from the breeding program. On the Friesian farm, weight was recorded for both the calf and dam once after each calving. On both farms all heifers, except a few with poor growth, were usually retained for breeding. Mature cows were normally not culled before they had completed their 4th lactation. This was done to regulate the total number of animals on the farm. However, cows could be culled for fertility and health reasons. Since 1990, cows had been culled based on production within contemporary groups. This policy was, however, not applied to purebred Boran cows. On the purebred Friesian farm cows were culled only for serious reproductive problems, poor health or old age. Therefore, the majority of animals had more than four lactation records completed. On both farms milking was done by hand, twice daily and milk yield of each individual cow was recorded at each milking. Cows were dried off at about 2 months before calving, if they had not been dry already. The same prophylactic health management practice was followed on both farms.

5.2.2 Data editing and analysis

The following data editing procedures were applied to the milk records of all cows: Each lactation record was considered normal if a cow had produced milk for at least 60 days and terminated with registered voluntary drying off date. The truncation point of 60 days was based on the recommendation of Kiwuwa *et al.* (1983) for the indigenous Ethiopian animals and their crosses. In addition, any record with lactation length of more than a 1000 days was also excluded from the data analysed. In this study, the lactation length between 60 to 1000 days was considered sufficient length to include all usable records of the indigenous B (this breed often have a short lactation length because of milk letdown problems) and crossbred or purebred F cows milked longer (because of reproductive problems). The acceptable lactation length for Zebu breeds is not well established and exclusion of short lactations are reported to minimizes the genetic variance for milk yield (Madalena, 1988). In contrast to this, Mackinnon *et al.* (1996) found no effect for either including or excluding short lactations on the estimation of genetic variance and crossbreeding parameters.

The traits analysed were milk yield per lactation (LMY), lactation length (LL), milk yield per day (DMY) calculated as LMY/LL, cow weight (BW), annual milk yield (AMY) and annual milk yield per metabolic body weight (AMYBW). AMY standardizes lactation milk yield of varying calving intervals (CI), and is calculated as (LMY/CI) x 365. AMYBWT measures the efficiency of milk production of cows with respect to their body size and is calculated as $AMY/BW^{0.75}$.

Two methods were applied in conducting the data analyses: firstly a 'genotype model' and then a 'genetic model' were used. In the genotype model, genetic effects were fitted as genotype group effect and a mixed model analysis of variance was performed for each trait using the ASREML program (Gilmour *et al.*, 2000). A repeatability animal model was fitted, where direct additive effects plus permanent environmental effect due to repeated records per cow were fitted as random effects. The fixed effects fitted in the genotype model were genotype (10 classes); calving year, 24 classes (1977 to 2000); Cow parity, 4 classes (1,2,3 and 4+) and calving season, grouped into three classes, based on the pattern of annual rainfall distribution in the area (October to February: dry period; March to May: light showers and June to September: main rainy season). The effect of calving season was found to be non-significant for all traits and was dropped from the subsequent analysis. Selected contrast was performed within each fixed effect to test for significance difference between least-squares means.

The second analysis was performed using a model equivalent to that of the genotype model. The only difference was that breed additive, heterosis and recombination effects were fitted as covariates in the place of the genotype effects. The random residual, direct animal genetic and permanent environmental effects in both models were assumed to have an independent distribution with mean zero and variances σ_e^2, σ_a^2 and σ_c^2, respectively. The model has the following variance expectation: Var(y) = $\sigma_a^2 + \sigma_c^2 + \sigma_e^2$, where var(a)=A$\sigma_a^2$, var(c)=I$\sigma_c^2$, and var(e)=I$\sigma_e^2$, From these distributions the phenotypic variance (Vp), heritability (h^2), cow effect (c^2) and repeatability (r^2) were calculated as

Vp=Va+Vc+Ve, h^2=Va/Vp, c^2=Vc/Vp, and r^2 = (Va+Vc)/Vp respectively. In addition, bivariate analyses were carried out between AMY, LL and BW for all cows having complete records for these traits. The effects fitted in the genetic model can be written in matrix form as follows:

$$\mathbf{y} = \mathbf{X}_1\mathbf{b}_1 + \mathbf{X}_2\mathbf{b}_2 + \mathbf{Za} + \mathbf{Wc} + \mathbf{e}$$

Where $\mathbf{y}$ is a vector of observation for the traits of interest; $\mathbf{b}_1$ a vector of fixed effects (overall mean, parity and calving year), $\mathbf{a}$ is a vector of random animal effects, $\mathbf{c}$ vector of random permanent environmental effects plus unaccounted non-additive genetic effects in the cow, $\mathbf{X}_1$, $\mathbf{Z}$ and $\mathbf{W}$ are incidence matrices relating records to fixed, animal and permanent environmental effects, respectively. $\mathbf{X}_2$ is a matrix of covariance coefficients for breed additive, heterosis and recombination relating individual cow records to these effects. The fixed covariates fitted for breed additive effects were: g_F and g_J for expected proportions of F and J genes in the individual cow respectively, with the effect of Boran breed component, g_B being included in the overall mean; h_{FB} and h_{JB} for expected heterozygosity between F and B and J and B derived genes in the cow, calculated as $p_i^s p_j^d + p_i^d p_j^s$; r_{FB} and r_{JB} for the expected average recombination of pairs of loci originating from F or J and B breeds, respectively. The recombination effect was calculated as $p_i^s p_j^s + p_i^d p_j^d$, where p_i^s and p_i^d denote the proportion of breed i in the sire and dam of the cow (Wolf *et al.*, 1995). The genetic effects considered were all direct individual cows related and genetic effects associated with maternal or paternal genotypes were assumed negligible on the traits studied. In addition, for the three-breed crosses the non-additive effects for F x J combination were also assumed negligible.

5.3 Results and discussion

5.3.1 Fixed effects and genotype comparison

The least-squares analysis of variance for milk production traits and cow weights are presented in Table 5.1. Year of calving significantly ($P<0.01$) influenced all traits. Milk production traits (LMY, DMY, AMY, AMYBW) showed a declining trend for calving year, while the change in LL and BW was irregular. The least-square means for AMY, LL and BW depicted in Figure 5.1 illustrates those trends. In addition to the general declining trend, there was a substantial drop in milk production for the year 1991 (Figure 1). This was attributed to a breakdown of herd management caused by political unrest in the country during that year. A separate analysis carried out for each genetic group, showed that this effect was similar for all groups and was, therefore, not confounded with the genetic effects. The decline in milk production performance over years may not only be caused by inter-annual random change of the climatic factors, it may also include management changes. Inter-annual variation in milk production for grazing dairy cows is a common problem reported in several studies conducted on tropical dairy production (e.g. Thorpe *et al.*, 1993; Rege *et al.*, 1994; Tawah *et al.*, 1999).

Table 5.1 **Least-squares analysis of variance for milk yield per lactation (LMY), daily milk yield (DMY), lactation length (LL), annual milk yield (AMY), annual milk yield per metabolic body weight (AMYBW) and cow weight (BW)**

		Mean squares of traits					
Effect	DF	LMY (kg^2)	DMY (kg^2)	LL (d^2)	AMY (kg^2)	AMYBW (kg^2)	BW (kg^2)
Parity	3	18026558***	388***	141541***	42610976***	885***	310941**
Year	23	29296894***	249***	43074***	23042814***	1646***	8708***
Genotype	9	508194816***	3633***	1493365***	232859784***	8894***	902990***
CV%		41	32	31	37	34	13
R^2		0.47	0.54	0.21	0.49	0.37	0.54

**, $P<0.01$; ***, $P<0.001$

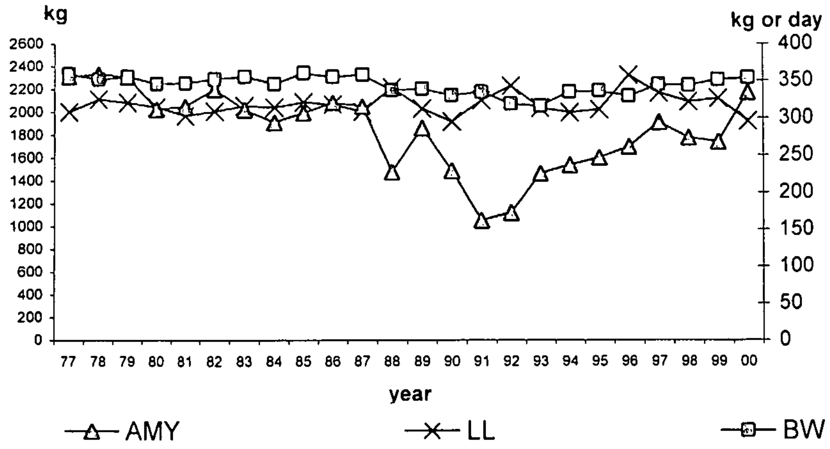


Fig. 5.1 **Least-squares means for annual milk yield (AMY), lactation length (LL) and cow weight (BW). Y-two axis scale is for LL and BWT**

As expected, cow parity significantly (P<0.01) affected all traits. All traits showed a significant (P<0.05) increase as cows became older, except for LL which was highest in the first parity and lowest for cows that calved four or more times. Consistent with this, significant changes in milk production for parity effect was reported by Thorpe *et al.* (1993), Rege *et al.* (1994), Tawah *et al.* (1999) and Kahi *et al.* (2000) for parity.

For all traits the B had the lowest performance (Table 5.2). As expected, crossing the B with F and J breeds increased milk production of the progeny three to fourfold (P<0.001). For instance, in comparison to the B, the F (average of F1, F2 and ¾) and the J (average of F1, F2 and ¾) crossbred cows produced on average 1721 and 1358 kg LMY, 3.7 and 2.8 kg DMY, 1481 and 1189 kg AMY, 16.5 and 15.2 kg AMYBW more milk and were milked for 142 and 135 d longer, respectively. Only the F crosses had a significantly (P<0.01) heavier BW (62 kg) than the Boran. Except for the magnitude of differences, the superior performance of crossbred progeny compared to the B for milk production traits is as expected and is in agreement with comparative results reported for *Bos indicus* and their crosses with European dairy breeds in the tropics (e.g. Kiwuwa *et al.*, 1983; Thorpe *et al.*, 1993; Rege *et al.*, 1994; Tibbo *et al.*, 1994; Udo *et al.*, 1995).

Table 5.2 Least-squares means (with s.e) for milk production traits and cow weight for different genotypes

		Traits[1]								
Genotype[2]	n[3]	LMY (kg)	DMY (kg)	LL (d)	n	AMY (kg)	n	AMYBW (kg)	n	BW (kg)
Boran	614	529±65	2.8±0.15	193±6	365	514±61	298	7.8±0.7	492	304±3
Friesian and its crosses										
1/2F:1/2B (F1)	860	2355±71	7.1±0.17	348±6	647	2057±57	531	25.7±0.7	714	382±3
1/2F:1/2B (F2)	225	1928±108	5.4±0.24	308±9	150	1740±94	84	20.7±1.2	125	353±6
5/8F:3/8B	67	2187±203	6.2±0.46	351±17	46	2091±178	21	24.7±2.2	37	367±10
3/4F:1/4B	129	2528±141	7.2±0.32	331±12	87	2093±120	31	26.1±1.8	47	363±9
Friesian	2259	3319±55	10.1±0.12	346±4	1833	2879±45	1166	28.3±0.5	1474	443±3
Jersey crosses										
1/2J:1/2B (F1)	875	2092±75	6.2±0.17	343±6	665	1861±60	587	24.4±0.7	769	326±3
1/2J:1/2B (F2)	234	1613±107	4.5±0.24	304±9	153	1480±94	98	19.8±1.1	159	294±5
3/4J:1/4B	172	1956±133	6.1±0.31	337±11	134	1758±110	47	24.7±1.5	65	292±8
Three-breed cross										
1/4F:1/4J:1/2B	111	1790±143	5.4±0.32	325±13	68	1752±131	54	21.8±1.5	94	316±7

[1] Traits defined in Table 5.1

[2] Sire breeds are written first; B, Boran, F, Friesian, J, Jersey and the fraction values are the proportion of breed contributions to each genotype class.

[3] number of observations (n) for LMY, DMY and LL.

When the F and J crossbred cows were compared, the F crossbred cows (average of F_1, F_2 and ¾) produced a significantly ($P<0.01$) higher LMY (383±89 kg), DMY (1±0.3 Kg) and AMY (260±130 kg) and was heavier (62±9 kg) than J crossbred cows (F_1, F_2 and ¾). However, the differences in LL and AMYBW between the two crossbred groups were not significant. This is in agreement with previous comparative results reported for F and J crossbred cows in Ethiopia (Kiwuwa *et al.*, 1983) and elsewhere (Tibbo *et al.*, 1994).

A comparison within each sire breed indicated that J F_1 crossbred cows were significantly ($P<0.05$) superior in all traits to J F_2 cows. Likewise the difference between F F_1 and F F_2 cows was also significant ($P<0.01$) for all traits. Both F and

J 3/4 crossbred cows were not significantly different compared to their respective F_1 cows, except for BW. These results agree to those reviewed for the different generations of *Bos taurus* x *Bos indicus* crosses (Syrstad 1989, 1990). The three-breed crosses were not different from the F_2 cows (average of F and J crosses) in all traits. However, their performances were significantly lower in all the traits, except in LL and AMY, compared to the average of F_1 F and J cows. Thus, the formation of a three-breed composite from F_1 F and J crosses did not improve the performance in the second generation crosses and it could not be considered as a better breeding alternative. The mean performance as well as the ranking order of different generations of the F and J crosses for milk production traits are in general agreement with results reviewed for crosses of these two dairy breeds with *Bos indicus* cattle in the tropics (e.g. Cunningham and Syrstad, 1987; Syrstad, 1989, 1990; Tibbo *et al.*, 1994; Rege, 1998).

5.3.2 Crossbreeding parameter estimates

The higher performances observed in all traits for the crossbreds, except for BW in J crosses, compared to B, was mainly attributed to the positive and significant ($P<0.001$) additive breed contribution of both the F and J breeds (Table 5.3). The estimates for the additive breed difference between the B and J breeds for LMY, LL and AMY were similar to those reported as a breed difference for the J from the Ghana shorthorn and Gudali breeds by Rege *et al.* (1994). The breed additive contributions of the F breed for milk production traits are generally higher than corresponding estimates reported for this breed elsewhere in the tropics (e.g. Sharma and Pirchner, 1991; Thorpe *et al.*, 1993). This might be a result of the lower milk production of the B breed compared to other milking type tropical indigenous cattle, such as the Sahiwal, which is commonly used in several other crossbreeding studies (e.g. Cunningham and Syrstad, 1987; Mackinnon *et al.*, 1996; Kahi *et al.*, 2000). The mean LMY of the B obtained in this study is even lower than that reported for the same breed (850 kg; ILCA 1993) and other indigenous breeds, the Arsi (809 kg) and mixed Zebu (809 kg) in Ethiopia (Kiwuwa *et al.*, 1983). The lower milk yield obtained for the B in the current study might be attributed to the milking practice that was followed, i.e. cows were milked without stimulation by their calves as is usually done under the traditional animal production systems. Though the current estimates might underestimate the potential yield of the B, it was measured under similar conditions as the other genotypes and is thus comparable.

Table 5.3 **Estimates and standard errors of crossbreeding parameters for milk production traits and cow weight**

	Traits[1]					
Parameter[2]	LMY (kg)	DMY (Kg)	LL (d)	AMY (kg)	AMYBW (kg)	BW (kg)
m	534±65	2.8±0.1	193±6	520±61	7.7±0.7	305±4
G_F	2774±81***	7.1±0.2***	152±7***	2345±71***	20.6±0.9***	140±4**
G_J	1473±362**	4.8±0.8**	146±31***	1238±319**	18.9±4.3**	-21±22
h_{FB}	454±81***	0.8±0.2***	81±7***	402±73***	7.8±0.8***	8.0±4.0*
h_{JB}	825±184***	1.1±0.4*	77±16***	726±164***	7.2±2.2***	32±11**
r_{FB}	-526±192**	-3.0±0.4***	4±17	-349±174*	-1.4±2.1	-68±11**
r_{JB}	-132±328	-2.2±0.7*	2±28	5±293	-1.4±3.6	-33±16*

[1] Traits are defined in Table 5.1

[2] m is the least-squares mean of Boran breed, G_F and G_J are breed additive estimates of Friesian and Jersey breeds as a deviation from the Boran breed, respectively; h_{FB} and h_{JB} are estimates of heterozygosity and r_{FB} and r_{JB} are estimates of recombination loss due to crossing Boran with Friesian and Jersey breeds, respectively.

Significance **, $P<0.01$; ***,$P<0.01$

Despite the large differences relative to the B, the mean LMY and AMY estimated for the F (3319±55 and 2879±45 kg) and that predicted for the J (2007±360 and 1758±317 kg) breeds were within ranges of performance values reported for these breeds in the tropics (e.g. Njubi *et al.*, 1992; Tibbo *et al.*, 1994; Tawah *et al.*, 1999; Ojango and Polott, 2001).

The contribution of heterosis to the performance of J x B and F x B crossbred cows was positive and significant ($P<0.01$) for all traits (Table 5.3). The estimated heterotic values for all traits in J x B crosses are higher than the corresponding estimates obtained for F x B crosses. However, the estimates for J x B had also higher sampling errors. The heterosis estimated as a deviation of F_1 means from the mid-parent mean values for F x B crosses were very close to the estimates obtained from the whole data set using the regression model (Table 5.3). These estimates were: 431±81 kg (22%) for LMY, 0.7±0.2 kg (11%) for DMY, 79±8 d (29%) for LL and 360±81 kg (21%) for AMY. These estimates are within the range of reported heterotic effects for milk production traits of other *Bos taurus* x *Bos indicus* crosses (e.g. Sharma and Pirchner, 1991; Thorpe *et al.*, 1993; Rege *et al.*, 1994; Rege, 1998).

The recombination effects estimated for F x B were significant ($P<0.01$) and negative for all traits, except for LL and AMYBW, while for J x B crosses it was only significant ($P<0.05$) and negative for DMY and BW. The negative recombination estimates for the majority of milk production traits in the crosses of F x B were expected. The F breed has been selected for generations with the main aim of increasing milk yield per cow. As a result of this, favourable epistatic interactions between genes in different loci may have been evolved. Thus, by crossing the F with the unselected B, these interactions may have been lost due to recombination. The reported recombination estimates for milk production traits for *Bos taurus* x *Bos indicus* crosses are generally limited and inconsistent (e.g. Sharma and Pirchner, 1991; Mackinnon *et al.*, 1996; Kahi, *et al.* 2000; Rutledge, 2001). Rutledge (2001) recently estimated a significant recombination loss of -277±55 for LMY and -345±56 kg for AMY, using the *Bos indicus* x *Bos taurus* crossbred data reviewed by Rege (1998); whereas individual experimental studies did not found any significant recombination loss on milk production traits (e.g. Sharma and Pirchner, 1991; Mackinnon *et al.*, 1996; Kahi *et al.*, 2000). The non-significant estimate for most of milk production traits in J x B crosses agrees with the latter reports and seems to be affected by large sampling errors. In general, the efficient separation of the dominance and recombination effects as components of heterosis, requires several diverse genotypes (Sölkner and James, 1990). In contrast to the inconsistent results of recombination loss in *Bos taurus* x *Bos indicus* crosses, several studies reported negative recombination losses in milk production traits for *Bos taurus* x *Bos taurus* crossbred cows under temperate (e.g.

Van Der Werf and De Boer, 1989; Akbas *et al.*, 1993; Grosshans *et al.*, 1994; Wolf *et al.*, 1995) and tropical climates (Khalil *et al.*, 2000).

5.3.3 Heritabilities and genetic correlations

Estimates for variance components, heritabilities (h^2), permanent environmental effects (c^2) and repeatabilities (r^2) are presented in Table 5.4. Both heritability and repeatability estimates were significantly ($P<0.05$) different from zero for all traits. The highest heritability estimate was for LMY (0.24±0.05) and the lowest was for BW (0.1±0.03). The heritability estimates for LMY and LL were closer to those reported for the Kenyan-Holstein-Friesian cattle (Ojango and Pollot, 2001), but were higher than estimates reported for the crossbred populations which comprised Ayrshire, Brown Swiss and Sahiwal crosses by Mackinnon *et al.* (1996). On the other hand, Lôbo *et al.* (2000), in their review of heritability estimates published for tropical dairy cattle, reported higher average heritability values for LMY (0.41) and LL (0.25) in crossbred dairy cattle. However, the current estimate for LMY is closer to what they have reported as an overall mean heritability (0.25). The large difference in the estimated heritabilities for the milk production traits between the current estimates and those reviewed for crossbred dairy cattle could be the result of differences in the analytical procedures followed. As indicated by Lôbo *et al.* (2000), very few studies have used animal models for estimating heritabilities. On the other hand, Dahlin *et al.* (1998) reported heritability estimates ranging from 0.09 to 0.22 for the first three-lactations of Sahiwal cattle in Pakistan using an animal model. In general, the moderate heritability estimates for milk production traits indicate that there is sufficient additive genetic variance for these traits that could be used for selection within each genotype in conjunction with crossbreeding.

Khan *et al.* (1999) reported higher heritability estimate ranging from 0.18 to 0.20 for Sahiwal cow weight at calving than the current estimates. However, comparable low heritability estimates were also reported for temperate breeds (e.g. Moore *et al.*, 1990; Ahlborn and Dempfle, 1992).

Table 5.4 **Estimates of variance components, heritabilities (h^2±s.e.) cow effects (c^2±s.e.) and repeatabilities (r^2+s.e.) for milk production traits and cow weight[1]**

Estimate[2]	LMY	DMY	LL	AMY	AMYBW	BW
V_a	252138	1.1	1355	154075	12.1	256
V_c	164751	0.65	652	92369	15.6	639
V_e	653797	4.07	8354	424372	43.0	1713
V_p	1070686	5.82	10361	670816	70.7	2608
h^2	0.24±0.03	0.19±0.03	0.13±0.03	0.23±0.04	0.17±0.05	0.10±0.03
c^2	0.15±0.03	0.11±0.03	0.06±0.03	0.14±0.03	0.22±0.05	0.25±0.03
r^2	0.39±0.02	0.30±0.02	0.19±0.02	0.37±0.02	0.39±0.02	0.34±0.02
e^2	0.61±0.02	0.70±0.02	0.81±0.02	0.63±0.02	0.61±0.02	0.66±0.02

[1] traits are defined in Table 5.1.

[2] V_a is additive genetic variance, V_c is permanent environmental variance, V_e is residual variance and V_p is phenotypic variance.

The phenotypic, direct genetic and permanent environmental correlations between selected milk production traits (AMY and LL) and BW are presented in Table 5.5. As expected, the direct genetic and permanent environmental correlations between AMY and LL were high and significantly different from zero. The phenotypic (0.31±0.02) and residual correlations (0.16±0.02) between these traits were also different from zero. The direct genetic (0.17±0.18) and permanent environmental (0.23±0.23) correlations between AMY and BW were moderate, but had also high standard errors. The implications of these results is that much of the observed genetic variation in milk production between and within genetic groups is strongly associated with LL, but not with cow size. In general, the correlation estimates between various traits are within the range of reviewed estimates reported for tropical dairy cattle (Lôbo *et al.*, 2000).

Table 5.5 **Estimates of phenotypic (p_1p_2) and direct genetic (a_1a_2) and permanent environmental (c_1c_2), and residual correlations (e_1e_2) between milk production traits and cow weight, from bivariate analyses**

Trait 1 and Trait 2[1]	p_1p_2	a_1a_2	c_1c_2	e_1e_2
AMY and LL	0.32±0.02	0.71±0.08	0.82±0.15	0.16±0.02
AMY and BW	0.13±0.02	0.17±0.18	0.23±0.13	0.10±0.02
LL and BW	0.01±0.02	0.23±0.20	0.01±0.17	0.03±0.02

[1] traits are defined in Table 5.1.

5.4 Conclusions

The findings of this study have indicated that the milk production of the Boran cattle is too low to support dairy production that is geared towards producing surplus milk for the market. However, by crossing Boran with the Friesian and Jersey breeds, milk production in the first generation crosses increased more than threefold, because of the significant additive and heterotic contributions. This high level of production could, however, not be maintained in the second or latter generation crosses, because of the significant epistatic loss caused by the recombination effects. Thus, the best breeding strategy based on the traits studied is to apply selection on the purebred base populations and then crossing them to produce the F_1 that could be used as a dairy cow. The current study did not include important dairy traits such as milk fat, protein, longevity and survival, thus further investigations are needed for a breeding decision based on total dairy merit.

Chapter 6

Genetic effects on reproductive traits in Boran, Friesian and crosses of Friesian and Jersey breeds with Boran breed

6.1 Introduction

Reproduction is of the utmost importance in any dairy farming enterprise. The size of the calf crop is all-important for herd replacement, and the production of milk depends on reproductive activity. Fertile cows should have their first calves at an early age followed by short calving intervals thereafter. It is therefore obvious that possible genetic improvement in traits of economic importance in dairy cattle is closely tied to the reproductive rate. Differences in reproductive performances are largely due to environmental effects, although small, between and within breed genetic differences also contribute to the variation.

Breed and crossbred differences in reproductive efficiency have been reported for several *Bos taurus* breeds and their crosses with *Bos indicus* breeds in the tropics (e.g. Kiwuwa *et al.*, 1983; Galina and Arthur, 1989a,b; Syrstad, 1989, 1990; Madalena, *et al.*, 1990a; Sharma and Pirchner, 1991; Haile-Mariam *et al.*, 1993; Thorpe *et al.*, 1993; Rege *et al.*, 1994; Mackinnon *et al.*, 1996; Negussie *et al.*, 1998; Rege, 1998; Tawah *et al.*, 1999; Kahi *et al.*, 2000). However, only a few studies have attempted to partition these differences into its various genetic components (e.g. Madalena, *et al.*, 1990a; Rege *et al.*, 1994; Thorpe *et al.*, 1993; Mackinnon *et al.*, 1996; Kahi *et al.*, 2000).

Purebred European dairy cattle (mainly Friesian) and crosses of Friesian and Jersey with indigenous breeds are commonly used for dairy production in the highlands of Ethiopia. Because of the lack of a clearly defined breeding program, many farmers often keep mixed purebred and a variety of crossbred cows for their alleged good milk production and adaptability to the prevailing physical and socio-economic environment. The available studies in the literature are limited to performance comparisons of a few crossbred genotypes only (Albero 1983; Kiwuwa *et al.*, 1983; Haile-Mariam *et al.*, 1993; Negussie *et al.*, 1998). No estimates have yet been reported on the relative breed differences and non-additive genetic effects on reproductive performance of the different purebred and crossbred animals used for dairy production in Ethiopia. The aim of this study, using data gathered from a long-term breeding program on purebred Boran, Friesian and crosses of Boran with Friesian and Jersey breeds was, therefore, to compare the performance of the different genotypes and estimate breed differences, heterotic and recombination effects as well as heritabilities and repeatabilities for age at first calving (AFC), calving interval (CI), days open (DO) and number of services per conception (SPC).

6.2 Material and methods

6.2.1 Animals and management

Reproduction data collected from 1496 cows, comprising purebred Boran (B), Friesian (F), and crosses of Friesian and Jersey (J) with Boran were used. The crossbred cow group included four F x B crosses (1/2F:1/2B(F_1),1/2F:1/2B(F_2), 5/8F:3/8B and 3/4F:1/4B), three J x B crosses (1/2J:1/2B(F_1), 1/2J:1/2B(F_2) and 3/4J:1/4B) and one three-breed cross (1/4F:1/4J:1/2B). The number of reproduction records used from each genotype is shown in Table 6.1.

Cows and heifers were all reared in a similar environment with fairly constant management over years. A detailed description of the management of the experimental herds has been given in Chapter 5. Heifers and cows were diagnosed for possible oestrus twice daily, once in the morning from 7h 00 to 8h 00 and once in the afternoon from 15h 00 to 16h 00. In addition, herdsmen and night guards reported cows showing oestrus behaviour. Cows and heifers were mated year round using AI or natural mating. All mated animals were checked after two months for pregnancy by trained inseminators through rectal palpation. Since both AI and natural mating were used on all groups, the effect of service type was assumed negligible.

6.2.2 Traits and statistical analysis

The following traits were studied: age at first calving (AFC), calving interval (CI), days open (DO) and number of services per conception (SPC). Days open (DO) measures the period in days between parturition and conception for subsequent calvings.

Data were analysed using the mixed model restricted maximum likelihood procedure of the ASREML program (Gilmour *et al.*, 2000). Two similar models, based on a repeatability animal model were used for the analyses of CI, DO and SPC. In the first model a genotypic group effect was fitted, in the second model each genotype class was substituted by expected breed additive, heterozygosity and recombination effects fitted as covariates. Additional fixed effects fitted in both models were calving year: twenty-four classes (from 1977 to 2000) and parity: four classes (1, 2, 3, 4+). Calving season was also fitted, but found to be non-significant and excluded from the final analysis. In addition, the direct additive individual cow effect and permanent environmental effects due to repeated records per cow were fitted as random effects. AFC was analysed using a unitrait animal model fitted with fixed effects of birth year: twenty-four classes (from 1974 to 1998) and season of birth: three classes (October to February: dry period; March to May: light showers and June to September: main rainy season) in both genotypic group and genetic models. The general structure of the full model that was used to analyse the majority of traits can be presented in matrix form as follows:

$$\mathbf{y} = \mathbf{X}_1\mathbf{b}_1 + \mathbf{X}_2\mathbf{b}_2 + \mathbf{Za} + \mathbf{Wc} + \mathbf{e},$$

where y represents one of the traits studied; b_l represents all fixed effects other than genotype; b_2 represents genotype effects in Model 1 or genetic effects (breed additive difference, heterosis and recombination) in Model 2; a and c stand for random individual additive effects and permanent environmental effects, respectively. $\mathbf{X}_1$, $\mathbf{Z}$ and $\mathbf{W}$ represent the incidence matrices relating individual cow records to the fixed environmental effects, random individual additive effect and permanent environmental effects, respectively. $\mathbf{X}_2$ is an incidence matrix that relates individual cow records to the genotype class in Model 1 or expected genetic coefficients for breed additive, heterosis, recombination effects in Model 2. The random residual effects are represented by $\mathbf{e}$. The random individual additive effects, permanent environmental effects and residual effects were assumed to be uncorrelated and have expected means of zeros and variances σ_{a}^2, σ_{c}^2 and σ_{e}^2, respectively. From these expectations the direct heritability and repeatability for each trait was estimated.

The coefficients for expected genetic effects (Model 2) for breed additive, heterosis and recombination loss were derived following the hypothesis of Dickerson (1969, 1973). The equations used to calculate breed additive (g_i), heterosis (h_{ij}) and recombination loss (r_{ij}) were: $g_i = 1/2(\alpha_i^s + \alpha_i^d)$, $h_{ij} = \alpha_i^s \alpha_j^d + \alpha_j^s \alpha_i^d$ and $r_{ij} = 4 g_i g_j - h_{ij}$, respectively (Wolf *et al.* 1995), where α_i^s and α_i^d denote the gene proportion of breed i in the sire and dam of the cow, respectively. The breed additive effects for F and J were estimated as deviation from the B breed. The genetic coefficients fitted are presented in Table 6.1. The crossbreeding effects fitted were for the direct individual genotype and crossbreeding effects associated with maternal or paternal genotypes were assumed negligible on the traits studied. In addition, for the three-breed crosses, the heterotic and recombination effects for F x J were also assumed negligible.

Table 6.1 Number of cows and reproduction records and expected genetic effects

Cow genotype[1]	Number of cows	Number records	Genetic coefficients[2]					
			g_F	g_J	h_{FxB}	h_{JxB}	r_{FxB}	r_{JxB}
Boran (B)	188	452	0	0	0	0	0	0
Friesian and its crosses								
1/2F:1/2B (F_1)	192	703	0.5	0	1	0	0	0
1/2F:1/2B (F_2)	60	172	0.5	0	0.5	0	0.5	0
5/8F:3/8B	19	53	0.625	0	0.5	0	0.438	0
3/4F:1/4B	38	93	0.75	0	0.5	0	0.25	0
Friesian (F)	674	1983	1	0	0	0	0	0
Jersey crosses								
1/2J:1/2B (F_1)	174	704	0	0.5	0	1	0	0
1/2J:1/2B (F_2)	68	174	0	0.5	0	0.5	0	0.5
3/4J:1/4B	46	133	0	0.75	0	0.5	0	0.25
Three-breed cross								
1/4F:1/4B:1/2B	37	80	0.25	0.25	0.25	0.25	0.25	0.25

[1] The first symbol in the crossbred genotype indicates the breed of sire; B, Boran, F, Friesian, J, Jersey.

2 g_F and g_J are F and J breed direct contributions relative to B; h_{FxB}, h_{JxB} are expected within locus heterozygosity for crossing F and J with, respectively. r_{FxB} and r_{JxB} are expected recombination loss due to the breakdown of parental epistatic gene complex when crossing F and J with B breeds, respectively.

6.3 Results and discussion

6.3.1 Fixed effects and genotype performances

Results of least-squares analysis of variance are presented in Table 6.2. In all traits, the effects considered accounted for less than 50% of the variation. However, all factors had a significant influence on all traits. As commonly noted for grazing animals under tropical conditions (e.g. Kiwuwa *et al.*, 1983; Haile-Mariam *et al.*, 1993, Nugussie *et al.*, 1998) birth year on AFC and calving year on CI, DO, and SPC were significant ($P<0.01$). The trend of influence was, however, irregular and not similar for all traits. This inter-annual variation in reproductive traits may indicate a failure to maintain a uniform reproductive management over years. As expected, parity significantly ($P<0.01$) affected CI, DO and SPC. For most traits, the significant ($P<0.01$) change was noticed up to the second parity after which no significant change was noticed. The observed direction of influence for cow parity on reproductive traits is in general agreement to the results reported for indigenous and crossbred cows in Ethiopia (e.g. Kiwuwa *et al.*, 1983; Albero, 1983; Haile-Mariam *et al.*, 1993; Negussie *et al.*, 1998).

Table 6.2 Results of least-squares analysis of variance for age at first calving (AFC), calving interval (CI), days open (DO), number of service per conception (SPC) for calving/birth year, parity and season of birth

		Mean squares of traits			
Effect	DF	AFC (mo^2)	CI (days^2)	DO (days^2)	SPC (no^2)
Birth season		78*	-	-	-
Parity	3	-	482823***	65936***	6.41***
Year	23	248***	133952***	39328***	2.31***
Genotype	9	592***	138930***	35928***	10.69***
R^2		0.34	0.14	0.11	0.06

*, $P<0.05$; ***, $P<0.001$

Genotype difference was a significant ($P<0.01$) source of variation for all traits. As shown in Table 6.3, crossing the F and J with the B had improved the reproductive performance of the crossbred cows. Selected contrasts performed between the genotypes indicate that the F_1 cows (both F and J crosses) were significantly younger at AFC, had shorter CI and DO and required less SPC than either purebred B or F cows. For all reproductive traits the F did not differ from the B, except for AFC. The J crossbred cows showed a tendency to perform better in all traits than the F crossbred cows, although, the difference was not significant. A comparison of crossbred cows within the F and J crossings also singled out the F_1 cows as significantly superior in all traits compared to their F_2 contemporaries. The average performance of the three-breed crossbred cows was not better than that of the inter se F_2's (average of F and Jersey crosses). In general, the estimates of reproductive performances obtained for the different crossbreds are within the range of reported estimates for Friesian and Jersey crosses with indigenous tropical cattle elsewhere (e.g. Kiwuwa *et al.*, 1983; Madalena *et al.*, 1990a; Thorpe *et al.*, 1993; Haile-Mariam *et al.*, 1993; de Albas and Kennedy 1994; Tibbo *et al.* 1994; Rege *et al.* 1994; Negussie *et al.*, 1998; Tawah *et al.*, 1999; Kahi *et al.*, 2000). In a comparative review of performances studies on purebred Jersey, Friesian, indigenous breeds and their crosses in the tropics, Tibbo *et al.* (1994) estimated an average of 62 and 341 days early AFC, 21 and 55 days shorter CI for the Jersey crosses relative to the Friesian crosses and the indigenous breeds, respectively.

Further comparisons of the current results with those obtained by Kiwuwa *et al.* (1983), Haile-Mariam *et al.* (1993) and Negussie *et al.* (1998) from a similar crossbreeding study in Ethiopia is envisaged. For crossbred cows of F and J with Arsi or mixed Zebu, Kiwuwa *et al.* (1983) and Negussie *et al.* (1998) reported relatively younger AFC (28.5 to 34 months) and fewer DO (70 to 108 days), but similar CI (393 to 468 days) compared to the current results. Except for AFC, the estimates for CI and DO reported for the indigenous Arsi breed by Kiwuwa *et al.* (1983) and Negussie *et al.* (1998) is similar to those obtained for the B in the current study. Likewise, compared to the current findings, Haile-Mariam *et al.* (1993) also reported younger AFC for F_1 (31.5±0.2 months) and 3/4 Friesian x Boran crosses (32.7±0.9 months). Their estimates for AFC for Boran heifers (45.2 months), CI and SPC for both Boran and crossbred cows are, however, similar to current estimates. The difference, particularly regarding AFC, of the crossbred heifers between the current study and the previous studies is mainly a reflection of differences in heifer rearing practices followed; otherwise the ranking orders of different genotypes are similar. Thus, the more advanced AFC obtained in the current study compared to the previous studies indicates the potential that could be exploited by merely improving management.

Table 6.3 Least-squares means and standard errors for different reproductive traits by genotype class

Genotype[1]	Traits[2]			
	AFC (mo)	CI (days)	DO (days)	SPC (no)
Boran	42.5±0.5	473±7	158±8	1.71±0.04
Friesian and its crosses				
1/2F:1/2B(F1)	36.0±0.4	417±6	133±7	1.49±0.04
1/2F:1/2B(F2)	39.6±0.6	435±10	141±9	1.60±0.06
5/8F:3/8B	38.5±1.0	426±18	131±15	1.41±0.11
3/4F:1/4B	36.7±0.7	444±13	148±13	1.70±0.09
Friesian	37.3±0.3	459±4	154±3	1.73±0.03
Jersey crosses				
1/2J:1/2B (F1)	35.4±0.5	408±6	123±7	1.31±0.04
1/2J:1/2B (F2)	39.2±0.6	430±10	146±9	1.44±0.06
3/4J:1/4B	37.7±0.7	426±11	141±11	1.46±0.08
Three-breed cross				
1/4F:1/4J:1/2B	40.2±0.8	411±14	122±14	1.42±0.09

[1] genotypes are defined in Table 6.1.

[2] Traits are defined in Table 6.2 .

6.3.2 Crossbreeding parameter estimates

Estimates for breed additive, heterozygosity and recombination effects are presented in Table 6.4. These results indicate that the direct additive contribution of the F and J breeds to the improvement of the reproductive performance of the progeny was only significant for AFC. However, the crossing of F and J with B resulted in desirable heterosis ($P<0.01$) in all reproduction traits. The heterotic estimates expressed relative to the mid-parent values were 9 and 11% for AFC, 10 and 11% for CI, 15 and 19% for DO, 14 and 21% for SPC for F x B and J x B crosses, respectively. Although the data set contained inter se and backcross generations, the recombination loss was only significant for AFC ($P<0.05$) in the F x B crosses.

Table 6.4 **Crossbreeding parameter estimates and standard errors for reproduction traits**[1]

Genetic effects [2]	AFC (mo)	CI (days)	DO (days)	SPC (no)
g_F	-5.4±0.6***	-13±7	-4±5	0.03±0.05
g_J	-5.5±1.9***	-26±33	-12±26	-0.09±0.23
h_{FB}	-3.7±0.5***	-50±7***	-23±5***	-0.24±0.05***
h_{JB}	-4.5±0.9***	-52±18**	-29±14*	-0.35±0.12**
r_{FB}	2.9±1.0*	-17±18	-14±14	-0.07±0.11
r_{JB}	3.4±1.8	-14±31	12±24	-0.10±0.20

[1] Traits are defined in Table 6.2.

[2] Genetic effects are defined in Table 6.1.

Significance: *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$

Several reports have shown that when *Bos taurus* dairy breeds are crossed with tropical indigenous breeds, the crossbreds exhibit a reduction in age at first calving as result of the additive breed contributions of dairy breeds or heterosis or both (e.g. Cunningham and Syrstad, 1987; Sharma and Pirchner, 1991; Thorpe *et al.*, 1993; Rege *et al.*, 1994; Rege, 1998). In general agreement to the current results, several studies reported non-significant differences for CI, DO and SPC between European dairy breeds and tropical indigenous cattle in tropical environments (e.g. Teodoro *et al.*, 1984; Madalena *et al.*, 1990a; Sharma and Pirchner, 1991; Rege *et al.*, 1994). In contrast to this, Thorpe *et al.* (1993) reported significant breed differences in calving intervals between the Sahiwal and *Bos taurus* dairy breeds (Friesian, Ayrshire and Brown Swiss breeds combined). Kahi *et al.* (2000) also reported a 42 days shorter calving interval in the Sahiwal than in the Ayrshire breed.

The significant heterosis estimated, particularly for AFC and CI, is consistent with reports in the literature (Sharma and Pirchner, 1991; Thorpe *et al.*, 1993; Rege, 1998; Kahi *et al.*, 2000). The current desirable heterotic estimates for AFC and CI are comparable to the average heterosis estimated for AFC (4.2 months) and CI (42 days) as revealed in several crossbreeding studies between *Bos taurus* x *Bos indicus* crosses in the tropics by Rege (1998). In contrast to this, no heterosis in crossing *Bos taurus* dairy breeds with *Bos indicus* cattle was found for CI, DO and SPC (Rege *et al.*, 1994), for SPC (Teodoro *et al.*, 1984) and for CI (Madalena *et al.*, 1990a).

The estimate for recombination loss reported in the literature for the reproductive traits of crossbred cows in the tropics are generally limited and apply mainly to AFC and CI. In most studies the recombination effects were reported to be a non-important genetic factor for CI (e.g. Mackinnon *et al.*, 1996; Kahi *et al.*, 2000; Khalil *et al.*, 2000; Rutledge, 2001). The estimates for the genetic effects obtained for AFC indicated that about 2.9±1.0 months delay in AFC could be attributed to the recombination loss. In general agreement to this result, Rutledge (2001), based on the reviewed performance data of *Bos taurus* x *Bos indicus* crosses, estimated about 8.9±7.2 months delay in AFC for second generation crosses due to what he called "recombination load" or for the loss of the "intact ancestral gene complex". Thus, the recombination effect seems to be an important component of heterosis for AFC in F x B crosses.

6.3.3 Heritability and repeatability estimates

Variance components, heritability (h^2), cow effect (c^2) and repeatability (r^2) estimates for AFC, CI, DO and SPC are presented in Table 6.5. The direct heritability estimate for AFC (0.44±0.05) was high when compared to the literature average of 0.31 for tropical dairy cattle reviewed by Lôbo *et al.* (2000). The estimates of the direct heritabilities and repeatabilities for CI, DO and SPC were low, but they are within ranges of estimates reported in the literature for tropical dairy cattle (e.g. De Alba and Kennedy, 1984; Mackinnon *et al.*, 1996; Khan *et al.*, 1999; Lôbo *et al.*, 2000; Ojango and Pollott, 2001). The high heritability estimates for AFC indicate that there is a potential for improvement of this trait through selection within each genetic group or from a synthetic population. The low heritabilities for CI, DO and SPC indicate that improvement in these traits could primarily be achieved genetically through crossbreeding or by improving herd reproductive management practices.

Table 6.5 **Estimates of variance components, heritabilities (h^2±s.e.), cow effects (c^2±s.e.) and repeatabilities (r^2±s.e) for reproduction traits[1]**

Estimate[2]	AFC	CI	DO	SPC
V_a	7.60	770	170	0.038
V_c	-	601	466	0
V_e	9.66	8616	4047	0.550
V_p	17.27	9987	4683	0.588
h^2	0.44±0.05	0.08±0.03	0.04±0.03	0.08±0.02
c^2	-	0.06±0.03	0.10±0.04	0
r^2	-	0.14±0.02	0.14±0.02	0.08±0.01
e^2	0.56±0.05	0.86±0.02	0.86±0.02	0.92±0.01

[1] traits defined in Table 6.2.

[2] V_a is additive genetic variance, V_c is permanent environmental variance, V_e is residual variance and V_p is phenotypic variance.

6.4 Conclusions

It may be concluded that crossbreeding the Friesian and Jersey breeds with the indigenous Boran improved the reproductive performance of the crossbred progenies, primarily as a result of increased heterozygosity. Thus, taking into consideration the relatively high milk production and reproductive performance of F_1 cows, the breeding program aimed at using the first generation Friesian and Jersey crosses as dairy cows might give the maximum cumulative benefit to the producers under the current dairy production conditions in Ethiopia. The use of both Friesian and Jersey crosses would provide a wider option to accommodate future shifts in the demand for traits that are not evaluated in the current study. In face of the current poor performance and the low heritability of most traits, as well as the non-existence of an organized breeding infrastructure, continued crossbreeding to produce F_1 cows as dairy animals, might be a more cost effective breeding option than selection within a synthetic population or the indigenous breeds. However, for such breeding decision an economic evaluation of different breeding programs is needed.

Chapter 7

General conclusions and recommendations

Animal breeding data from long-term experiments that are conducted under limited infrastructure and resources, are generally expected to present several problems. This study was no exception. However, the crossbreeding project used in this study has one important quality. It includes three of the most important indigenous breeds and their contemporary crossbred progenies with the three *Bos taurus* breeds. This allowed for the comparisons of the performance of several crossbred genotypes at the same time. The results, as well as some of the problems noted in this study, have important implications in designing breeding programs for similar resource poor environments.

It has been noted, as in all comparable previous studies in Ethiopia (e.g. Kiwuwa *et al.*, 1983; Haile-Mariam *et al.*, 1993; Haile-Mariam and Kassa Mersha, 1995; Negussie *et al.*, 1998), that animal performance has declined over years in almost all the traits studied (Chapters 4, 5, and 6). The recurrent drought and political instability are among the major causes, however, improper resource planning for long-term breeding programs could also be contributing factor. This negative environmental influence generally limited the expression of the genetic potential and the expected marginal differences between different genotypes. In order to evaluate animal performance, a proper definition of the environment (in terms of feeding and health management and other resources) is required. It should also be maintained as uniform as possible throughout the evaluation period. As a result of the low level of management (particularly feeding), the performance of animals measured in terms of growth, milk production and reproduction for all genotypes is generally lower than expected. As McDowell (1985) puts it: "this might be a result of the miss-interpretation of the concept that: crossbreds are more efficient in utilizing locally available resources". This does not mean that they can withstand sever malnutrition and disease infestation. Crossbred animals, because of the blend of genes (productivity and adaptability) they are carrying from the two parental breeds, are efficient in utilizing local resources, however, to obtain acceptable levels of biological efficiency, their intake should be approximately twice its maintenance requirements (McDowell, 1996). However, although no measurement in feed intake was obtained in the current study, the feeding levels of experimental animals, was definitely lower than this general recommendation.

The other limitation in this crossbreeding design was that the purebred *Bos taurus* and their reciprocal crosses were not involved. This means that only individual direct genetic effects, under the assumption of non-maternal effects, could be estimated. The assumption of non-maternal effects, particularly for early growth traits, is generally not true. For example, the unexpected negative direct heterosis and positive recombination loss, estimated for birth weight (Chapter 3), could not be further investigated by fitting additional maternal effects, because of the mentioned limitation in data structure. Likewise, the accuracy of estimates for additive and non-additive effects for other traits might also be lower, because of the absence of reciprocal crosses and purebred *Bos taurus* information (Sölkner and James, 1990).

In spite of the aforementioned limitations in animal management and breeding design, the following major conclusions and recommendation can be drawn from this study.

As indicated in Chapter 2, the model based on dominance alone has a lower goodness of fit compared to the models with epistatic effects included to describe the genetic differences between different genotypes. The implication of this result is that epistasis seems to be an important component of heterosis and need to be considered in performance evaluation of *Bos taurus* x *Bos indicus* crosses, as exemplified for breed crosses involved in this study. The significant negative estimates for the recombination loss for the majority of the traits investigated (Chapters 3, 5 and 6) indicate that synthetic breed formation should not be considered as a promising breeding option unless a very effective selection program based on large population size is implemented, in order to counteract the loss from negative recombination effects. Swan and Kinghorn (1992) indicated that, if functionally related genes are linked, the recombination loss will appear in several generations of crosses to come. This further will limit the genetic progress that could be expected from a selection program within a composite population.

The Friesian crosses were superior to Jersey crosses for the majority of traits studied, except for reproductive traits (Chapter 6) and milk yield expressed in terms of metabolic body weight (Chapter 5). In a previous study (Kiwuwa *et al.*, 1983) that included milk quality traits, the productivity of the Friesian and Jersey crosses was alike. Since the present study did not include traits such as feed efficiency, milk quality and viability traits, it is difficult to make firm conclusions regarding these two breed crosses. It would rather be better to use both breeds (with some known differences in merit) in future crossbreeding programs, this would provide different options in order to meet possible changes in demand.

The total crossbred and purebred dairy cattle population in Ethiopia is very small and the majority of these are in small herds scattered all over the country with in institutional herds. Furthermore, virtually no performance is recorded in any of the privately owned herds. Even in the institutional herds, where there are some performance records available, the quality of information is not always up to standard. These conditions plus the low heritability estimates obtained for growth (Chapter 4), milk production (Chapter 5) and reproduction (Chapter 6) traits in the current and similar previous studies (Haile-Mariam, 1994) practically limits the application of selection. Therefore, the short term breeding program particularly for the dairy traits under Ethiopian conditions, can only be based on crossbreeding. However, concurrent other measures, such as the implementation of an effective performance recording systems for economically important traits and improved animal management should be implemented as well.

In general, the first generation crosses (F_1) showed superiority in growth traits (Chapter 3; Banjaw and Haile-Mariam, 1994), milk production traits (Chapter 5; Kiwuwa *et al.*, 1983; Haile-Mariam, 1994) and reproduction traits (Chapter 6; Kiwuwa *et al.*, 1983; Haile-Mariam *et al.*, 1993; Negussie *et al.*, 1998). Furthermore, studies on preweaning viability and abortion rate in cows (Haile-Mariam, 1994) also favoured the F_1 crosses compared to their purebred parental breeds and other generations of crosses. This overall superiority of F_1 crosses is primarily attributed to the significant heterosis obtained in all traits studied.

This study as well as previous experience indicated that a breeding strategy aimed at production and utilization of F_1 crosses, primarily for the improvement of milk production and secondarily for meat and draft power, as a by-product, would yield the highest benefit to the farmers as well as to the nation at large. The question that needs to be investigated is how F_1 females could be economically produced continuously. The disadvantage of this system is that it requires the maintaining of both purebred parental populations. It is, however, more flexible and could easily be changed into another system of crossbreeding, if desired.

As an alternative to the F_1 system, the three-breed composite formation attempted using the Friesian and Jersey crosses did not show any improvement in all traits studied compared to the performances of direct *inter se* F_2 crosses (Chapter 3 to 6). However, further research of the three-breed crossing systems is needed. For example, systems such as crossing of the indigenous breeds first to, either Friesian or Jersey for the production of F_1 crosses and then mating them to the alternative breed (Friesian or Jersey) that was not involved in the F_1 formation. This system is similar to a three-breed terminal sire breeding system in beef production and is expected to generate higher levels of heterosis while maintaining the possible recombination loss at lower levels (Swan and Kinghorn, 1992).

Finally, there are several aspects of cattle improvement that need to be addressed in future research:

- Since Ethiopia experiences recurrent droughts and climatic changes, survival of different crossbred animals at different ages is an important economic trait that needs to be investigated.
- Economic evaluation of different alternative crossbreeding strategies
- Optimum feeding and health care of crossbred animals and its economic feasibility under Ethiopia conditions.
- So far, all crossbreeding or breed improvement studies were based on data collected from government institutions; there is a need to collect and analyse performance data local farmers.

Last but not least, successful long-term breeding programs can only be possible with the participation of farmers, particularly those investing for profit. There is sufficient experience world wide about the role and participation of farmers in breeding programs. These experiences could be applied in Ethiopia as well. For example, the Boran cattle, which originated in Ethiopia, have commercial breeding societies working towards its improvement in several countries in Africa and elsewhere, but not in Ethiopia. As a result of this, the performance of the Boran and its crosses, particularly for growth traits as reported in this study and those from other countries, are non-comparable (e.g. Herring et al. 1996, in USA; Frisch and O'Neill 1998, in Australia).

Abstract

Five separate studies were conducted to investigate the genetic factors affecting growth, milk production and reproduction traits in *Bos indicus* x *Bos taurus* crosses in Ethiopia. The first three studies were based on early growth data collected from the purebred Boran (Bo), Barca (Ba), Horror (Ho) (*Bos indicus*) and their crosses with the Friesian (F), Jersey (J) and Simmental (S) breeds (*Bos taurus*). Early growth data were for calves that were representing three purebred *Bos indicus* and 38 crossbred genotypes and were separated from their dams one day after birth and fed milk from a bucket. The fourth and fifth studies were based on milk and reproduction data collected from cows of two purebreds (Boran and Friesian) and eight crossbred (crosses of Friesian and Jersey with Boran) genotypes.

In the first study, five genetic models were evaluated for goodness of fit and estimation of crossbreeding parameters. These models were: 1) Dominance model, 2) Dickerson's model (recombination loss), 3) Additive x dominance interaction model, 4) Dominance x dominance interaction model and 5) Kinghorn's model (x). Models 2 to 5 are epistatic models that included all effects in model one plus one type of epistatic interaction based on a two-locus gene model. The models were evaluated using data for birth, weaning, yearling weights and preweaning average daily gain. All five models tested provided high levels of fit, with adjusted R^2 values averaging 93% over traits. All the epistatic models fit the data significantly ($P<0.05$) better than the dominance model for all the traits. Among the epistatic models, Dickerson's model (Model 2) gave significantly ($P<0.05$) higher R^2 values compared to the other epistatic models. Crossbreeding parameters estimated from this model has relatively lower sampling correlations and correspondingly lower standard errors. This model could, therefore, be considered as the most appropriate one for parameter

estimation and prediction of performances of untested genotypes for future crossbreeding decisions for the breeds involved in this study.

In the second study, breed difference, heterosis and recombination loss were estimated for birth weight (BWT), weaning weight (WWT), preweaning average daily gain (ADG) and yearling weight (YWT), fitting an animal model. Differences between genotypes were significant ($P<0.01$) for all traits. Genetic group means adjusted for environmental effects ranged from 20 to 30 kg for BWT, 88 to 114kg for WWT, 122 to 157kg for YWT and 358 to 492g for pre-weaning average daily gain (ADG). The breed additive effect of the F as a deviation from the Bo was significant ($P<0.01$) and positive for all traits. Relative to the Bo mean, the additional breed additive contribution of the F breed on BWT, WWT, ADG and YWT was 39.3, 16.5, 9.3 and 10.3%, respectively. On the other hand, the breed additive effects of the Ho and J breeds were significantly ($P<0.01$) negative for all traits. The heterotic effects were significantly negative ($P<0.01$) for BWT for all F and S crosses, but positive ($P<0.01$) for all other traits for all types of crosses. The average heterosis estimated within the F, J and S breeds were: -2.1±0.6, 0.2±0.6 ($P>0.05$) and -2.3±0.6 kg for BWT, 8.8±2.1, 11.8±2.3 and 13.7±2.4 kg for WWT, 60.4±11.3, 64.8±12.3 and 90.6±12.7 g for ADG and 19.8±2.6, 19.5±2.8 and 20.8±2.9kg for YWT, respectively. The recombination effects were significant ($P<0.01$) for the majority of crosses for all traits. The estimates for the recombination loss were negative for all traits, except for BWT. The average recombination effects estimated within the F, J and S breeds were: 2.6±0.8, 2.9±0.9 and 2.4±1.0 kg for BWT, -13.6±3.2, -4.2±3.4 ($P>0.05$) and -16.0±4.0 kg for WWT, -88.0±17.1, -39.4±18.4 and -102.2±21.3 g for ADG and -14.4±4.0, -0.1±4.4 ($P>0.05$) and -17.5±4.9 kg for YWT, respectively.

In the third study, variance components and direct and maternal heritabilities were estimated for weight at birth, weaning and yearling and preweaning average daily gain. Data were analysed using six alternative animal models (direct and including or excluding maternal effects). The direct heritability estimates from the "best" model for each trait were: 0.14±0.03 for birth weight, 0.08±0.03 for weaning weight, 0.06±0.02 for preweaning average daily gain and 0.13±0.03 for yearling weight. The direct maternal heritability estimates were small, but significantly different from zero for only birth weight (0.07±0.02), weaning weight (0.04±0.02) and preweaning average daily gain (0.04±0.02). Direct genetic correlations between birth weight and the other three traits were: 0.66±0.08, 0.55±0.19 and 0.50±0.12 with weaning weight, preweaning average daily gain and yearling weight, respectively. The genetic correlation between weaning weight, preweaning average daily gain and yearling weight was high and ranged from 0.82±0.11 to 0.97±0.01. Small, but non-zero maternal heritabilities estimated for weaning and preweaning average daily gain for artificially reared calves in this study should be interpreted cautiously because of potential bias from unaccounted breed additive and non-additive effects of the dam. Results of this study also showed that estimates of variance components and genetic parameters suitable for general use can be obtained from mixed purebred and crossbred data after appropriately accounting for breed additive and non-additive effects.

In the fourth study, breed additive and non-additive effects plus heritabilities and repeatabilities for milk yield per lactation (LMY), milk yield per day (DMY), lactation length (LL), annual milk yield (AMY), annual milk yield per metabolic body weight (AMYBW) and cow weight at calving (BW) were estimated. In addition, genetic, phenotypic and permanent environmental correlations were estimated between AMY and LL, AMY and BW and LL and BW. Data for each trait were analysed, using two equivalent repeatability animal models: first, fitting genotype as a fixed group effect and in the second model substituting genotype with breed additive, heterotic and recombination effects as fixed covariates. Among the genotypes the Bo had the lowest and the F the highest performance for all traits. The least-squares means for the Bo breed were 529±65 kg for LMY, 2.8±0.1 kg for DMY, 193±6 d for LL, 514±61 kg for AMY, 7.8±0.7 for AMYBW and 304±3 kg for BW. Both F and J breed additive effects, measured as a deviation from the Bo breed were significant (P<0.01) for all traits, except for BW of the J. The F and J additive contributions were 2774±89 and 1473±362 kg for LMY, 7.1±0.2 and 4.8±0.8 kg for DMY, 146±8 and 81±7 d for LL, 2345±71 and 1238±319 kg for AMY, 20.6±0.9 and 18.9±4.3 kg for AMYBW and 140±4 and -21±22 kg ($P>0.5$) for BW, respectively. The heterotic contributions to the crossbred performance were also positive and significant ($P<0.01$) for all traits, except for BW in the F x Bo crosses. The F_1 heterosis expressed as a deviation from the mid-parent values were 22 and 66 % for LMY, 11 and 20% for DMY, 29 and 29% for LL, 21 and 64 % for AMY, 42% ($P>0.05$) and 42 % for AMYBW and 2% ($P>0.5$) and 11% for BW for the F x Bo and J x Bo crosses, respectively. The recombination effect estimated for the F x Bo crosses was negative and significant for LMY (-526±192 kg, $P<0.01$), DMY (-3.0±0.4 kg, $P<0.001$) AMY (-349±174, $P<0.05$) and BW (-68±11 kg, $P<0.001$). For the J x Bo crosses the recombination loss was only significant and negative for DMY (-2.2±0.7 kg, $P<0.05$) and BW (-33±17, $P<0.05$). The direct heritabilities (h^2) and repeatabilities (r^2) estimated for each trait after correcting for the fixed environmental and breed additive and non-additive effects were 0.24±0.04 and 0.39±0.02 for LMY, 0.19±0.03 and 0.30±0.02 for DMY, 0.13±0.03 and 0.19±0.02 for LL, 0.23±0.04 and 0.37±0.02 for AMY, 0.17±0.05 and 0.39±0.02 for AMYBW and 0.10±0.03 and 0.34±0.02 for BW, respectively. The estimated genetic correlations between AMY and LL, AMY and BW, LL and BW were 0.71±0.08, 0.17±0.18 and 0.23±0.20, respectively.

In the fifth study, estimates of breed additive differences, heterosis and recombination loss, as well as heritabilities were obtained for age at first calving (AFC), calving interval (CI), days open (DO) and number of services per conception (SPC). The genetic parameters were estimated using a repeatability animal model for CI, DO and SPC and a unitrait animal model for AFC. The overall least-squares means estimated were: 38.3±0.26 months, 435±4 days, 145±10 days and 1.58±0.03 (number) for AFC, CI, DO and SPC, respectively. The breed additive effects of F and J were only significant ($P<0.01$) for AFC. Relative to the Bo, both the F and the J additive contributions for AFC were

–5.4±0.5 and –5.5±1.9 months, respectively. Crossing the F and J breeds with the Bo breed also resulted in significant heterosis ($P<0.05$) ranging from 10 to 21% in all traits. The estimated recombination loss was only significant for AFC (2.8±1.0 months) for the F x Bo crosses. Heritability estimates were high for AFC (0.44±0.05) and low for CI (0.08±0.03), DO (0.04±0.03) and SPC (0.08±0.02). The corresponding estimates for the repeatability (r^2) were 0.14±0.02 and 0.14±.0.02 for CI and DO, respectively. The repeatability estimate for SPC was zero.

Opsomming

Vyf afsonderlike studies is uitgevoer om die genetiese faktore te ondersoek wat groei, melkproduksie en voortplantingseienskappe in *Bos indicus* x *Bos taurus*-kruisings in Ethiopië affekteer. Die eerste drie studies is op vroeë groeidata wat versamel is van suiwergeteelde Boran (Bo)-, Barca (Ba)-, Horro (Ho)-rasse (*Bos indicus*) en hul kruisings met Fries (F)-, Jersey (J)- en Simmentaler (S)- rasse (*Bos taurus*) versamel is gebaseer. Vroeë groeidata was van kalwers wat drie suiwergeteelde *Bos indicus* en 38 kruisgeteelde genotipes verteenwoordig het en wat een dag na geboorte van hulle moeders geskei is en melk uit 'n emmer gevoer is. Die vierde en vyfde studies is gebaseer op melk- en voortplantingsdata gebaseer wat van koeie van twee suiwergeteelde (Boran en Fries) en agt kruisgeteelde (Boran met Fries en Jersey) genotypes versamel is.

In die eerste studie is vyf genetiese modelle geëvalueer vir geskiktheid van passing en beraming van kruistelingsparameters. Hierdie modelle was: 1) dominansiemodel, 2) Dickerson se model (rekombinasie verlies), 3) additiewe x dominansie interaksie-model, 4) dominansie x dominansie interaksie-model en 5) Kinghorn se model (x). Modelle 2 tot 5 is epistatiese modelle wat al die effekte in model 1 ingesluit het, plus een tipe epistatiese inter-aksie gebaseer op 'n twee-locus gene-model. Die modelle is geëvalueer deur gebruik te maak van data vir geboorte-, speen- en jaaroudgewigte, asook voorspeense gemiddelde daaglikse toename. Al vyf modelle wat getoets is het hoë vlakke van passing vertoon, met aangepaste R^2-waardes wat 'n gemiddeld van 93% oor eienskappe bereik het. Al die epistatiese modelle het die data betekenisvol ($P<0.01$) beter vir al die eienskappe gepas as die dominansiemodel. Van die epistatiese modelle het Dickerson se model betekenisvol ($P<0.01$) hoër R^2-waardes getoon, vergeleke met die ander. Kruistelingparameters wat van hierdie model beraam is het relatief laer monsteringkorrelasies en ooreenstemmend laer standaardfoute gehad. Hierdie model kan derhalwe beskou word as die mees geskikte vir parameterberamings en voorspelling van die prestasie van ongetoetste genotipes vir toekomstige teeltbesluite oor raskruisings wat in hierdie studie betrokke is.

In die tweede studie is rasverskille, heterose en rekombinasieverliese vir geboortegewig (Ggew), speengewig (Sgew), voorspeense gemiddelde daaglikse toename (GDT) en jaaroudgewig (Jgew) deur 'n dieremodel te gebruik beraam. Verskille tussen genotipes was betekenisvol ($P<0.01$) vir alle eienskappe. Genetiese groepgemiddeldes aangepas vir omgewingseffekte het van 20 tot 30kg gewissel vir Ggew, 88 tot 114 kg vir Sgew, 122 tot 157 kg vir Jgew en van 358 tot 429g vir voorspeense gemiddelde daaglikse toename (GDT). Die ras-additiewe effek van F as 'n afwyking van die Bo, was betekenisvol ($P<0.01$) en positief vir alle einskappe. Relatief tot die Bo-gemiddelde was die bykomende additiewe bydrae van die F-ras op Ggew, Sgew, GDT en Jgew onderskeidelik 39.3, 16.5, 9.3 en 10.3%. Hierteenoor was die additiewe effekte van die Ho- en J-rasse betekenisvol ($P<0.01$) negatief vir alle eienskappe. Die heterose-effekte was betekenisvol negatief ($P<0.01$) vir Ggew vir alle F- en S-kruisings, maar positief ($P<0.01$) vir alle ander eienskappe vir alle tipe kruisings. Die gemiddelde heterose wat binne die F-, J- en S-rasse beraam is, was onderskeidelik -2.1±0.6, 0.2±0.6 ($P>0.05$) en -2.3±0.6 vir Ggew, 8.8±2.1, 11.8±2.3, en 13.7±2.4 kg vir Sgew, 60.4±11.3, 64.8±12.3 en 90.6±12.7 g vir GDT en 19.8±2.6, 19.5±2.8 en 20.8±2.9 kg vir Jgew. Die rekombinasie-effekte was betekenisvol ($P<0.01$) vir die meerderheid van kruisings vir alle eienskappe. Die beramings van die rekombinasie-verlies was negatief vir alle eienskappe, behalwe vir Ggew. Die gemiddelde rekombinasie-effekte wat beraam is binne die F-, J- en S-rasse was onderskeidelik 2.6±0.8, 2.9±09 en 2.4±1.0 kg vir Ggew, -13.6±3.2, -4.2±3.4 ($P>0.05$) en -16.0± 4.0 kg vir Sgew, -88.0±17.1, -39.4±18.4 en -102.2±21.3 g vir GDT en -14.4±4.0, -0.1± 4.4 ($P>0.05$) en -17.5±4.9 kg vir Jgew vir genoemde drie rasse onderskeidelik.

In die derde studie is variansiekomponente en direkte en maternale oorerflikhede vir gewig by geboorte, speen en jaaroud en voorspeense gemiddelde daaglikse toename onderskeidelik beraam. Data is deur die passing van ses alternatiewe dieremodelle (direk en met in- of uitsluiting van maternale effekte) ontleed. Die direkte oorerflikheidsberamings van die “beste” model vir elke eienskap was: 0.14±0.03 vir geboortegewig, 0.08±0.03 vir speengewig, 0.06±0.02 vir voorspeense gemiddelde daaglikse toename en 0.13±0.03 vir jaaroudgewig, Die direkte maternale oorerflikheidsberamings was klein, maar betekenisvol verskillend van slegs zero vir geboortegewig (0.07±0.02), speengewig (0.04±0.02) en voorspeense gemiddelde daaglikse toename (0.04±0.02). Direkte genetiese korrelasies tussen geboortegewig en die ander drie eienskappe was onderskeidelik 0.66±0.08, 0.55±0.19 en 0.50±0.12 met speengewig, voorspeense gemiddelde daaglikse toename en jaaroudgewig. Die genetiese korrelasies tussen speengewig, voorspeense gemiddelde daaglikse toename en jaaroudgewig was hoog en het tussen 0.82±0.11en 0.97±0.01 gewissel. Klein, maar nie-zero maternale oorerflikhede wat speengewig en voorspeense gemiddelde daaglikse toename vir kunsmatig-grootgemaakte kalwers in hierdie studie beraam is, moet met omsigtigheid geïnterpreteer word vanweë die potensiële sydigheid van onverklaarde ras-additiewe en -nie-additiewe effekte van die moeder. Resultate van hierdie studie het ook getoon dat beramings van variansie-komponente en genetiese parameters wat geskik is vir algemene gebruik, verkry kan word van gemengde, suiwergeteelde en kruisgeteelde data na behoorlike inagneming van ras-additiewe en -nie-additiewe effekte.

In die vierde studie is ras-additiewe en –nie-additiewe effekte beraam, asook oorerflikhede en herhaalbaarhede vir melkopbrengs per laktasie (LMO), melkopbrengs per dag (DMO), lengte van laktasie (LL), jaarlikse melkopbrengs (JMO), jaarlikse melkopbrengs per metaboliese liggaamsgewig (JMOLgew), en koeigewig met kalwing (Lgew). Bykomend is genetiese, fenotipiese en permanente omgewingskorrelasies tussen JMO en LL, JMO en Lgew en LL en Lgew beraam. Data vir elke eienskap is ontleed deur twee ekwivalente herhaalbaarheids-dieremodelle te gebruik: eerstens, deur genotipe as ‘n vaste groep-effek te pas en in die tweede model genotipe te vervang deur ras-additiewe, heterose en rekombinasie-effekte as vaste ko-veranderlikes. Van die genotipes het die Bo die laagste en die F die hoogste prestasie vir al die eienskappe gehad. Die kleinste vierkantgemiddeldes vir die Bo-ras was 529±65 kg vir LMO, 2.8±0.1 kg vir DMO, 193±6d vir LL, 514±61 kg vir JMO, 7.8±0.7 vir JMOLgew en 304±3 kg vir Lgew. Beide F en J ras-additiewe effekte, wat gemeet is as 'n afwyking van die Bo-ras was betekenisvol ($P<0.01$) vir alle eienskappe, behalwe vir Lgew van J. Die F en J additiewe bydraes was onderskeidelik 2774±89 en 1473±362 kg vir LMO, 7.1±0.2 en 4.8±0.8 kg vir DMO, 146±8 en 81±7 d vir LL, 2345±71 en 1238±319 kg vir JMO, 20.6±0.9 en 18.9±4.3 kg vir JMOLgew en 140±4 en -21±22 kg ($P>0.5$) vir Lgew. Die heterose-bydrae tot die kruisteeltprestasie was ook positief en betekenisvol ($P<0.01$) vir alle eienskappe, behalwe vir Lgew in die FxBo kruisings. Die F_1 heterose, uitgedruk as 'n afwyking van middelouerwaardes was onderskeidelik 22 en 66 % vir LMO, 11 en 20% vir DMO, 29 en 29% vir LL, 21 en 64% vir JMO, 42% ($P>0.05$) en 42% vir JMOLgew en 2% ($P>0.5$) en 11% vir Lgew vir F x Bo- en J x Bo- kruisings. Die rekombinasie-effek vir F x Bo kruisings was negatief en betekenisvol vir LMO (-526±192 kg, $P<0.01$), DMO (-3.0±0.4kg, $P<0.001$), JMO (-349±174, $P<0.05$) en Lgew (-68±11 kg, $P<0.001$). Vir J en Bo- kruisings was die rekombinasie-verlies slegs betekenisvol en negatief vir DMO (-2.2±0.7 kg, $P<0.05$) en Lgew (-33±17, $P<0.05$). Die direkte oorerflikhede (h^2) en herhaalbaarhede (r^2) wat vir elke eienskap beraam is nadat vir die vaste omgewings- en ras-additiewe en –nie-additiewe effekte gekorrigeer is, was onderskeidelik 0.24±0.04 en 0.39±0.02 vir LMO, 0.19±0.03 en 0.30±0.02 vir DMO, 0.13±0.03 en 0.19±0.02 vir LL, 0.23±0.04 en 0.37±0.02 vir JMO, 0.17±0.05 en 0.39±0.02 vir JMOLgew en 0.10±0.03 en 0.34±0.02 vir Lgew. Die beraamde genetiese korrelasies tussen JMO en LL, JMO en Lgew, LL en Lgew was onderskeidelik 0.71±0.08, 0.17±0.18 en 0.23±0.20.

In die vyfde studie is beramings van ras-additiewe verskille, heterose en rekombinasie-verliese, sowel as oorerflikhede gemaak vir ouderdom met eerste kalwing (OEK), kalwings-interval (CI) , dae oop (DO) en aantal dekkings per bevrugting (DPB). Die genetiese parameters is beraam deur 'n herhaalbaarheidsdieremodel vir CI, DO en DPB en 'n enkeleienskap-dieremodel vir OEK te pas. Die algehele kleinste kwadraatgemiddeldes wat beraam is, was onderskeidelik 38.3±0.26 maande, 435±4 dae, 145±10 dae en 1.58±0.03 (getal) vir OEK, CI, DO en DPB. Die ras-additiewe effekte van F en J was slegs vir OEK betekenisvol ($P<0.01$). Relatief tot die Bo, was beide die F en J additiewe bydraes vir OEK onderskeidelik -5.4±0.5 en -5.5±1.9 maande onderskeidelik. Kruising van die Bo met die F- en J-rasse het ook betekenisvolle heterose tot gevolg gehad ($P<0.05$) wat van 10 tot 21% in alle eienskappe gewissel het. Die beraamde rekombinasie-verlies was slegs vir OEK (2.8±1.0 maande) vir F- en Bo-kruisings betekenisvol. Beramings van oorerflikheid was hoog vir OEK (0.44±0.05) en laag vir CI (0.08±0.03), DO (0.04±0.03) en DPB (0.08±0.02). Die ooreenstemmende beramings vir die herhaalbaarhede (r^2) was onderskeidelik 0.14±0.2 en 0.14±0.02 vir CI en DO. Permanente omgewingseffek vir DPB was zero.

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