

Phenotypic and genetic characterization of South African Boran cattle

By

Denis Lochner

Dissertation submitted in partial fulfilment of the requirements for the
degree MAGISTER SCIENTAE AGRICULTURE ANIMAL SCIENCE

With specialization in Animal Breeding and Genetics

In the

Department of Animal and Wildlife Sciences

Faculty of Natural and Agricultural Sciences

University of Pretoria

Pretoria

South Africa

November 2018

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Denis Lochner

Supervisor: Prof Este van Marle-Köster

Co-supervisor: Dr Carina Visser

Department: Animal and Wildlife Sciences

Degree: MSc (Agric) Animal Breeding and Genetics

Acknowledgement

I first want to thank the Lord Almighty for giving me the strength and ability to finish this degree. As Philippians 4:13 says “I can do all things through Him who strengthens me”; with Him on my side I can do anything.

Next I want to thank my supervisor, Prof Esté van Marle-Köster, and my co-supervisor, Dr Carina Visser, for their endless patience – always greeting me with a smile and a door wide open for any questions I had any time of the day.

To my mom and dad, I want to say thank you for all the emotional and financial support – not just for the MSc degree, but also for the BSc (Agric) degree. Thank you both for always being there for me through all the challenges. Luckily there were good times as well and I would not have come so far in life without your support every step of the way.

To Oom Johan Erasmus, president of the Boran Cattle Breeders’ Society, thank you for allowing me permission to access the Boran data and for allowing me to come visit you on your farm. Your knowledge that you shared with me has also contributed to my success in this degree.

To Dr Bobby van der Westhuizen and Dr Helena Theron from SA Studbook, I want to thank you for the help with understanding some of the programs I used and for providing the data that I needed for this degree.

I also want to thank the BGP and TIA for their support for livestock genotyped data of genomics for SA beef cattle.

Lastly I want to thank Rulien Grobler in the Animal and Wildlife Science Department at the University of Pretoria for always lending a hand with my dissertation whenever I was struggling. You were always there when I needed you and I thank you for that.

Abstract

Boran cattle are classified as Zebu and have only been recognized as a breed in South Africa since 1995, with the establishment of the Boran Cattle Breeders' Society of South Africa on 17 May 2003. Although Boran breeders have been participating in animal recording since 2003 and also joined the BGP (Bovine Genomics Project) in 2016, limited scientific research has been performed on the South African Boran. The aim of this study was to perform a phenotypic and genetic characterisation of the South African Boran based on available data to provide reference data for compiling breeding objectives and further genomic applications. The phenotypic data consisted of pedigree data from 1995 to 2016 and Estimated Breeding Values (EBVs) for seven different traits recorded over the same time period. Pedigree completeness varied from 22.6%, six generations ago with improvement, to 100% in generation one. Furthermore, complete recording for production traits was limited to seven years. This affected the accuracy of the EBVs and could result in incorrect prediction and potential adverse effects on genetic improvement. Maternal birth weight and maternal weaning weight decreased, while birth weight direct and weaning weight direct increased. Yearling weight and final weight increased as well. This indicates that the genetic trends for the previously mentioned production traits were positive except for mature weight. Birth weight remains low which is positive in order to prevent dystocia. Decreased maternal traits can cause cows not being able to raise a calf to weaning due to not sufficient milk produced. Both age at first calving and calving interval also increased over time, resulting in heifers giving birth later in life and longer periods between calving. The genotypic data indicated low inbreeding (-0.027) and revealed high heterozygosity (0.371) for the South African Boran population. Population structure revealed two dominant groups for the Boran. In comparison with other breeds (Bosnmara, Hereford), the Boran was confined as a separate cluster. The Boran breed contributes a well-adapted genetic resource for the beef industry in South Africa. Results confirmed that more attention to breeding objectives and animal recording is required to improve and ensure long-term sustainability.

Declaration

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I have not allowed anyone to copy any part of my dissertation.

I have not previously submitted this dissertation for a degree at this or any other tertiary institution.

Signature:

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List of abbreviations

\$	American dollar
%	Percentage
ΔF	Rate of inbreeding
ADG	Average daily gain
AFC	Age at first calving
ARC	Agriculture research council
ATT	African tsetse fly-transmitted Trypanosomosis
BC	Before Christ
BCBS	Boran cattle breeders society
BGP	Bovine Genomic Project
BLUP	Best linear unbiased prediction
CI	Calving interval
CV error	Cross validation error
DD	Dam to daughter
DNA	Deoxyribonucleic acid
DS	Dam to son
EBV	Estimated Breeding Value
EBVs	Estimated Breeding Values
EVA	Evolutionary algorithms
F	Inbreeding coefficient
F_{IS}	Inbreeding per individual
FMD	Foot-and-mouth disease
Freq	Frequency
F_{ST}	Degree of differentiation among population
GCTA	Genome wide complex trait analysis
GDP	Gross domestic product
GEBV	Genomic estimated breeding value

Gen	Generation
GGP	Geneseek genomic profiler
GI	Gastro-intestinal
GxE	Genotype-environment interaction
h^2	Heritability
He	Heterozygosity expected
HO	Heterozygosity observed
HWE	Hardy-Weinberg equilibrium
IBD	Identical by descent
ICP	Inter-calving period
ID	Identification
Ig	Generation intervals
K	1000
Kg	Kilogram
K-value	Number of ancestral populations
L	Generation intervals
LD	Linkage disequilibrium
MAF	Minor allele frequency
MAS	Marker-assisted selection
MtDNA	Mitochondrial DNA
NCE	National cattle evaluations
N_E	Effective population size
p-value	Statistical significance levels
PCA	Principal Component Analysis
PCR	Polymerase chain reaction
PGD	Population genetics data
QC	Quality control
QTL	Quantitative trait loci

RFLPs	Restriction fragment length polymorphisms
R/kg	Rand per kilogram
RTU	Real time ultrasound
SAS	Statistical analysis software
SD	Sire to daughter
r_g	Genetic correlation
SNP	Single nucleotide polymorphisms
SS	Sire to son
T	Tonnes
TBD	Tick-borne diseases
U.S.A	United State of America
WGS	Whole-genome sequence

Chapter 1: Introduction

1.1 Introduction

Humans changed from hunting to the taming of wild animals which led to the domestication of livestock species (cattle, sheep, goats, pigs and buffalo) approximately 10 000 years ago (Ajmone-Marsan et al., 2010). Livestock species have the capability to turn plant material that is not suitable for human consumption, into animal protein. This source of protein provided the means for humans to survive and thrive in a wide range of environments (Blench & MacDonald, 2006). Since domestication selection became a continuous process to select and breed livestock for desirable traits, modern livestock breeds exhibiting genetic variation for a large variety of traits were produced (Wright, 2014). This led to the occurrence of remarkable phenotypic changes and contributed to the evolution of domesticated cattle (Stock & Gifford-Gonzalez, 2013).

All taurine and Zebu cattle decent from the wild Auroch, called *Bos primigenius* (Upadhyay et al., 2017). Fossil records identified three distinct sub-species of Auroch, namely the *B. p. africanus* that inhabited Northern Africa from the Middle Pleistocene period onwards (Linseele, 2004). Western Eurasia was inhabited mostly by *B. p. primigenius* and South Asia by *B. p. nomadicus*, who is supposedly wild ancestor of Zebu (Stock & Gifford-Gonzalez, 2013). Estimating the time period when *Bos taurus* and *Bos indicus* deviated from a common ancestor ranges from 2 million to 330 000 years ago, depending on the genetic markers applied for the analyses (Ajmone-Marsan et al., 2010).

Based on archaeological and molecular data, inferences have been made with regard to the history of African cattle, including their possible migration routes (Figure 1.1) on the African continent (Hanotte et al., 2002; Blench & MacDonald, 2006). Archaeological evidence and pictorial accounts support the statement that humpless *Bos taurus* were one of the first cattle on the African continent (Blench & MacDonald, 2006). These cattle spread from the north-eastern part of the continent to West and East Africa (Hanotte et al., 2002). The humpless longhorns were apparently introduced first, followed by humpless shorthorn cattle approximately 2 500 years later (Epstein, 1971; Rege, 1999). However, this “two waves” scenario of taurine cattle arriving in Africa has not yet been supported by any molecular evidence. After the initial taurine cattle dispersion, Zebu cattle were introduced to the African continent in two different stages (Hanotte et al., 2002). Zebu-introgressed taurine cattle may have been the first African cattle reaching the Southern part of Africa through the horn of the continent (Epstein, 1971; Hanotte et al., 2002). This route was linked with the expansion of

the 'Swahili-Arabs' cultivation that took place along the East African coast from the 7th century AD.

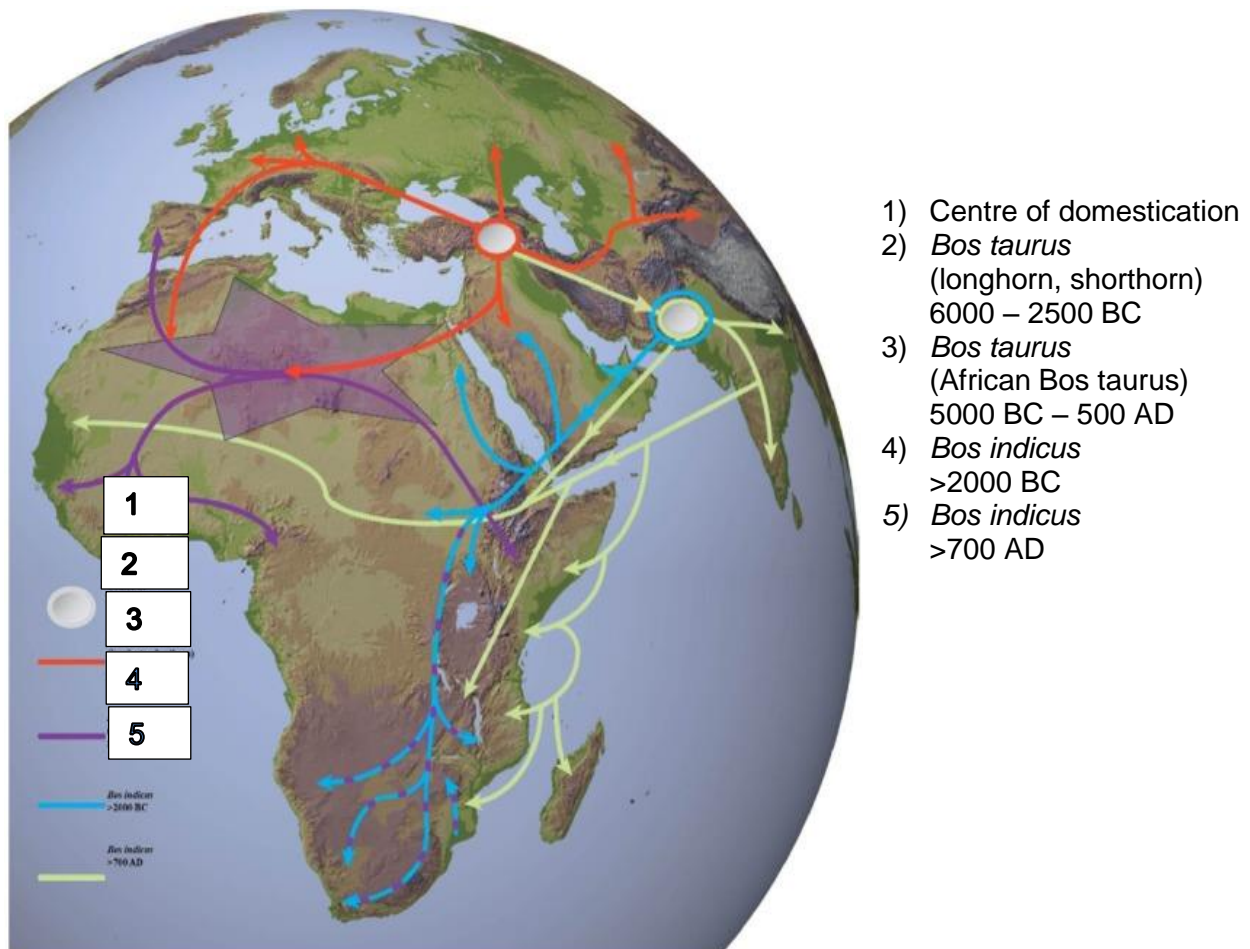


Figure 1.1: Migration route of cattle into Africa. Adapted from Mwai et al., (2015)

Currently, African cattle are divided into five different groups; namely Taurine (humpless), Zebu (humped *Bos indicus*), Sanga, Zenga and composite breeds (Felius et al., 2011). Some of these groups will be discussed in detail in the following section. The majority of cattle in Africa are classified as Zebu, which includes the Boran (Rege & Tawah, 1999; Felius et al., 2011). Research has suggested that Zebu cattle may have been present in Africa earlier than 2000 BC (Epstein, 1971). There are 150 recognised indigenous African breeds of which 25% are found in Southern Africa (Rege, 1999; Rege et al., 2007). African cattle, including the Boran, are known for their ability to tolerate high temperatures and drought conditions and to exhibit disease resistance (Mwai et al., 2015). Expression of traits will depend on the environment, genetics and genotype-environment (GxE) interactions (Stock & Gifford-Gonzalez, 2013). Although indigenous breeds are adapted to the local environments, they are relatively poor milk and meat producers compared to the commercial breeds raised in the extensive systems (Chan et al., 2010).

The largest proportion of Zebu cattle consists of Boran cattle and is kept in arid and semi-arid areas in Kenya (Ajmone-Marsan et al., 2010). Even though Boran cattle can be used for multiple purposes such as milk production, meat and draft power (Rege, 2001), in Kenya, Boran cattle are used mostly for beef and milk production (DAGRIS, 2010). However, in South Africa the Boran is predominantly used as a beef breed. Boran cattle are known for a high fertility rate, drought resistance, low disease susceptibility, and heat tolerance that all contribute to their ability to adapt to a variety of climates including large regions of South Africa (Chan et al., 2010; Mirkena et al., 2010).

Selection on phenotypes is limited to the traits that can be recorded during the production cycle of an animal within a specific environment (Makina, 2015). It is therefore of utmost importance that animal recording is performed with high accuracy for effective selection (Bergh, 2010; Goddard et al., 2011). Furthermore, genomics holds potential for increasing accuracy of selection via genomic selection and is achievable with complete and accurate animal recording (Goddard et al., 2011).

1.2 Aim of the study

Limited scientific research is available on the production performance of the South African Boran. Despite a relatively recent introduction in 1995 into South Africa the numbers of Boran cattle have increased to 36 048 registered Boran cattle in 2016. Boran breeders have been participating in animal recording since 2003, focussing on seven different traits of economic importance. Both pedigree and phenotypic records are submitted to SA Studbook for genetic evaluations. Estimated Breeding Values (EBVs) are provided to breeders for use in their selection programs. The Boran has also joined the BGP (Bovine Genomic Project) in 2016, to generate genotypic data. The University of Pretoria was approached by the Boran Breeders Society to perform a production analyses on the available phenotypic data and genotypic data.

The aim of this study was to perform a phenotypic and genetic characterisation of the South African Boran based on available phenotypic and genotypic data to provide reference data for compiling breeding objectives and further genomic applications through these objectives:

1. Evaluate the available phenotypic data to provide descriptive data for birth weight, weaning weight, yearling weight, final weight, mature weight, age at first calving and calving interval period.
2. Evaluate available EBV data and provide genetic trends for all traits
3. Analyse genotypic data for estimation of genetic diversity parameters and inbreeding
4. Estimate population structure of the Boran based on available genotypic data

Chapter 2: Literature review

2.1 Introduction

In South Africa there are 30 registered beef breeds using different service providers for genetic analyses, such as SA Studbook, ARC and Breedplan. The 2017 agricultural statistics report of the Department of Agriculture, Forestry and Fisheries (DAFF, 2017), reported 13.4 million beef cattle in South Africa which produces 1.19 million tonnes of beef annually, with a per capita consumption of 20.93 kg/year. This section provides an overview of the South African beef industry with reference to the Boran and traits related to beef cattle production focusing on the Boran breed. Further discussion will include genomics and the application thereof in the improvement of beef cattle.

2.2 Breed classification in Africa

African cattle breeds can be classified into two major types, namely Taurine cattle (*Bos taurus*) and Indicine cattle (*Bos indicus*) (Bradley et al., 1996). *Bos indicus* is phenotypically identifiable through the presence of a significant cervico-thoracic hump and further divided into Zebu proper and Zebu crossbred types (Rege, 1999). Zebu proper and Zebu crossbred types are classified into cervico-thoracic-humped and thoracic-humped depending on the hump's position on the animal's back (Epstein, 1971). Zebu cattle (*Bos indicus*) represent the majority of cattle types in Africa. Studies based on Y chromosome, autosomal and mtDNA analyses suggest that Zebu introgression on the Africa continent was primarily a male Zebu process (Bradley et al., 1994; Hanotte et al., 2002; Porto-Neto et al., 2013). It should also be noted that all African cattle carry Taurine mitochondrial DNA (Mwai et al., 2015).

Sanga cattle are crossbreds humped and thoracic-humped Zebu cattle with a cervico-thoracic hump (Hanotte et al., 2002). By crossbreeding Sanga and Zebu cattle, a new cattle group called "Zenga" was developed adding to the classification of cattle (Rege, 1999; Hanotte et al., 2002). Composite breeds are a mixture of two or more breeds (Felius et al., 2011). African cattle are therefore classified into five main groups; namely Taurine, Zebu, Sanga, Zenga and composite breeds (Felius et al., 2011). Figure 2.1 represent the distribution of indigenous cattle in Africa.

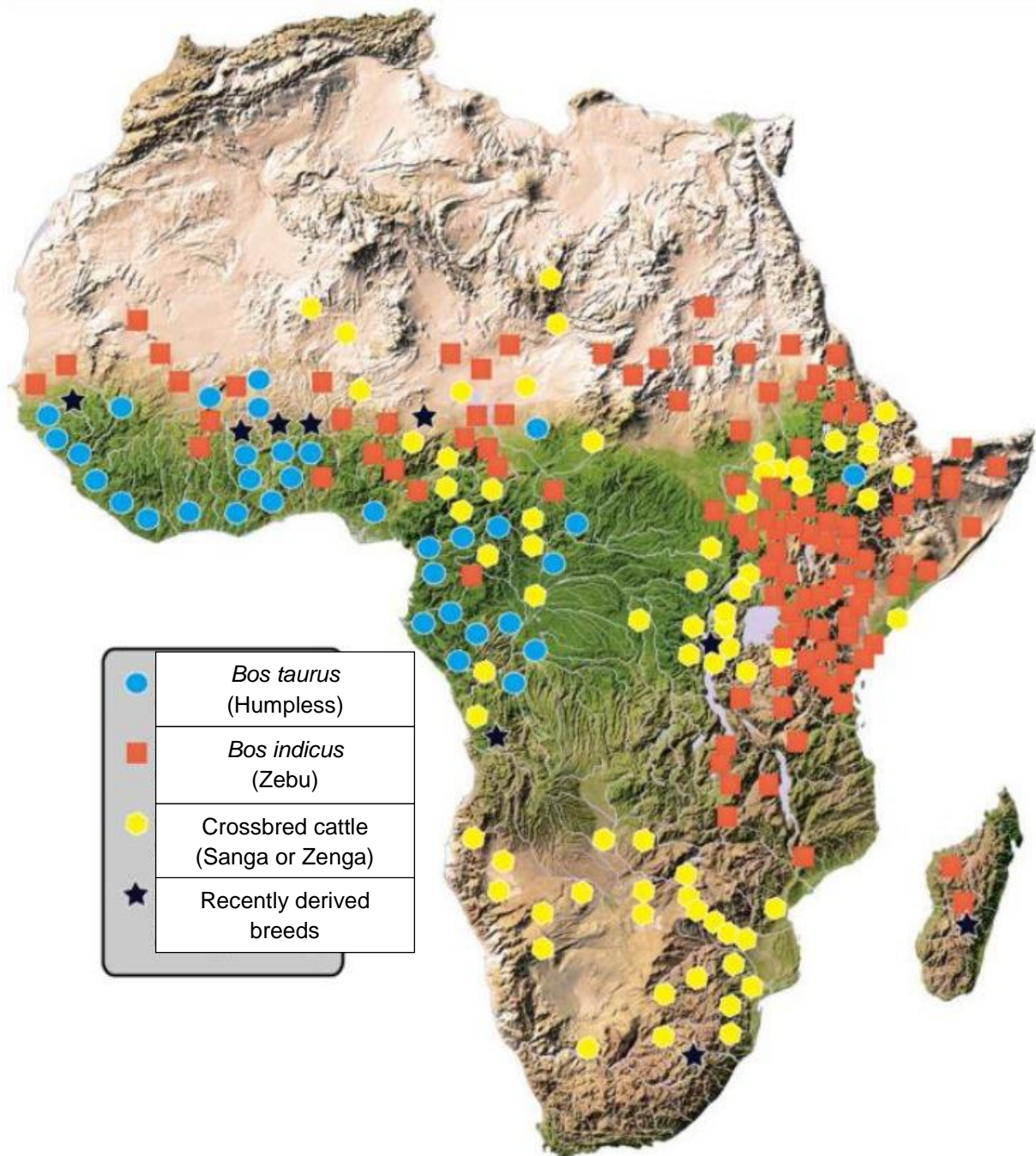


Figure 2.1: Distribution of cattle through Africa (Mwai et al., 2015)

Sanga cattle mainly reside in Eastern and Southern Africa and are recognised by their ability to adapt to seasonal changes and climatic harsh conditions (Mirkena et al., 2010). Sanga cattle consist of approximately 30 different breeds/strains and are sub-divided further into different ecotypes depending on their location (Felius et al., 2011). The entrance of the second Zebu wave in the Abyssinian regions and the coastal areas led to the introduction of Sanga cattle to the southern parts of Africa, such as Malawi and Zambia (Hanotte et al., 2000). Sanga cattle arrived in the most southern parts of Africa during the second wave of Zebu introgression, entering countries such as Zimbabwe, Mozambique and South Africa, for trading between tribes (Hanotte et al., 2000). These breeds included the Afrikaner and Nguni cattle (Makina et al., 2014). Drakensberger cattle are also classified under Sanga

types, but the origin of the Drakensberger cattle is unclear with a history dating back to the early settlers in the late 1700s (Scholtz et al., 2010).

Zebu cattle are the most abundant cattle on the African continent and are highly adapted to the varying environmental conditions in Africa (Rege, 1999; Chan et al., 2010). Zebu cattle include approximately 75 breeds of which approximately 61 are found in Eastern Africa and Southern-central Africa and the rest in the western parts of Africa (Bradley et al., 1994; Porto-Neto et al., 2013). Zebu cattle entered the Southern parts of Africa, such as Zimbabwe, Mozambique and South Africa, through the Zebu introgression stage (Hanotte, et al., 2000; Mwai, 2015). Table 2.1 shows a summary of indigenous cattle types in Africa.

One of the Zebu types found in South Africa is the Boran breed whose ancestors arrived in the horn of Africa approximately 1 300 to 1 500 years ago from Southwest Asia (DAGRIS, 2010; Decker et al., 2014). These cattle were located in the arid and semi-arid plateaus of Southern Ethiopia and then spread across Ethiopia, Northern Kenya and South-western Somalia (Hanotte et al., 2002; Ajmone-Marsan et al., 2010). The Kenyan Boran breed evolved from the Ethiopian Boran cattle, which were selected for beef production but are also currently used for milk production (DAGRIS, 2010). Between 1992 and 1995 Boran cattle were imported from Kenya into South Africa. In August 1995, the Department of Animal Improvement recognized the Boran as a breed and the Boran Cattle Breeders' Society of South Africa was established on 17 May 2003 (www.boran.org.za/Breed-History.htm).

Table 2.1: Summary of indigenous cattle breeds in Africa (<http://dagris.info/>)

Group	Breed name	Characteristics
Southern Africa Sanga	Shangan	Strain of Nguni cattle in South Africa
	Afrikaner	Walking and grazing ability, good mothering ability, longevity
	Watusi	Long, massive horns, medium body size and relatively short neck with weak legs
	Pedi	Mainly grey or black in colour with white patches as a result of selection
	Landim	Well adapted to hot, humid weather as well as dry periods, very resistant to Foot and Mouth disease
	Tswana	Tolerance to ticks, resistance to the endemic heartwater
	Nguni	High fertility, early sexual maturity, good foraging and walking ability, good mothering ability
	Kaokoveld	Phenotypically similar to the Ovambo, but larger in body size
	Okavango	Medium body size, between the Ovambo and Kaokoveld
	Damara	The original Damara cattle had typical Sanga characteristics, including cervico-thoracic hump and long horns. The modern Damara have shorter but spreading horns, and they resemble the Kaokoveld cattle
Humplless Longhorn	Ovambo	Phenotypically similar to Okavango cattle, but generally small and well-proportioned body size
	Tuli	High fertility, good mothering ability, low calf mortality
	Mashona	Highly fertility, strong maternal instinct, docile disposition
Zenga	Nkone	Genetically improved Nkone have good beef characteristics
	N'Dama	Tolerance to Trypanosomosis and cattle ticks
Small East African Zebu	Bovines of Tete	Thought to have trypanotolerance
	Angoni	Adapted to browsing during dry season, variable coat colour and horn size
Large East African Zebu	Arsi	Poor milkers, extremely active and often very aggressive
	Kenyan	Walking ability, highly adapted to harsh conditions, herd instinct, mothering ability, longevity, large sex dimorphism
	Boran	Tolerance to trypanosomosis
	Orma Boran	Survive on very poor pasture and scarce water, walking ability
	Turkana	

2.3 The South African beef industry

In South Africa, the livestock production industry's contribution to GDP (Gross Domestic Product) of 47.33% is well above the average in comparison to other agricultural sectors with beef contributing 26.24% towards the animal production industry (DAFF, 2017). DAFF showed an increase in beef production over the years. In 1980/1981 there were 12.9 million cattle in South Africa and this number increased by 0.5 million cattle in 2015/2016 to 13.4 million. The number of cattle slaughtered per year increased from 2.4 million in 1980/1981 to 3.4 million in 2015/2016. The number of calves being slaughtered per year decreased from 158 000 in 1980/1981 to 20 000 in 2015/2016. The production of beef and veal increased from 545 200t in 1980/1981 to 1 million tonnes in 2015/2016 with the price of beef increasing from R2.02/kg in 1980/1981 to R35.17/kg in 2015/2016. Per capita consumption decreased from 21.9 kg/year in 1985/1986 to 20.93 kg/year in 2015/2016. However, the total amount of beef consumed annually has increased from 630 000t in 1985/1986 to 1.17 million tonnes in 2015/2016.

The beef industry is driven by the terms 'efficiency and productivity' and the enterprise's performance is evaluated on the basis of economic returns (Van Marle-Köster et al., 2013). In extensive grazing systems, the efficiency and productivity of beef enterprises are influenced by how well the animals are adapted to the prevailing environmental conditions (Mirkena et al., 2010). Competition for natural resources, quantity and quality of feeds, diseases, heat stress and biodiversity loss affects production (Wright, 2014) but to a lesser extent in more adapted cattle (Philips, 2010).

The Southern African region has a high proportion of indigenous beef cattle breeds such as the Afrikaner, Tuli, Tswana, Boran, Mashona, Nkone, Angoni, and Nguni. The South African beef cattle industry includes an assorted number of cattle breeds which include those that can be classified as exotic, composite and indigenous (Abin et al., 2016). Indigenous cattle (*Bos indicus*) are more adapted to the harsh South African climate and tend to be more productive on natural grazing/external production when compared to exotic breeds (*Bos taurus*) (Scholtz, 2010). However, exotic breeds have improved feed efficiency compared to indigenous cattle and are preferred in feedlots (Frylinck et al., 2009). It has been shown that the *Bos indicus* cattle tend to reach puberty later compared to *Bos taurus* because of their exposure to the adverse environmental conditions and poor nutrition in the tropics (Koch et al., 2004).

Beef cattle in South Africa have a relatively long history of performance recording as official performance testing for beef cattle that dates back to 1959. Performance testing has developed over the past six decades with the larger amount of beef breeds take part in performance recordings; this also includes South African indigenous breeds (Bergh, 2010). The available recording schemes assist breeders to submit data on quality traits, production and fitness (reproduction) (FAO, 1998; Bergh, 2010). Not all breeds take part in national performance recording schemes or in private recording schemes, due to performance testing not being enforced by all breed societies (Chagunda et al., 2015). Participation in the recording scheme for beef cattle in South Africa varies from as low as 5% (Chianina) to 100% (Bonsmara, Tuli, Drakensberger) (Scholtz, 2010).

South Africa is one of the few countries in Africa where there are national programme for animal recording for genetic evaluation of livestock breeds (Van Marle-Köster et al., 2015). Logix is a system used for animal recording and consists of a collection of databases and programmes that address the animal recording needs of a broad spectrum of role-players within the livestock industry (<http://www.boran.org.za/Breed-Logix.htm>). According to Studbook's 2016 annual report, a total of 1859 beef cattle herds are registered and only 69% of these registered herds participate in Logix beef. There are a total of 33 1857 individual beef cattle registered with only 86% of animals participating in Logix beef. Of the males and females, 88% and 85% are participating respectively in Logix beef (SA Studbook, 2016).

2.4 Selection for genetic improvement

Genetic improvement is the intentional change in genetic composition in a population of animals through selection and breeding in order to make them more suitable for the purpose for which they are kept (Goddard & Hayes, 2009). The potential for genetic improvement of traits depend upon genetic variation existing in the population (Wright, 2014; Hill, 2014). The genetic expression of a trait can be affected by the heritability of a trait and environmental factors affecting the performance of an individual in that population (Dekkers & Hospital, 2002). Precise and accurate knowledge of genetic parameters are important for planning appropriate selection and breeding strategies in order to reach the set breeding objective (Scholtz, 2010).

Breeding objectives are achieved through the correct selection criteria which consist of economically important traits (Miller, 2002; Bergh, 2008). Traits that can be considered for selection criteria in the beef industry are traits that influence productivity, including those which focus on reproductive performance, growth rate and survival (Scholtz, 2010). Other traits that can be considered are traits that influence cost of production such as feed intake and also traits that influence product quality such as tenderness and taste (Frylinck et al., 2009; Bolormaa et al., 2013). In recent years, farmers also consider including traits that influence production efficiency such as individual animal measures of inputs (FCR and ADG) and outputs (different stages of weight measurements) (Day & Nogueira, 2013). Traits that influence the quality of the eating experience (Philips, 2010), traits that influence animal health and traits that influence the human health are also considered (Berry et al., 2014).

Breeders use different tools to improve beef which include: the choice of breed, the choice of mating plan to exploit complementarities and heterosis, and selection for within-breed improvement (Scholtz et al., 2010). In order to successfully select beef cattle, one must take into account the measurements of phenotypic traits combined with statistical computer software in order to predict accurate breeding values (Muir, 2007). For selection within-breed, estimated breeding values (EBV) and corresponding indices developed from national cattle evaluations (NCE) are the main tools that can be applied (Golden et al., 2009). An estimated breeding value (EBV) is an estimate of the additive genetic merit for a particular trait that an individual will pass on to its descendent (Goddard & Hayes, 2009). The Best Linear Unbiased Prediction (BLUP) animal model is an effective methodology to predict EBVs (Dekkers, 2004; Goddard, 2011). Genetic markers can also be used in order to provide genomic EBV for traits that influence the breeding goal but have not been available from conventional performance recording (Jeon et al., 2006)

Selective breeding has led to the improvement within livestock. However, there are still a few new objectives that will need to change in both direction and pace of selective breeding approaches (Hayes et al., 2013). One of the objectives to consider is that little genetic improvement has been achieved in some important traits due to it being too expensive to measure, such as feed conversion (Bolormaa et al., 2013) or because genetic variation in the trait has been ignored, such as fertility (Nino-Soto & King, 2004). These days, farmers put more emphasis on fertility due to its large impact on system efficiency in livestock production (Foote, 2003). Secondly, there are novel traits that have not yet been included in the breeding objective but may form part of it in the future (Scholtz et al., 2010), such as methane emissions (Hayes et al., 2013). Strong genetic correlation exists between dry matter intake and emission levels and by selecting for reduced dry matter intake while maintaining production will lead to a better feed conversion efficiency, which will lead to

reduction in emissions (Bolormaa et al., 2013). And thirdly, changes in breeding objectives will occur due to increase in human population and global warming (Scholtz, 2010). Temperatures will increase and this will affect cattle reproduction and production (Renaudeau et al., 2012). Farming with animals suited to these hot conditions or crossbreeding with animals adapted to hot conditions will become the solution (Hayes et al., 2013). This will force producers to place more emphasis on adapted breeds for specific environment

Beef production based on the Boran breed has operated outside a stratified breeding programme without formal performance evaluation and selection for many years after their introduction into South Africa (Scholtz, 2010). With time a breeding programme was developed and an evaluation of genetic and economic efficiency of the breeding programme based on the Boran Cattle Breeders Society (BCBS) was completed (Scholtz et al., 2010). Another study focused on the barriers presented by the formation of a breeding programme that will include entire herds from the BCBS and also for an expanded population of Boran cattle producers, the majority of whom are non-members of BCBS. The major challenge is convincing farmers to take part in animal recording and give continuous, accurate records for years to come (Bergh, 2010).

2.5 Traits of economic importance in African Zebu with special reference to Boran cattle

Boran cattle

The South African Boran genetic makeup consist of 64% *Bos indicus*, 24% *European Bos taurus* and 12% African *Bos taurus* (Hanotte et al., 2002). The breed standards for Boran cattle recognise that the Boran is a medium framed type of cattle with a good body conformation (Figure 2.2) (Kios et al., 2017) and is multi coloured with the majority being white, light grey, fawn or light brown (Wasike et al., 2009). Some of these colours contain grey, black or dark brown shading on the head, neck, shoulders and hindquarters (SABCBS, 2010). The horns are short, erect and pointing forwards but thick at the base (SABCBS, 2010). The hump is pyramidal in shape and overhanging to the rear or to one side and is more prominent in males (Makina et al., 2014). The males have a short and wide head with broad muzzle, prominent eyebrows and a short strong neck which is deep and muscular with a well-developed dewlap with plenty of loose skin (Räisänen, 2015). The Boran breed has deep shoulders with a broad brisket and a straight back with broad hindquarters (Kios et al., 2017)



Figure 2.2: Typical South Africa Boran bull (Denis Lochner)

Boran cattle are known for high fertility rates, drought and disease resistance. They are heat tolerant and have the ability to adapt to a variety of climates (Gaughan et al., 1999; DAGRIS, 2010). These traits enable them to be productive and fertile in harsh environmental conditions (Wasike et al., 2009). Characteristics of the Boran such as digestive and metabolic efficiency, low maintenance requirements and the above mentioned traits all contribute to its ability to adapt to Africa's climate (Shabtay, 2015; Kios et al., 2017). Some of the most important traits will be discussed in more detail.

Adaptability

Adaptability of an animal can be defined as its ability to survive and reproduce within a defined environment or the degree to which an organism, population or species can become or remain adjusted to a wide range of environments by physiological or genetic means (Mirkena et al., 2010). African cattle are adapted to environments with high temperatures and long periods of drought, and show a high tolerance to diseases (Hayes et al., 2013; Mwai et al., 2015).

In certain areas of South Africa, heat stress is the biggest challenge that animals have to deal with for the largest part of the year (Renaudeau et al., 2012). Temperatures that exceed the thermo-neutral zone can lead to significant changes in the physiological processes of cattle, such as feed intake. This is mostly due to the direct effects of thermal stress (Hansen, 2004). Hot environments can also impair production with regards to growth, meat, milk yield and quality, and reproductive performance, metabolic and health status, and immune response (Nardone et al., 2010). African indigenous cattle have a higher tolerance towards

heat in comparison to humpless *Bos taurus* breeds (Shabtay, 2015). This ability of indigenous cattle to tolerate warmer conditions is due to less heat production and an increase in heat loss to the environment (Hansen, 2004). Their physiological, morphological and cellular characteristics enable them to adapt to tropical conditions (Kim et al., 2017).

Indigenous cattle have the ability to adapt to drought conditions (Collins-Lusweti, 2000). One of the major influences on the amount of energy essential to maintain an animal's ability to take on every day physiological processes that is necessary for survival, such as tissue building and repair and the cardiac cycle, is body size (Hansen, 2004). The small to medium size of the indigenous breeds occurred due to the genotype of the animal naturally harmonising with available feed resources (Mirkena et al., 2010). Therefore, large size breeds will suffer more compared to small to medium size breeds in conditions where feed and water are limited (Shabtay, 2015).

Diseases and parasites cause major losses for farmers including treatment and prevention costs. However, genetic resistance against certain diseases does occur which makes indigenous cattle breeds better adapted to certain environments (Bahbahani & Hanotte, 2015). A major problem that farmers experience is tick infestation (Magona et al., 2011). Ticks and tick-borne diseases can cost up to \$160 million per annum in Africa alone (Smith & Parker, 2010). Studies have shown that indigenous cattle are more resistant to infestation when compared to *Bos Taurus* breeds (Mwai et al., 2015; Kim et al., 2017; Nyamushamba, 2017) Coat characteristics of a breed such as colour, hair length and density, has all contributed to tick resistance (Marufu et al., 2011). Grooming behaviour and delayed cutaneous hypersensitivity reaction to tick infestation also contribute to tick resistance (Mota et al., 2016b). Indigenous cattle also have a natural resistance to tick-borne diseases (Latif, 1993; Magona et al., 2011) which results in better performance under harsh environmental conditions and, although ticks may affect them, the damage will be minimal in comparison to European breeds (Latif, 1993; Shabtay, 2015).

Besides tick-borne diseases (TBD), parasites, such as gastro-intestinal (GI) nematodes, are one of the largest causes of disease and loss of productivity in livestock. Grazing livestock are the most at risk to be infected (Smith & Parker, 2010; Hayes et al., 2013). GI nematodes, are among the important parasites limiting cattle productivity in Southern Africa and can lead to blood loss and even death (Olwoch et al., 2008). It causes reduction in feed intake, feed conversion efficiency, growth performance (Nkrumah et al., 2004), draft power performance and cow fertility (Berry et al., 2014). A study was done on three different breeds, across seasons, on sweet rangeland in South Africa (Marufu et al., 2011). The results showed that indigenous breeds had the lowest egg count and worm problems which indicated that they

are more resistant to nematodes when compared to other breeds (Marufu et al., 2011; Nyamushamba et al., 2017).

African Tsetse fly-transmitted Trypanosomiasis (ATT), also known as “sleeping sickness”, affects a range of wild and domestic animals in large regions of West, East and Central Africa (Gifford-Gonzalez, 2000; Hanotte et al., 2003). It is caused by tsetse-transmitted *Trypanosoma congolense* and *Trypanosoma vivax* and can be transmitted through swallowing flies (Bahbahani & Hanotte, 2015). Infected animals will show signs of disease such as anaemia, weight loss, lymphadenopathy, infertility and abortion. In susceptible animals, death may occur from a few weeks up to several months after infection (d’Ieteren et al., 1999). In cattle alone, ATT cost the sub-Saharan African economy billions of U.S. dollars annually, due to expensive drugs which can be rendered ineffective as a result of drug resistance. Since there is no vaccine for ATT, vector control methods can damage the environment and it may be difficult or ineffective to control (Bradley et al., 1994). ATT is ranked among the world’s most serious livestock diseases and focusing on trypanotolerant breeds may provide a way to diminish the disease (Hanotte et al., 2003).

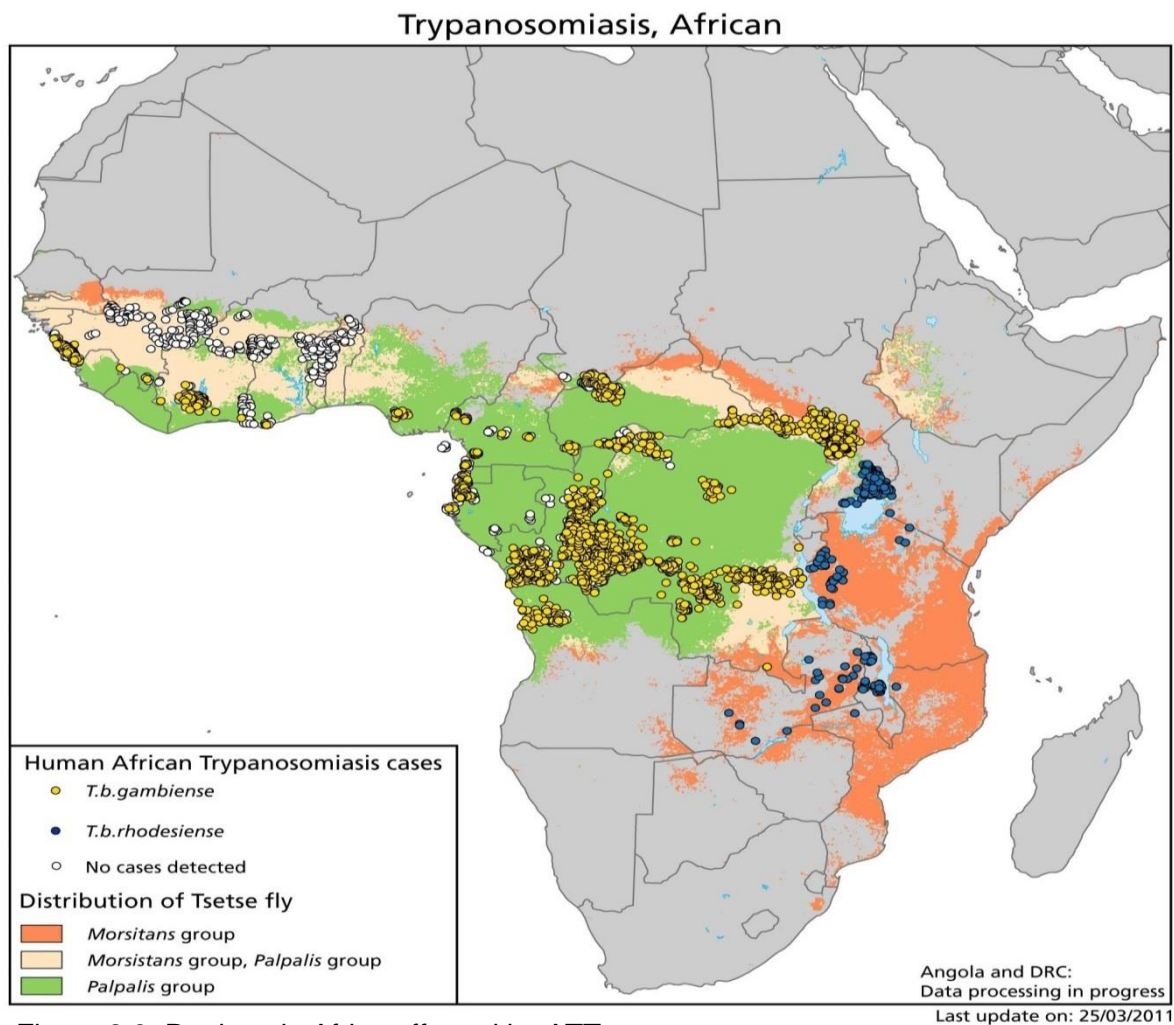


Figure 2.3: Regions in Africa affected by ATT

The trypanotolerance haplotype, that is a set of genetic determinants located on a single chromosome, appears to be derived from the Boran. However, it is unclear where the Boran trypanotolerant haplotypes originated from (Dolan, 1998). Evidence points to the Boran breed having developed over various regions which includes Southern Sudan across Southern Ethiopia to Southern Somalia (Dolan, 1998; Chan et al., 2010). Tsetse flies were present in parts of these regions where Boran cattle may have been exposed to ATT and developed a degree of tolerance (Rege, 2001). A study that was conducted on the mapping of quantitative loci for the control of trypanotolerance in Boran and N'Dama cattle found several QTL on several chromosomes that contribute to three major tolerance indicators, namely anaemia, body weight and parasitaemia controls (Hanotte et al., 2003). Figure 2.3 shows regions in Africa affected by ATT.

ATT does not occur in South Africa but the ability of the Boran to be trypanotolerant can be beneficial for other African countries where ATT poses a negative impact on the economy, such in Tanzania, Congo, Angola and other Western and Central African countries (Gifford-Gonzalez, 2000). A recent study showed that the tolerant allele at two of the QTLs originated from the Kenyan Boran ancestors. There is also a distinct QTL that could probably explain the genetic resistance against parasites and anaemia (Bahbahani & Hanotte, 2015). It has been indicated that trypanotolerant cattle have a lower mortality rate, parasitic infestation and degree of anaemia, and improved weight gain and reproductive performance, than susceptible animals (Mirkena et al., 2010; Berry et al., 2014). Table 2.2 shows the heritability of some adaptive traits

Table 2.2: A summary of heritability values for adaptive traits of beef cattle

Trait	h²	Reference
Heat tolerance	0.18 - 0.75	Gaughan, et al., 1999; Burrow, 2001; Renaudeau et al., 2012
Tick resistance	0.15 - 0.44	Marufu et al., 2011; Mapholi et al., 2014; Bahbahani & Hanotte, 2015; Mota et al., 2016b
Nematode resistance	0.30 - 0.38	d'Ieteren et al., 1999; Gifford-Gonzalez, 2000; Burrow, 2001; Bahbahani & Hanotte, 2015
Trypanotolerance	0.30 - 0.88	Dolan, 1998; Burrow, 2001; Hanotte et al., 2003; Bahbahani & Hanotte, 2015

Fertility and reproduction traits

Fertility traits can be described by the reproduction, survival, mothering ability and longevity of an individual (Foote, 2003). These traits vary from low to high in heritability (Table 2.3) and are more challenging to record (Bergh, 2010). Fertility traits that are easy to record include age at first calving, calving success, calving interval, calf survival, day to calving and calving date (Nino-Soto & King, 2004). Efficient reproduction is essential for profitable beef cattle production (Rust & Groeneveld, 2001). Fertility in females can be defined as the cow's ability to conceive normally and calve down producing enough milk until the calf reaches weaning successfully (Nino-Soto & King, 2004). Male fertility can be defined as the ability to produce semen that will result in a successful pregnancy (Foote, 2003).

Table 2.3: Summary of heritability estimates (h^2) for fertility traits in beef cattle

Traits	Heritability	Reference
Age at first calving	0.04 - 0.31	Rust & Groeneveld, 2001; Corbet et al., 2006; Berry et al., 2014
Calving date	0.02 - 0.09	Beffa, 2005; Corbet et al., 2006
Calving success	0.03 - 0.27	Van der Westhuizen et al., 2001; Rust & Groeneveld, 2001; Corbet et al., 2006
Calving rate	0.04	Rust & Groeneveld, 2001
Calving interval	0.02 - 0.13	Van der Westhuizen et al., 2001; Rust & Groeneveld, 2001; Demeke et al., 2004; Corbet et al., 2006, Berry et al., 2014
Days open	0.04	Demeke et al., 2004
Longevity	0.08	Van der Westhuizen et al., 2001

The reproductive performance of the breeding female is one of the most important factors that influences herd productivity (Patterson et al., 2016). Reproductive performance can be recorded by measuring age at first service, age at first calving, calving interval, days open and number of services per conception (Bologn et al., 2016). Age at first calving reverse to the period of time between birth and first calving and has an influence on both the productive and reproductive life of the female (Gutiérrez et al., 2002). In a breeding program, age at first calving has an influence on generation interval and response to selection (Day & Nogueira, 2013). The inter-calving period refers to the time between sequential births and is a function of postpartum anoestrus period (from calving to first oestrus), service period (first postpartum oestrus to conception) and gestation length (Van der Westhuizen et al., 2001). Calving interval is good indicator of cattle reproductive efficiency (Bologn et al., 2016).

South African beef farmers still rely on natural service and, therefore, acceptable bull fertility is also critical (Mukuahima, 2007). Factors that determine a bull's fertility and performance include plane of nutrition (Gaughan et al., 1999), structural soundness, capability of the reproductive organs, quality of the semen, libido level and servicing capacity (Patterson et al., 2016). Scrotal circumference can be used as an indicator for age at puberty for both male and female offspring (Nino-Soto & King, 2004). Selection based on scrotal circumference can be used to improve female fertility traits, such as age at puberty, due to the strong additive genetic relationship that exists (Foote, 2003). Table 2.4 shows the genetic correlation between fertility traits.

Table 2.4: Genetic correlations (r_g) between reproductive traits in beef cattle

Trait	r_g	Reference
Age at first calving and calving date	0.09 - 0.88	Van der Westhuizen et al., 2001; Corbet et al., 2006
Age at first calving and calving interval	-0.03 - 0.44	Van der Westhuizen et al., 2001; Corbet et al., 2006
Calving date and calving interval	0.01 - 0.75	Van der Westhuizen et al., 2001; Corbet et al., 2006
Calving success and calving date	-0.95	Beffa, 2005
Days to calve and pregnancy rate	-0.99	Corbet et al., 2006

Growth and carcass traits

The growth performance of cattle at various ages of the growth curve has a direct influence on the profitability in beef production systems (Koch et al., 2004). Growth rate and efficiency of gain were among the first traits to receive selection emphasis in beef cattle due to their early expression and ease of recording (Prayaga, 2003). Weights at different ages and production stages are the most common measurements for growth with moderate to high heritability (Van Marle-Köster et al., 2015).

Table 2.5 shows that birth weight and mature weight have the highest heritability among the production traits with ADG and FCR heritability also being high which will result in accelerated genetic progress when selecting for these traits (Akanno et al., 2018).

Table 2.5: A summary of estimates of beef cattle heritability values for specific production traits

Trait	h²	Reference
Birth weight (direct)	0.21 - 0.4	Norris et al., 2004; Van Niekerk et al., 2004; Corbet et al., 2006; Beffa, 2005; Wasike et al., 2009; Ndofor-Foleng et al., 2012; Nesper et al., 2012
Birth weight (maternal)	0.05 - 0.14	Norris et al., 2004; Corbet et al., 2006; Beffa, 2005; Ndofor-Foleng et al., 2012; Nesper et al., 2012
Weaning weight (direct)	0.12 - 0.29	Norris et al., 2004; Beffa, 2005; Corbet et al., 2006; Wasike et al., 2009; Ndofor-Foleng et al., 2012; Nesper et al., 2012
Weaning weight (maternal)	0.11 - 0.21	Norris et al., 2004; Beffa, 2005; Corbet et al., 2006; Ndofor-Foleng et al., 2012; Nesper et al., 2012
Yearling weight	0.13 - 0.26	Norris et al., 2004; Van Niekerk et al., 2004; Beffa, 2005; Corbet et al., 2006; Wasike et al., 2009; Ndofor-Foleng et al., 2012; Nesper et al., 2012
Final weight	0.13 - 0.42	Van Niekerk et al., 2004; Beffa, 2005; Corbet et al., 2006; Ndofor-Foleng et al., 2012; Nesper et al., 2012
Mature weight	0.24 - 0.41	Nephawe, 2004; Nesper et al., 2012
Average daily gain (ADG)	0.38	Bolormaa et al., 2013
Feed conversion ratio (FCR)	0.23 - 0.41	Nkrumah et al., 2007

Heavier birth weight will result in a heavier weaning weight and this will lead to overall heavier mature weight due to the positive genetic correlation that exists between the different stages (Table 2.6) (Santana et al., 2014).

Table 2.6: Summary of genetic correlations between growth traits of beef cattle

Traits	Genetic correlation	Reference
Birth and weaning weight	0.45 - 0.78	Maiwashe et al., 2002; Corbet et al.,2006; Nesper et al., 2012
Birth and yearling weight	0.28 - 0.57	Bosso et al., 2009;Nesper et al., 2012
Birth and final weight	0.45 - 0.6	Maiwashe et al., 2002; Nesper et al., 2012
Birth and mature weight	0.63	Nesper et al., 2012
Weaning and yearling weight	0.86	Nesper et al., 2012
Weaning and final weight	0.71 - 0.99	Maiwashe et al.,2002; Nesper et al., 2012
Weaning and mature weight	0.94	Nesper et al., 2012
Yearling and final weight	0.85	Nesper et al., 2012
Yearling and mature weight	0.43	Nesper et al., 2012
Final and mature weight	0.75	Nesper et al., 2012

Carcass quality is one of the most important determinants of price and purchasing (Seroba et al., 2011). Some of the traits used to assess carcass quality include marbling score, fat thickness, dressing percentage and hot carcass weight (Rios Utrera & Van Vleck, 2004). These traits can be classified into two groups: cutability traits and quality traits. Cutability traits include muscling and leanness while quality traits are represented by marbling (Bolormaa et al., 2013). Although carcass traits are moderately to highly heritable, the inclusion in selection criteria is hampered by late expression and recording of traits on large numbers of carcasses is expensive (Crews et al., 2010).

Real-Time Ultrasound (RTU) is the most reliable tool to record these traits. The limited availability of RTU scanners throughout South Africa and lack of breeders that scan their animals has resulted in low frequency of RTU scanning. However, progressive farmers believes has led to a increase in RTU measurements. According to SA Studbook's annual report of 2016, the number of Boran cattle (57) RTU is average compared to several other breeds with Bonsmare (1130) being the highest and Senepol (5) the lowest. Considering the rib fat thickness, Boran (2.85mm) is thinner on average with Tuli (4.03mm) being the thickest and Senepol (2.08mm) being the thinnest. Boran cattle's (4.09mm) rump fat thickness is above average with Tuli (5.39mm) being the thickest and Senepol (2.6mm) being the thinnest. Boran cattle's eye muscle area (55mm²) is below average with South Devon

(69.6mm²) being the thickest and Dexter (48.9mm²) being the thinnest. Considering marbling, Boran (2.18%) has the lowest marbling percentage while Dexter (3.5%) has the highest (SA Studbook, 2016). The genomic selection for carcass traits will act as a tool to assist in carcass evaluation in the future (Van Marle-Köster et al., 2013).

Behavioural traits

Zebu cattle have an ability to adapt their grazing behaviour in response to restricted grazing time or when no grazing is allowed during nights (Jung et al., 2002; Huber et al., 2007; Butt, 2010; Räisänen, 2015). Several studies show that different Zebu breeds spent more than 4% of their pasture time resting which varies between 4.4% and 10.12% (Bayer, 1990; Huber et al., 2007; Butt, 2010). In a study involving Boran, the resting time is as low as 2% (Jung et al., 2002). The high grazing frequency and low resting time of the Boran show its great ability to utilise the available resources efficiently during grazing time (Räisänen, 2015). The distance between observed cow and the nearest cow to her by every interval was recorded in a study. The results show that Boran spent their time more closely to each other (Huber et al., 2007). The closeness of the Boran herd is classified as a positive social behaviour due to less chance of being attacked by predators.

2.6 Brief history of genomics

In the past three decades, major advances and technological developments have been made in the field of molecular genetics (Womack, 2012). Technology such as the development of the polymerase chain reaction (PCR) by Mullis was a major advancement for molecular research (Beuzen et al., 2000). It contributed to the development of Sanger sequencing in 1977 by Fredrick Sanger which was based on chain-termination method (Green, 2001). In 1987, Applied Biosystems introduced the first automated sequencing machine (Dekkers & Hospital, 2002) based on capillary electrophoresis which made sequencing faster and more accurate (Chagunda et al., 2015).

The automatic sequencing instruments and associated software, which emerged in 1998, became the main tools for the completion of the Human Genome Project in 2001 (Green, 2001). The discovery of the hypervariable region in the human genome (Collins et al., 2003) paved the way for the discovery and mapping of different DNA markers (Dodgson et al., 1997; Beuzen et al., 2000). These have been applied widely in several livestock species (Dekkers, 2004; Pollak, 2005; Jeon et al., 2006). Microsatellites were the first widespread markers that took full advantage of PCR technology (Hardy et al., 2003). They are tandemly repeated sequences that are highly polymorphic, abundant and fairly evenly distributed

throughout the genome which led to microsatellites becoming one of the most popular genetic markers (Dorji & Daugjinda, 2014).

For livestock, this tool contributed to a better understanding of the evolution of species, domestication and breed formation, and the development of new theories of population genetics for improved selection and genetic improvement of animal production (Barendse et al., 2007; Barendse et al., 2009). Since the completion of the Human Genome Project, most farm animal species have been sequenced and mapped (Fan et al., 2010), creating new opportunities for genetic improvement in livestock that were previously beyond the reach of scientists (Eggen, 2012).

Single nucleotide polymorphism (SNP) genotyping arrays were developed primarily for the use of association mapping, admixture mapping, identity by descent mapping, and studies aimed at detecting phenotype and genotype associations (Albrechtsen et al. 2009; Goddard & Hayes, 2009). However, SNP chips have also been used in population genetic studies (Groeneveld et al., 2010; Edea et al., 2013; Makina et al., 2014). The preparation and utilisation of SNP arrays have considerable impacts on animal breeding and genetics (Fan et al., 2010). As dense SNP markers were becoming available and affordable, whole-genome marker data could be incorporated effectively in a breeding programme for a polygenic trait (Meuwissen et al., 2001). Currently, there are several commercial bovine SNP arrays available, as indicated in Table 2.7 (<http://genomics.neogen.com/en/beef-cattle>; Nicolazzi et al., 2015).

Table 2.7: Commercial SNP arrays that are available for cattle

Platform	SNP chips	Size
Affymetrix®	Axiom® Genome wide BOS1	648 875
Neogen-Geneseek®	GGP-LD version 2	19721
	GGP-LD version 3	26151
	GGP HD	76 879
	GGP HDi	12 189
	GGP indicus	35 090
	GGP150K	139 480
	GGP F250	230 000
Illumina®	Bovine LD version 1.1	6912
	Bovine SNP 150 version 2	54 609
	Bovine HD	777 962

These advances in DNA technology over recent years have led to the reduction in cost of generating the genotype of an animal (van Marle-Köster et al., 2013). South African beef cattle breeders are already exploiting DNA technology through DNA-based parentage verification and diagnostic testing (Van Marle-Köster et al., 2015). Beef cattle can be tested for meat tenderness with various diagnostic kits as well as for a few genetic disorders, including dwarfism and certain translocations (Nicolazzi et al., 2015).

2.7 Application of genomics for genetic diversity in beef cattle

For millions of farmers in Africa, indigenous cattle are the only option to farm due to the harsh climate of Africa (Nardone et al., 2010). Genetic variability is a key component enabling adaptation of natural populations to changing environments (Mirkena et al., 2010). Analysing the genetic diversity of African cattle may provide new insights into their ability to adapt to various ecosystems (Hanotte et al., 2010). In previous years, low density microsatellite markers and mitochondrial- or Y-chromosomes were used for genetic diversity and structure analyses (Bradley et al., 1994; Dorji & Daugjinda, 2014). Currently, SNPs are used in genetic diversity studies due to their abundance in the genome and their stability as well as the availability of genome wide SNP arrays (Edea et al., 2013; Decker et al., 2014).

Genetic diversity is expressed as the frequencies of genotypes and alleles, the proportion of polymorphic loci and the observed and expected heterozygosity (Bourdon, 2000). The most widely used parameter for measuring genetic diversity within a population is expected heterozygosity or gene diversity (Toro et al., 2009). Computer software such as ADMIXTURE can be used to describe population structure through implementing a model-based clustering method for inferring population structure using genotypic data (Alexander et al., 2009). It is suitable for the assignment of populations and assumes a model in which there are K populations where each is characterised by a set of allele frequencies at each locus (Decker et al., 2014).

Genome wide studies have unravelled historical events that shaped populations during domestication and breed formation (Womack, 2012). This information can assist in preserving the genetic diversity within endangered indigenous breeds and also with scientific conservation of adaptation traits (Fan et al., 2010). The use of SNP data proved that genetic diversity of breeds is linked to their areas of origin indicating that breeds that separated more recently are more closely linked geographically (Porto-Neto et al., 2013; Stock & Gifford-Gonzalez, 2013). The difference between taurine and indicine breeds may be due to greater

separation time (Upadhyay et al., 2017) and is supported by previous findings (Cymbron et al., 2005; Gautier et al., 2007; Decker et al., 2014).

Through nucleotide diversity one can measure the degree of polymorphism within a population. The reduced levels of nucleotide diversity may be the result of intensive artificial selection over generations, genetic drift and a low effective population size (Bourdon, 2000). Recently, a study was conducted on the genome characterization of five indigenous African cattle breeds, including the Boran breed, which is representative of the cattle diversity of the continent (Kim et al., 2017). In this study, the nucleotide diversity was the highest in the African Zebu (Boran, Ogaden, Kenana) and the Ankole sanga (Kim et al., 2017).

Principal component analysis (PCA), which is based on autosomal SNPs genotype data, reveals clear breed structures as samples from the same breed cluster together. This indicates separation between different breeds based on their genetics. Genomic selection, also known as genomic prediction or genomic evaluation, is one of the most fundamental changes that occurred to breeding and genetics in agriculture (Calus, 2010). It refers to the use of genome-wide genetic markers to predict the breeding value of selection candidates (Meuwissen et al., 2001). It is a statistical method that does not require identification of the genes or sites causing variation in the trait (Dorji & Daugjinda, 2014).

The advantage of genomic selection is that cattle can be selected accurately early in life based on their genomic predictions, and for traits that are difficult or expensive to measure such as fertility, disease resistance and feed conversion (Pryce et al., 2012; Berry et al., 2014). This will lead to greater rates of progress and the costs of genotyping can be at least partly offset by reducing or eliminating progeny testing (Hill, 2014). Using genomic selection, one can predict breeding values of animals using information offered by thousands of SNPs across the genome, namely genomic estimated breeding value (GEBV) (Calus, 2010; Bolormaa et al., 2013). Genomic tools present opportunities to study South African cattle breeds at a genomic level in order to discover their unique genetic structure and to unravel their genetic potential (Makina, 2015).

Chapter 3: Materials and methods

3.1 Introduction

The aim of this project was to analyse the South African Boran based on the available quantitative and genotypic data in order to provide reference for the breed with regard to the formulation of breeding objectives and its future role in the South African beef production system. Phenotypic and genotypic data were provided by SA Studbook and BGP respectively with consent from the SA Boran Breeders' Society. Ethical approval from the committee (Natural and Agricultural Science) was obtained to ensure compliance with the research ethics and integrity of the University of Pretoria (EC170513-143 / EC170913-148).

3.2 Materials

Phenotypic data

The quantitative data consisted of pedigree data and estimated breeding values (EBVs) for fertility and growth traits. For this study pedigree and performance data from 1995 to 2016 was analysed. The pedigree recordings consist of the animals' ID, sire, dam, birth date and sex. The EBV data represented seven traits namely: birth weight, weaning weight, yearling weight (12 month), final weight (18 months), mature weight, age at first calving and inter-calving period. In Table 3.1, a summary was provided indicating the number of animals for each production trait recorded.

Table 3.1: Summary of the number of animals included in genetic analyses

Year	AFC	ICP	BW (DIR)	BW (MAT)	WW (DIR)	WW (MAT)	YW (12 month)	FW (18 month)	Mature Weight
1995	107	90	106	107	87	88	78	78	77
1996	113	90	101	101	80	81	64	58	69
1997	95	82	90	91	74	73	64	60	65
1998	129	105	128	126	110	109	92	89	96
1999	167	124	172	171	126	128	96	89	98
2000	258	204	294	294	201	203	157	148	157
2001	305	241	361	359	261	267	222	196	204
2002	404	312	449	450	320	323	254	224	244
2003	665	552	818	817	557	557	503	466	502
2004	936	824	1104	1099	858	865	791	745	761
2005	1266	1051	1438	1439	1147	1155	1049	993	998
2006	2188	2019	2314	2316	2083	2086	1948	1805	1935
2007	3018	2773	3404	3405	2839	2857	2714	2566	2683
2008	4829	4485	5254	5257	4618	4633	4332	4178	4272
2009	6608	6242	7014	7017	6365	6385	6046	5808	5986
2010	8643	8201	9128	9125	8362	8379	8029	7668	7940
2011	10258	9958	10646	10623	10072	10078	9735	9315	9715
2012	11949	11601	12358	12310	11769	11766	11253	10661	11179
2013	12856	12450	13296	13267	12679	12670	12048	11443	12072
2014	11683	11331	12000	11978	11560	11546	10980	10245	10954
2015	9946	9567	10113	10088	9790	9787	8988	8165	8988
2016	8232	7963	8453	8441	8140	8099	7539	6830	7625
2017	994	974	1004	1000	989	986	927	852	936

AFC: Age at first calving; ICP: Inter-calving period; BB: Birth weight; WW: Weaning weight; YW: Yearling weight; FW: Final Weight; DIR: Direct; MAT:

Maternal

Genotypic data

The genotypic data consisted of 87 Boran cattle genotyped using the GGP Bovine 150K SNP array at the ARC Biotechnology Platform. An additional 83 Bonsmara and 83 Hereford cattle genotypes were used in order to compare and illustrate population structure. Bonsmara and Hereford genotype data were provided by the BGP after approval was given by the Bonsmara Breeders' Society and Hereford Breeders' Society. The Bonsmara and Hereford cattle were also genotyped using the GGP Bovine 150K SNP array at the ARC Biotechnology Platform.

3.3 Methods

Phenotypic data analyses

Pedigree data

Pedigree data were analysed using different software such as POPREP (Groeneveld, 2004) and EVA (Berg et al., 2006) and graphs were created through the use of Excel. The Boran pedigree records were uploaded into the POPREP software through the website <http://popreport.tzv.fal.de>. The input file consisted of a unique ID for each animal, its sire, dam, date of birth and sex. The population parameters included were pedigree completeness, generation intervals (GI), inbreeding (F_{IS}), age structure of parents by birth of offspring, distribution of dams by parity and effective population size (N_e).

Pedigree completeness is a parameter used to examine the completeness of a pedigree over generations (Groeneveld et al., 2009) and is calculated based on an algorithm index (Macluer et al., 1983).

$$Id = 4Id_{pat}Id_{mat} / Id_{pat} + Id_{mat} \text{ and } Id_k = \frac{1}{d} \sum_{i=1}^d a_i \quad k = pat, mat.$$

K represents the paternal (pat) or maternal (mat) line of an individual, a_i is the proportion of known ancestors in an identified generation and d is the number of generations considered in the calculation of the pedigree completeness. The value for pedigree completeness was expressed as percentage per generation that ranged from 0 to 100.

The generation interval for a given year was calculated as follows:

1. All animals born in a given year were considered (subset 1)
2. Animals in subset 1 that become parents in the later years were identified (subset 2)
3. The parents of animals in subset 2 were identified (subset 3)

4. The generation interval was calculated as the average age of the animals in subset 3 at birth of their offspring in subset 2.

Animals that were considered during computation were the selected offspring and those who produced at least one progeny. The generation intervals for each of the four selection paths (sire to son, sire to daughter, dam to son and dam to daughter) were calculated, also males, females and whole population that met the requirements in the pedigree records.

The number of breeding animals influences the dispersion of allele frequencies in a population and thereby determines the effective size (N_e). The number of breeding animals was counted on the year of birth of their first offspring. An animal was considered as a breeding animal when having a service record or identified as a parent in the birth record of an offspring (Groeneveld et al., 2009).

The inbreeding coefficient (F) and the rate of inbreeding (ΔF) are means to quantify the increase in pairs of homozygous genes in an individual relative to the population (Groeneveld et al., 2009). The inbreeding coefficients for all animals of the population were calculated with POPREP (Groeneveld et al., 2009). Inbred animals are defined as any animal with an inbreeding coefficient greater than zero. The level of inbreeding of the population per year was calculated by averaging inbreeding coefficients by year of birth. The inbreeding coefficient (F) was computed for all animals in the pedigree data set according to Falconer & Mackay, 1996 through the use of POPREP:

$$\Delta F = (F_t - F_{t-1}) / (1 - F_{t-1})$$

F_t and F_{t-1} are the average inbreeding of offspring and their parents where (t) is defined as all animals recorded and born in a given year and ($t-1$) uses the average generation interval to arrive at a theoretical parent's birth year.

Effective population size referred to the number of breeding animals in an idealized population which will give rise to the same rate of calculated or observed inbreeding as observed in the real population (Falconer & Mackay, 1996). It was estimated using the formula:

$$N_e = 1/2\Delta F$$

ΔF represent the rate of inbreeding (Falconer & Mackay, 1996). The rate of genetic progress in the Boran population depends on the turnover of breeding stock. To determine the rate of genetic progress in the Boran population, the number of sires and dams

contributing to the group of individuals in the successive generations were categorized by age (Groeneveld et al., 2009).

Production data

The EBV data set was provided by SA Studbook. SAS software (SAS, 2010) was used to calculate descriptive statistics and Excel was used for visual illustration in graphs. Statistical analysis was done on the measurements of each trait to calculate the average, standard deviation, minimum and maximum for each trait per year and average for each trait over the 22 years (SAS software). The estimated breeding values for the growth and reproductive traits for this data set were used to compile the genetic trends. Animals with EBVs within the data set parameters (1995 to 2016) were retrieved and the average for each trait per year was calculated in order to investigate the genetic trend, after which Excel was used to visually display the trends.

Genotypic data analyses

Sample- and marker-based QC was performed using PLINK software (Purcell et al., 2007). Samples with more than 10% missing genotypic data (sample call rate <90%) were removed from further analysis while SNPs were removed if average marker call rate was lower than 90%, minor allele frequency lower than 5% (MAF<0.05) and Hardy-Weinberg Equilibrium lower than 0.001 (HWE p-value <0.001). The Bonsmara and Hereford data sets were merged using PLINK software (Purcell et al., 2007) and were submitted to the same quality control as the Boran data. The Bonsmara and Hereford data were then merged with the Boran data and again submitted to the same parameters for quality control. For the analysis of genotypic data software, SNeP (Barbato et al., 2015) for estimating the effective population size was used. GCTA (Yang et al., 2011), ADMIXTURE (Alexander et al., 2009), PGD spider (Lischer & Excoffier, 2012), Arlequin (Excoffier et al., 2006) and Genesis (Buchmann & Hazelhurst, 2014) were used for population structure and genetic diversity.

Following quality control, LD-pruning was performed on both the Boran data set alone and combined data set to remove SNPs that were in linkage disequilibrium with one another using PLINK's simple pairwise threshold model (command:—indep-pairwise 50 5 0.4). MAF, heterozygosity (observed and expected) and inbreeding were calculated based on the data set after LD-pruning through PLINK's commands mentioned above (--freq, --het). The minor allele frequency (MAF) for each SNP was calculated by using PLINK's -freq command. For the calculation of heterozygosity and individual inbreeding PLINK's —het command was used. The heterozygosity observed and expected was calculated by the following formula:

$$HET (O \text{ or } E) = \frac{N(NM) - HOM(O \text{ or } E)}{N(NM)}$$

H_O and H_E is the observed or expected heterozygosity and $N(NM)$ is the number of non-missing genotypes. Inbreeding (F_{IS}) was estimated using PLINK's `-het` command and obtained through PLINK's output file in the F-value column while F_{ST} was calculated by converting PLINK input file to an Arlequin input file through PGD spider software (Lischer & Excoffier, 2012) followed by analyses using Arlequin (Excoffier et al., 2006).

Principal component (PCA) and population structure analyses were performed for LD-filtered mapped, autosomal SNPs using both the Boran data set alone and the combined data set. GCTA version 1.24 (Genome-wide Complex Trait Analysis) (Yang et al., 2011) was used to construct a genetic relationship matrix and, subsequently, to estimate eigenvalues and eigenvectors for the first three principal components (command: `-pca 3`). Using ADMIXTURE version 1.23 (Alexander et al., 2009), a cross-validation (CV) procedure was followed in order to determine the optimal K-value for population structure analyses. After CV errors were estimated for each K-value, the K-value with the lowest CV error was chosen as optimal. Genesis version 0.2.3 (Buchmann & Hazelhurst, 2014) was then used to generate population structure bar plots and Excel was used to generate scatter plots. Population structure analyses were performed for the combined Bonsmara and Hereford data and combined Boran, Bonsmara and Hereford data using the same commands as discussed above.

Effective population size (N_e) for the Boran was estimated using SNeP version 1.1 (Barbato et al., 2015) on the Boran data set alone. SNeP estimates N_e from genome-wide linkage disequilibrium (LD) using the following formula suggested by Corbin and co-authors (Corbin et al., 2012):

$$N_{T(t)} = \frac{1}{(4f(c_t))} \frac{1}{(E[r_{adj}^2|c_t])} - \alpha$$

$N_{T(t)}$ represents the past effective population size estimated t generations ago, c_t represents the recombination rate t generations ago, r_{adj}^2 represents the linkage disequilibrium estimation adjusted for sampling bias and α represents a constant. PLINK input files for quality filtered, autosomal SNP data sets were used for N_e calculation. The quality filtered, autosomal SNP data sets were converted to ped and map files using PLINK's `--convert` command. The newly formed ped and map files were then used to calculate the effective population size by running it through SNeP software (Barbato et al., 2015).

Chapter 4: Results

4.1 Phenotypic data

Pedigree data

In Figure 4.1, the number of animals born and recorded over 22 years is illustrated. There was an exponential increase in the number of Boran per year until 2006, after which the numbers declined slightly and then peaked in 2013 at 13 922 Boran cattle. After 2013, the numbers of Boran born declined with 8538 cattle recorded for 2016.

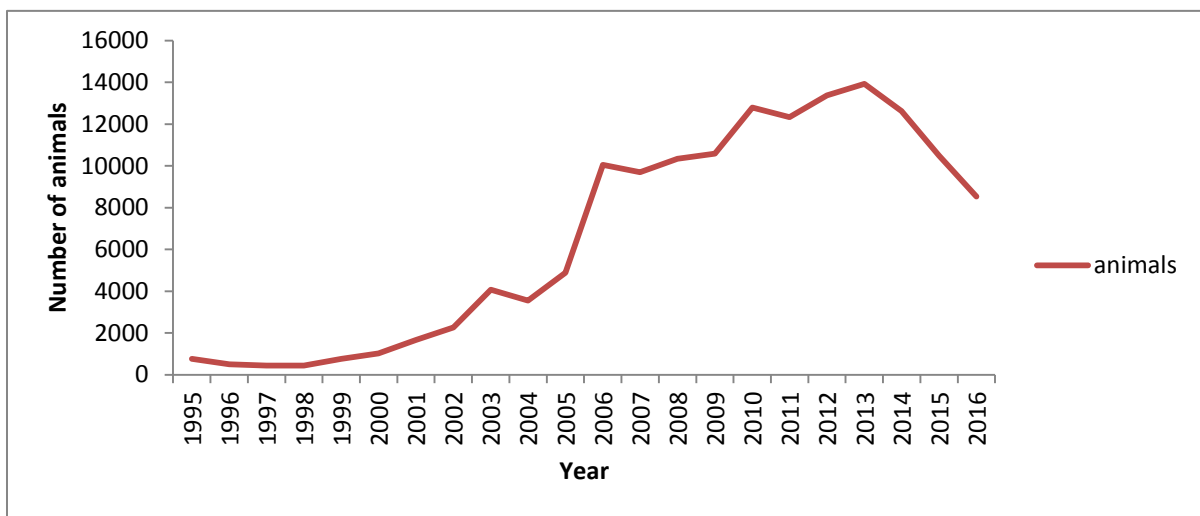


Figure 4.1: Variation in numbers of Boran cattle born and recorded from 1995 – 2016

The pedigree completeness was investigated over six generations as the percentage of known ancestors per parental generation in the whole pedigree data set. The pedigree completeness is shown in Figure 4.2.

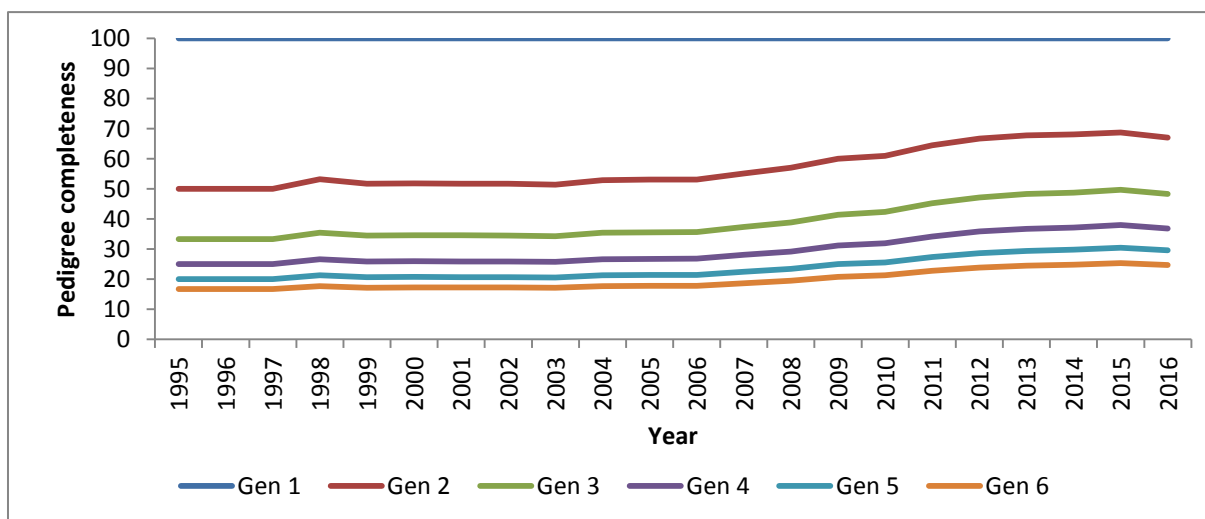


Figure 4.2: Average pedigree completeness (%) for six generations deep by year of birth between 1995 and 2016 for Boran breed

The Boran breed has shown consistent progress in the trend for pedigree completeness. The pedigree completeness of generation 1 is consistent at 100% over the last 22 years while generations 2-6 increased from 2006 to 2015. However, there was a slight decrease in 2016 for generations 2-6. This could be due to late recordings, causing 2016 records to be incomplete. The average pedigree completeness over the last ten years is indicated by Table 4.1.

Table 4.1: Average pedigree completeness (%) over the past 10 years

Breed	Gen 1	Gen 2	Gen 3	Gen 4	Gen 5	Gen 6
Boran	100	63.6	44.7	33.9	27.1	22.6

Gen: Generation

Figure 4.3 shows the trend for the generation intervals for the Boran breed while the average generation intervals for four pathways (sire-son, sire-daughter, dam-son and dam-daughter), males, females and the whole population are presented in Table 4.2.

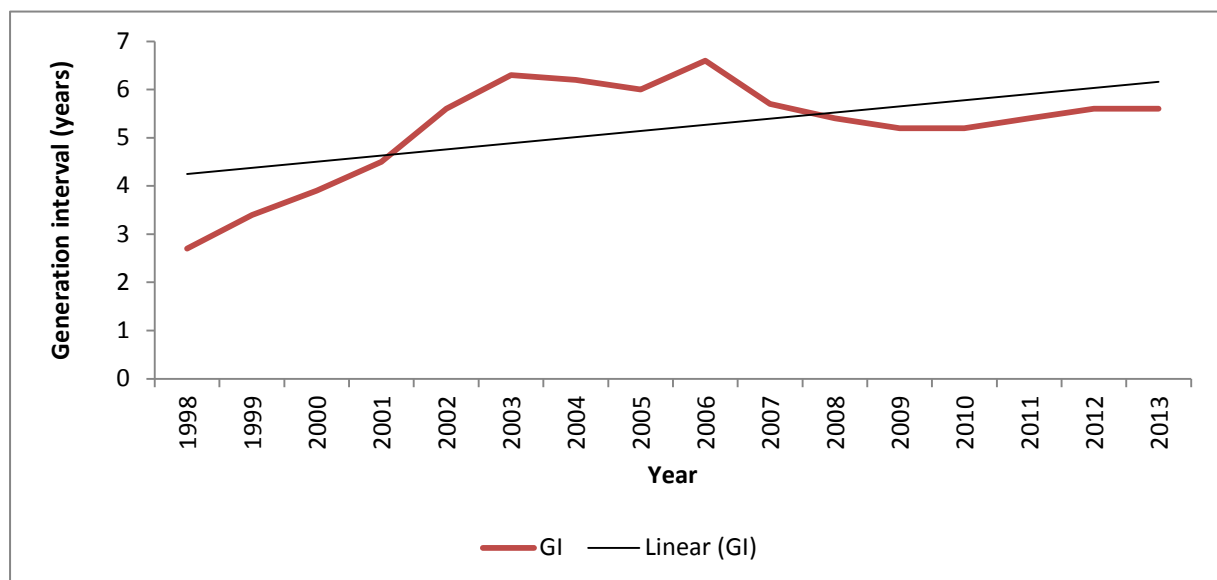


Figure 4.3: Average generation interval of the Boran breed

The generation interval increased from 1998 to 2003 with some improvement in 2005. After 2006, the generation interval decreased and stabilized at 5.6 years in 2013. Generation interval was also evaluated with EVA (Berg et al., 2006) with similar results.

Table 4.2: Estimated average generation intervals (years) for the four gametic selection pathways, male, female and the Boran population.

Breed	SS	SD	DS	DD	Male	Female	Population
Boran	5.9	5.9	5.8	5	5.9	5.1	5.5

SS: sire to son; SD: sire to daughter; DS: dam to son; DD: dam to daughter; population: Boran population

The overall Boran population generation interval was estimated at 5.5 years with the generation interval for males being longer compared to that of females.

The age distributions of parents by birth of offspring in the pedigree file are presented in Figure 4.4 and distribution of dams by parity in Figure 4.5.

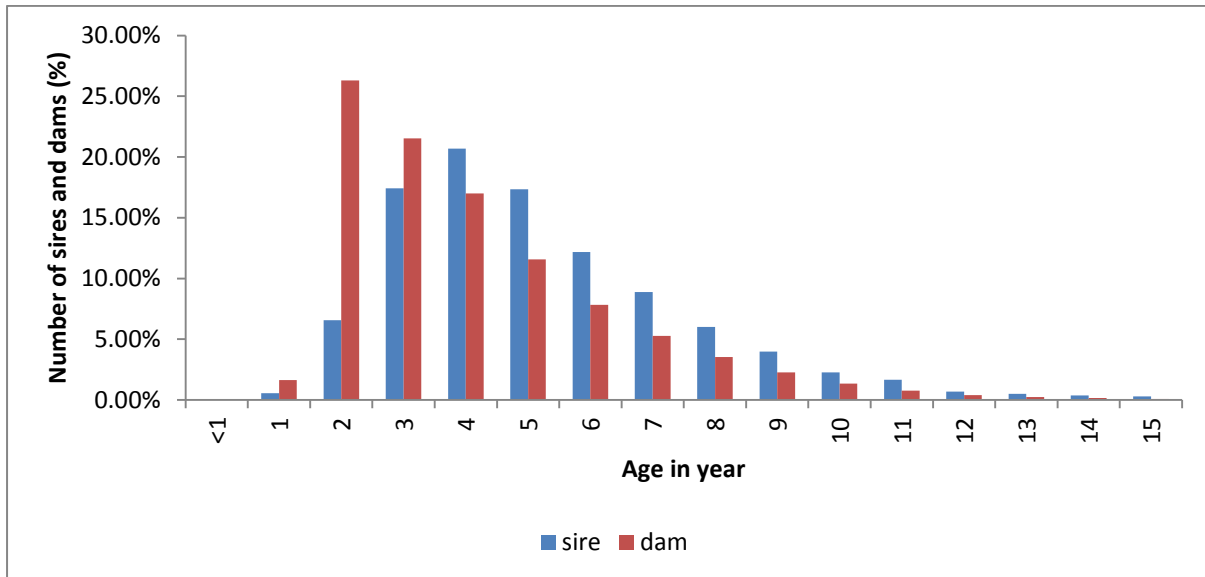


Figure 4.4: Age distribution of parents by birth of offspring

The proportion of sires in reproduction was the highest at the age of four years followed by three and five years of age while the proportion of dams in reproduction was the highest at two years of age followed by three and four years of age. The majority of sires and dams produce offspring between the age of two and five years with dams producing earlier in life than sires. The proportion of sires still producing offspring at an older age is greater than dams.

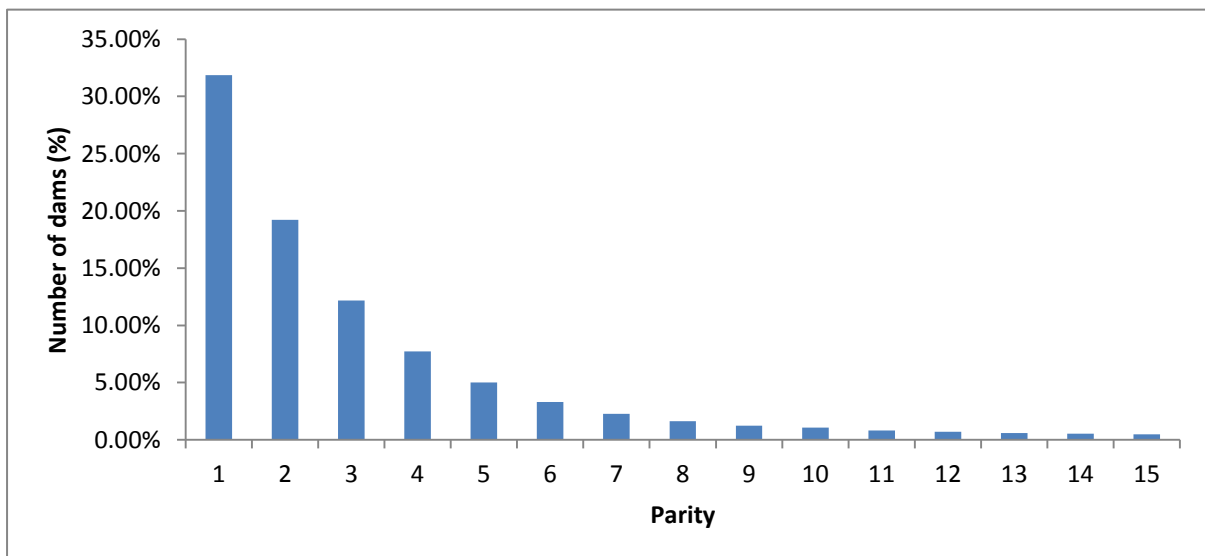


Figure 4.5: Distribution of Boran dams by parity

Figure 4.5 shows that parity 1 contains the highest proportion of dams with the number of dams decreasing with increase in parity.

The effective population size is a measure of genetic diversity within a population. Therefore, it is an important parameter in breeding of animals. The trend for number of animals used in reproduction is presented in Figure 4.6 and for effective population size over time is represented in Figure 4.7.

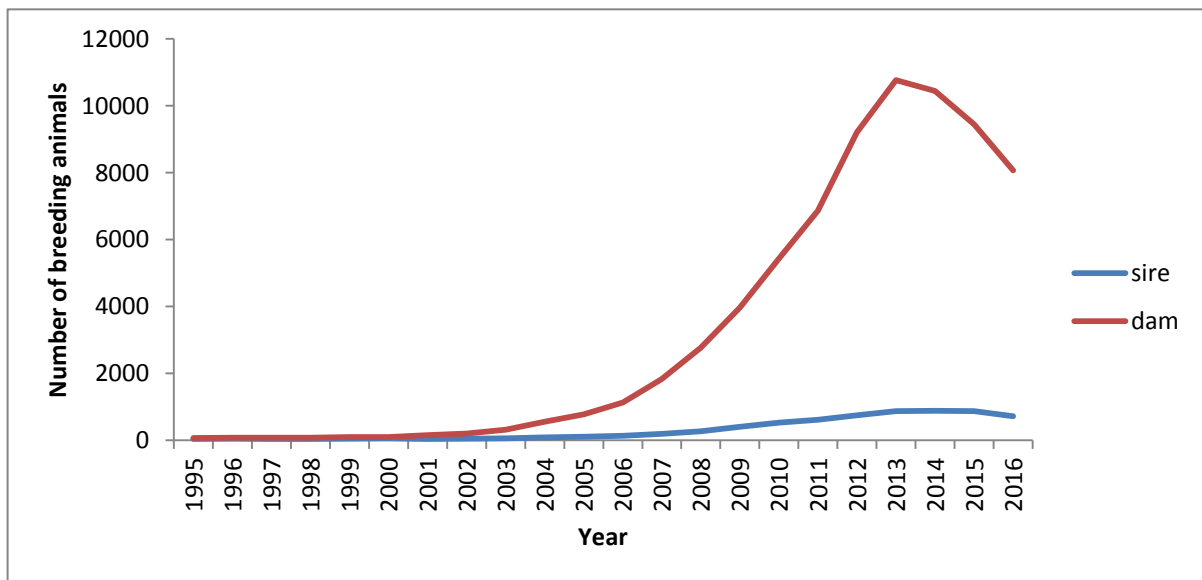


Figure 4.6: Trend in the number of Boran breeding animals from 1995 - 2016

The number of breeding animals (sires and dams) for the Boran is consistent until 2003 after which an exponential increase occurred in the amount of breeding dams with a small consistent increase in the amount of breeding sires.

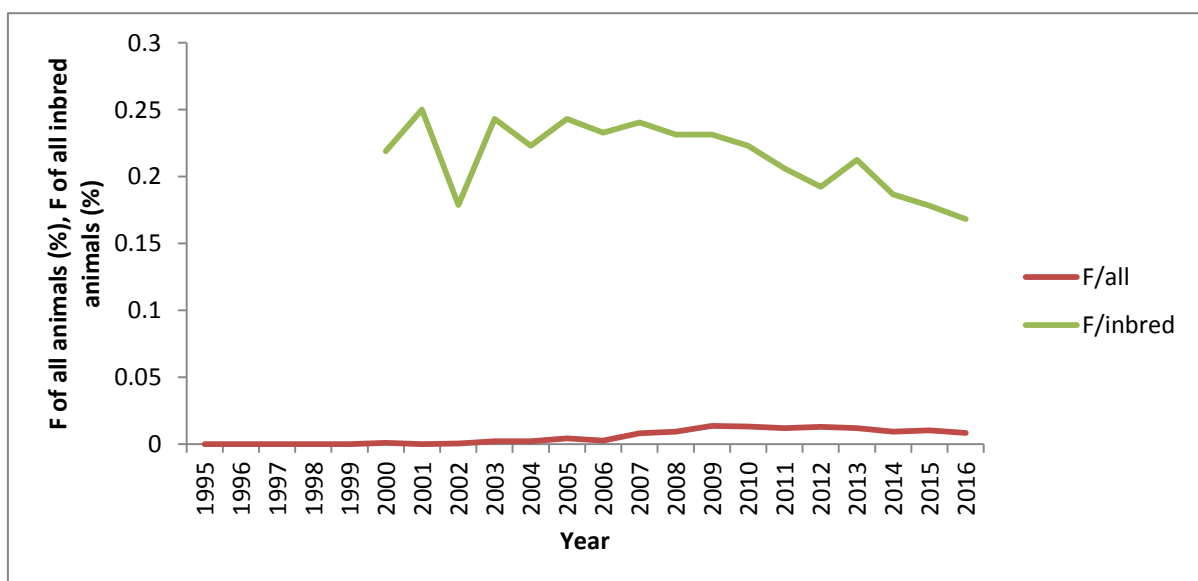


Figure 4.7: Trend of inbreeding coefficient for all Boran cattle and inbred Boran cattle

The rate of inbreeding (ΔF) was calculated to determine the level of inbreeding. Figure 4.7 shows the trend for inbreeding coefficient of all animals, as well as inbred animals, computed by year of birth of the individual animal in the whole pedigree. Inbreeding of inbred animals was only available from 2000 after breeding in SA had occurred and had decreased over the years from 0.22% to 0.17%. Inbreeding of all animals increased from 0% to 0.014% until 2009, after which it decreased to 0.008% in 2016. The inbreeding coefficient for all animals was also evaluated with EVA (Berg et al., 2006) and the result was similar for the year 2016 (0.007%).

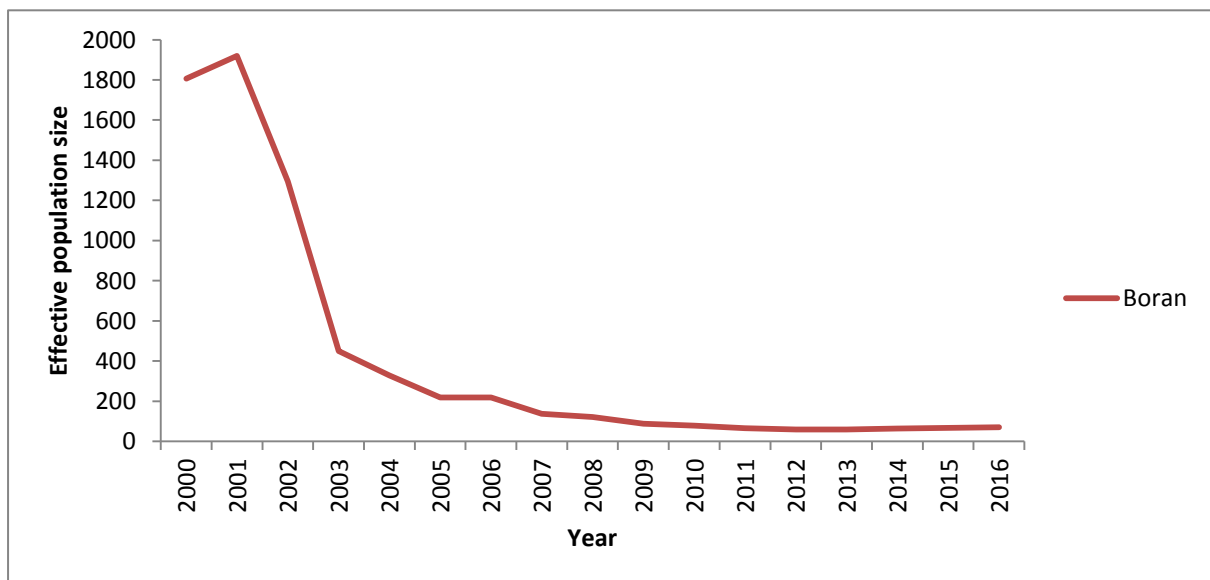


Figure 4.8: South African Boran effective population size over time

The trend for effective population size over the years has decrease rapidly from 2000 (1806) until 2008 (122) with an effective population size of 71 cattle in 2016. For the period 1995 to 1999, no effective population size could be estimated due to incomplete data.

Production data

In Table 4.3 the descriptive statistics for each trait over 22 years were shown. Details per year are included as Addendum A.

Table 4.3: Descriptive statistics for recorded traits over 22 years

Traits	Mean	sd	Min	Max
AFC	1100.37	141.00	814.20	1543.67
ICP	487.60	111.86	343.05	772.15
BW (DIR)	29.43	4.22	18.65	46.20
BW(MAT)	29.43	4.26	18.06	46.20
WW (DIR)	203.70	30.54	126.50	309.75
WW (MAT)	203.70	30.54	126.50	309.75
YW	256.76	59.55	172.00	390.67
FW	326.63	51.49	235.67	437.70
MW	393.97	53.54	296.00	510.71

AFC: Age at first calving; ICP: Inter-calving period; BB: Birth weight; WW: Weaning weight; YW: Yearling weight; FW: Final Weight; MW: Mature weight; DIR: Direct; MAT: Maternal

The genetic trends for seven economically important traits in the Boran breed were estimated by averaging the predicted breeding values on birth year for each trait between 1995 and 2016. The most important point in these trends is the slope of the line (Figure 4.9-4.13) and the rate of genetic change per year (Table 4.4) which will indicate the direction of selection and traits of priority of the Boran breeders.

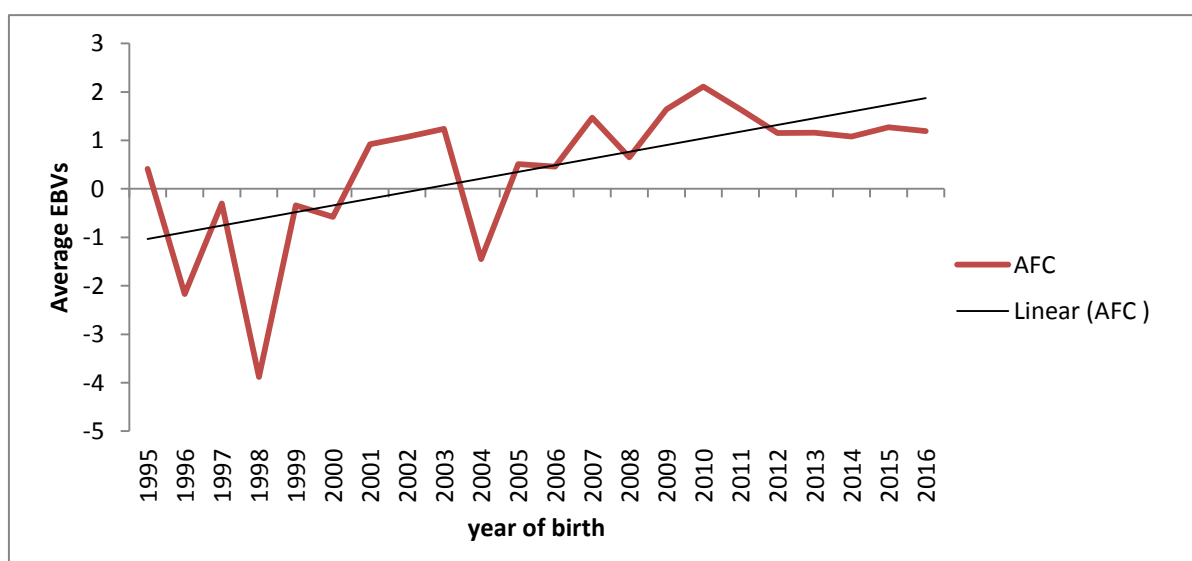


Figure 4.9: Genetic trend for age of first calving (AFC)

EBVs for age at first calving (AFC) (Figure 4.9) varied over the years but also showed a steady increase over time. The variation in EBVs for AFC was extreme at first until 2004 after which the variation decreased over the years due to more complete recording. AFC is 1.19 in 2016.

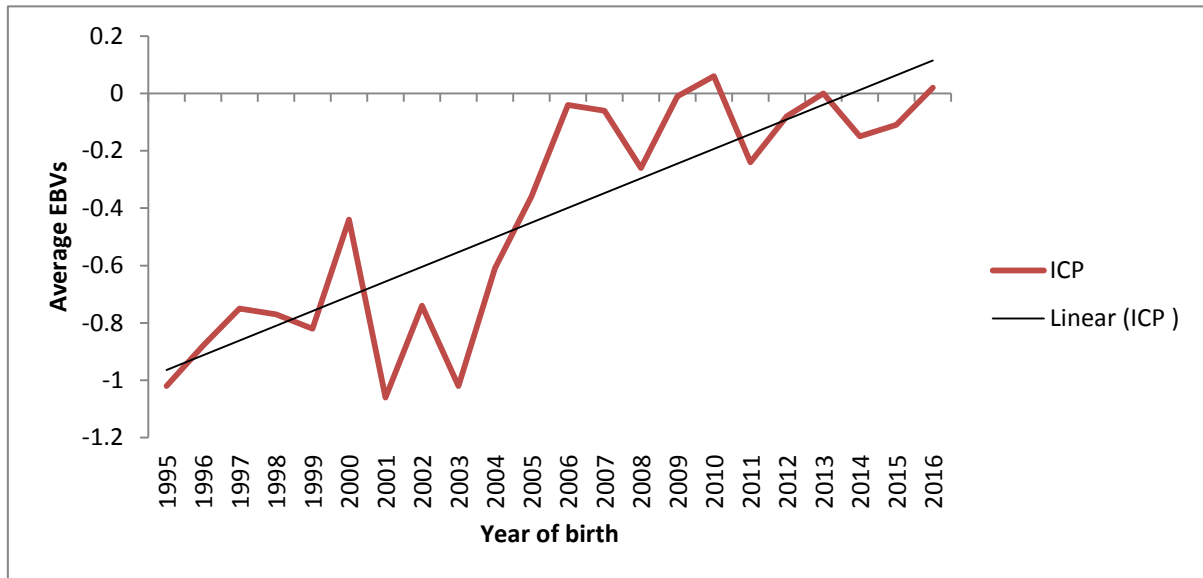


Figure 4.10: Genetic trend for inter-calving period (ICP)

EBVs for inter-calving period (ICP) (Figure 4.10) varied over the years. Erratic variation occurred until 2003 with a rapid increase that followed until 2006 and erratic variation occurring again until 2016. The EBVs for ICP is 0.02 in 2016. The trend shows a clear increase in ICP over the years.

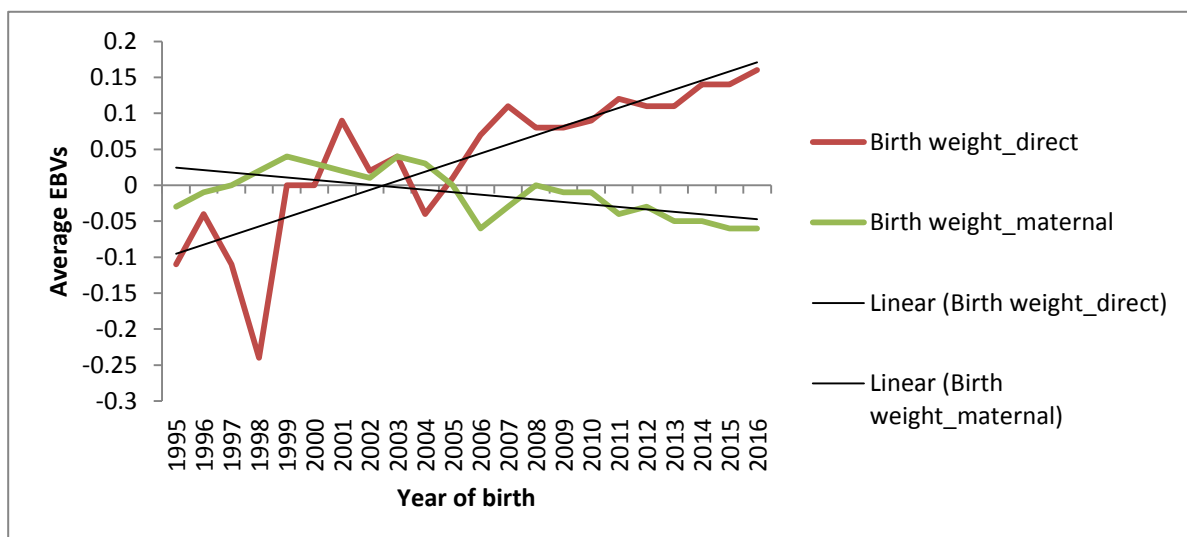


Figure 4.11: Genetic trend for birth weight (direct and maternal)

The trends for maternal and direct EBVs are variable. Since the availability of more complete animal recording, the EBVs for birth weight (direct) and birth weight (maternal) indicate a steady increase and decrease respectively.

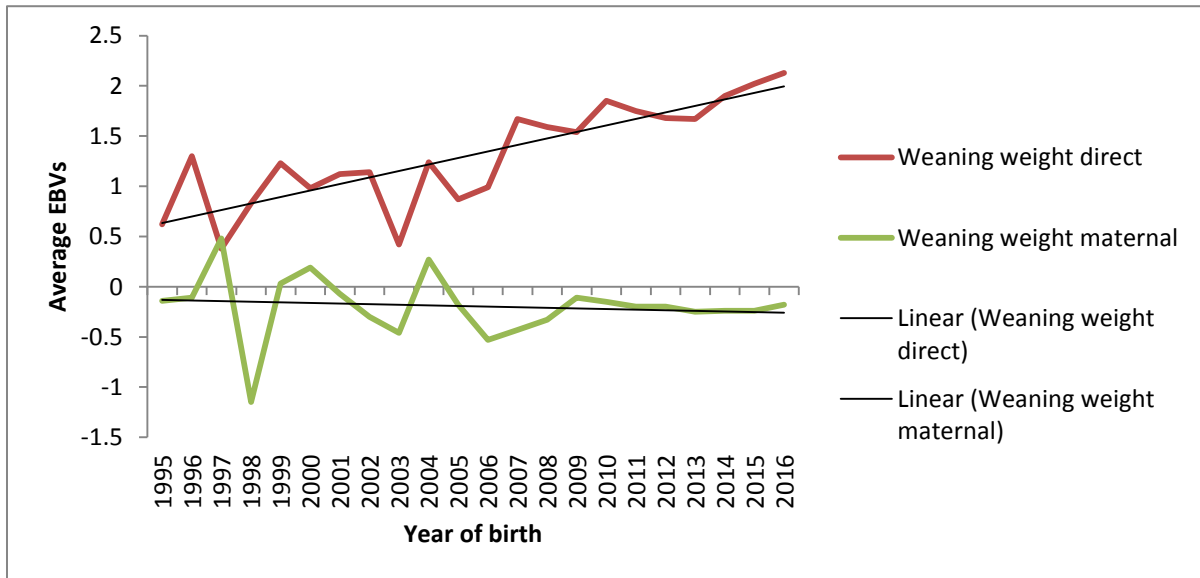


Figure 4.12: Genetic trend for weaning weight (direct and maternal)

The trends for maternal and direct weaning weight EBVs vary before 2003 and from 2004 the EBVs for weaning weight (direct) increased over the years, while the EBVs for weaning weight (maternal) decreased. In 2016, weaning weight (direct) was 2.13 and weaning weight (maternal) was -0.18.

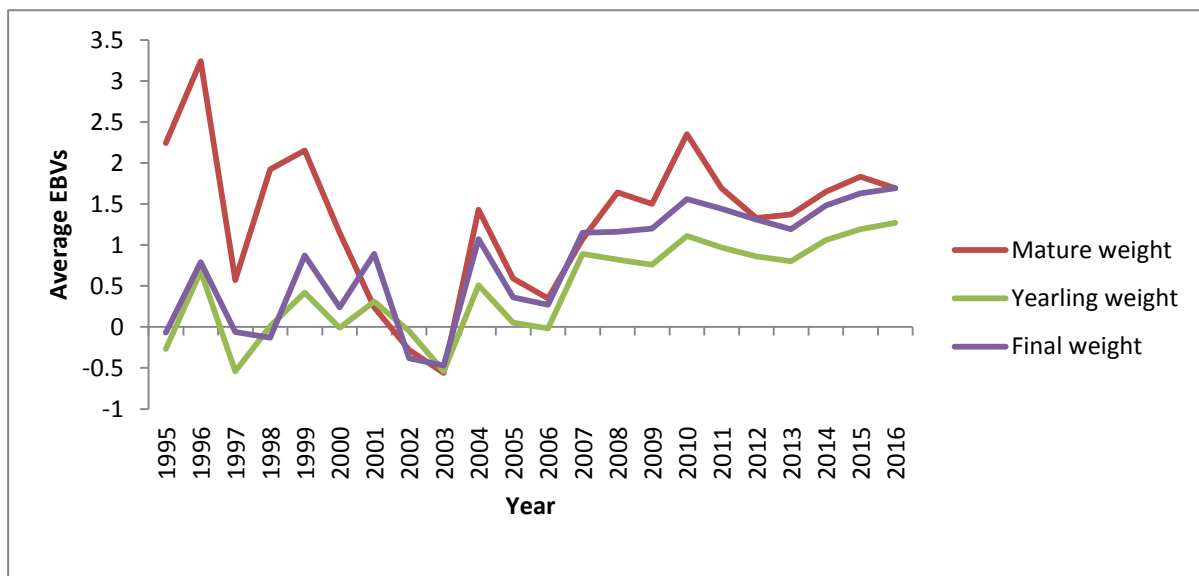


Figure 4.13: Genetic trend for yearling, final and mature weights

The genetic trend for yearling weight, final weight and mature weight were erratic but similar (Figure 4.13) with an increase for all observed from 2007. There is no clear trend for yearling, final and mature weights due to incomplete data.

Table 4.4: Estimated annual rate of genetic change based on EBVs of traits measured between 1995 and 2016

Trait	Rate of genetic trend
Birth weight direct (kg)	0.00173913
Birth weight maternal (kg)	-0.000434783
Weaning weight direct (kg)	0.056956522
Weaning weight maternal (kg)	-0.008695652
Yearling weight (12 months) direct (kg)	0.020434783
Final weight (18 months) direct (kg)	0.033913043
Mature weight direct (kg)	0.057826087
Age at first calving (days)	0.01826087
Inter-calving period (days)	-0.01826087

Slight changes were observed which indicate very slow genetic changes for all traits except for birth weight (maternal) and weaning weight (maternal) which changes is so small that it is insignificant. The direction for birth weight (direct) and age at first calving is positive but unfavourable. The direction for weaning weight (direct), yearling weight, final weight and mature weight is also positive but favourable. However, the inter-calving period is negative favourable.

4.2 Genotypic data

A total of 83 samples (63 males and 20 females) were analysed and after quality control 5 animals were removed due to missing genotype data. 140 113 SNP variants and 78 cattle passed quality control and no founders were detected. For marker quality control, 12 060 SNPs were removed due to missing genotype data with 100 449 SNPs available for analyses. Table 4.5 shows the results for MAF, heterozygosity (observed and expected) and inbreeding after marker-based quality control and LD-pruning were performed in the Boran population.

Table 4.5 shows the summary statistics of the Boran. Minor allele frequency, heterozygosity observed and expected and inbreeding coefficient were lower after quality control than after LD-pruning.

Table 4.5 Summary of statistics of the Boran population

Population	Boran
Average MAF	0.258
Average H_e	0.348
Average H_o	0.355
Inbreeding coefficient	-0.019
Average MAF	0.276
Average H_E	0.361
Average H_o	0.371
Inbreeding coefficient	-0.027

*Top was calculated after quality control and bottom was calculated after LD-pruning

An effective population size of 5133 Boran was estimated based on genotypic data of 958 years ago. The effective population size drastically decreased over time with a current estimation of 184 Boran cattle (Figure 4.14).

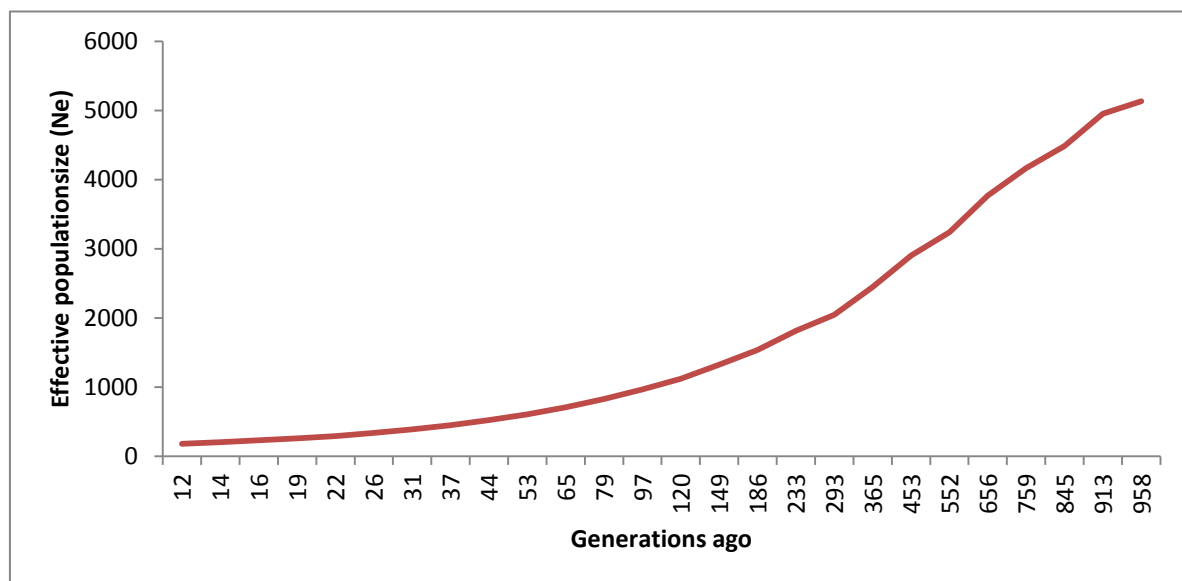


Figure 4.14: Effective population size of Boran cattle based on genotypic data

Principal Component Analysis (PCA) was used to visualize individual relationships within the Boran population (Figure 4.15) and between the three breeds (Boran, Bonsmara and Hereford) (Figure 4.16). Figure 4.15 indicates a wide spread of the Boran population without any distinct clusters.

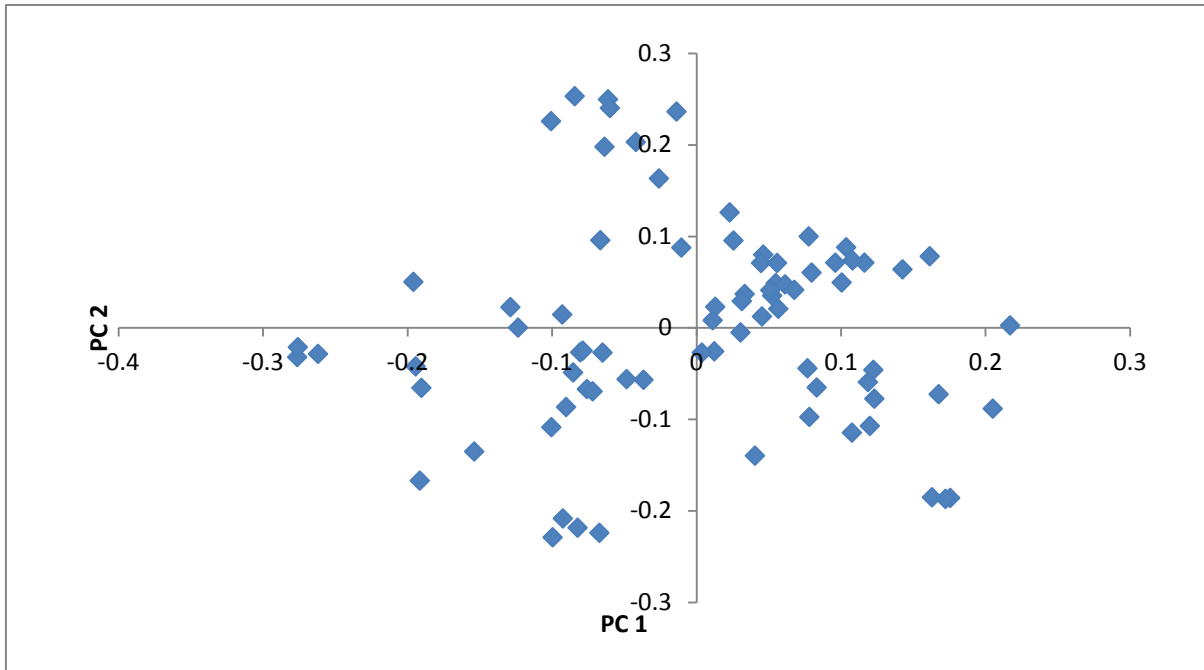


Figure 4.15: Principal Component Analysis of the SA Boran population

In Figure 4.16, the PCA for the Boran with Hereford and Bonsmara clearly illustrates three distinct clusters.

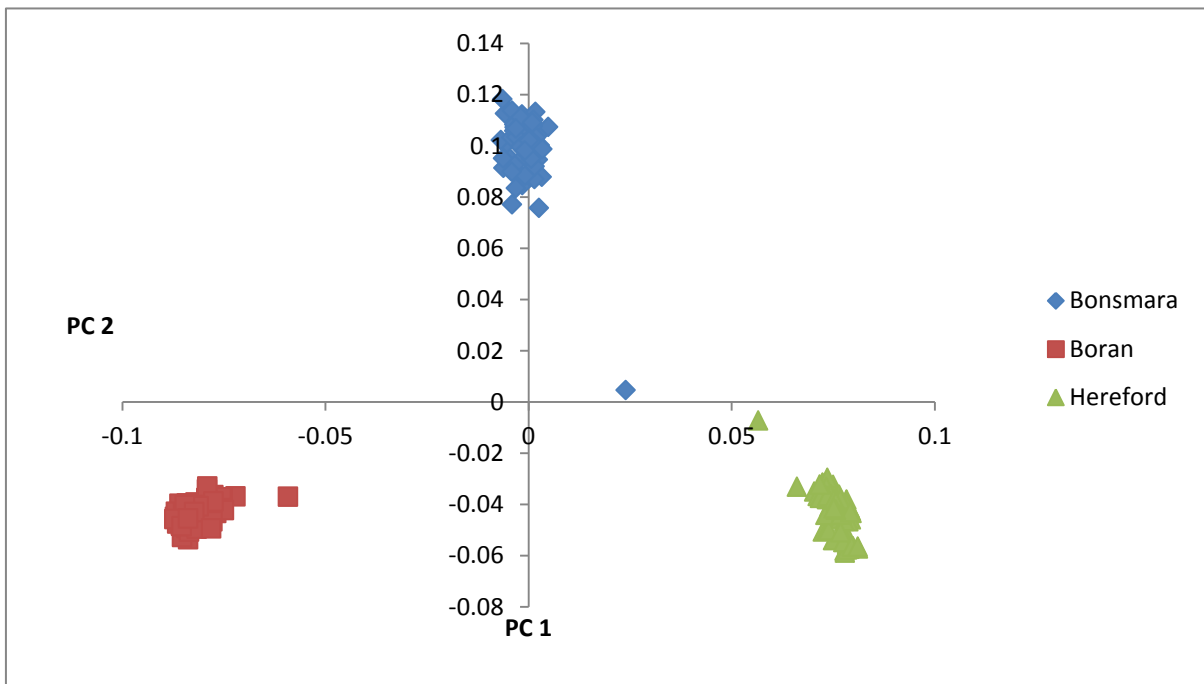


Figure 4.16: PCA of the three combined breeds (Boran, Bonsmara and Hereford)

The Boran population is located furthest from the other two breeds and forms a tight cluster. Two outliers were observed for the Hereford population and one for the Bonsmara with one outlier observed for Boran. Table 4.6 shows the F_{ST} -values between Boran, Bonsmara and Hereford.

Table 4.6: Population differentiation among the three breeds (Boran, Bonsmara, Hereford)

	Bonsmara	Boran	Hereford
Bonsmara	***		
Boran	0.11338	***	
Hereford	0.17807	0.0996	***

Between Bonsmara and Hereford there is the most differentiation (0.18) and between Boran and Hereford there is the least comparison (0.1). This indicates that Bonsmara and Hereford are less distinctive compared to Bonsmara is related to Boran.

Likelihood scores for runs of various K-values in Admixture showed a decrease in cross-validation error values with an inflection point at K=6 (Figure 4.17) for the combined population (Boran, Bonsmara and Hereford).

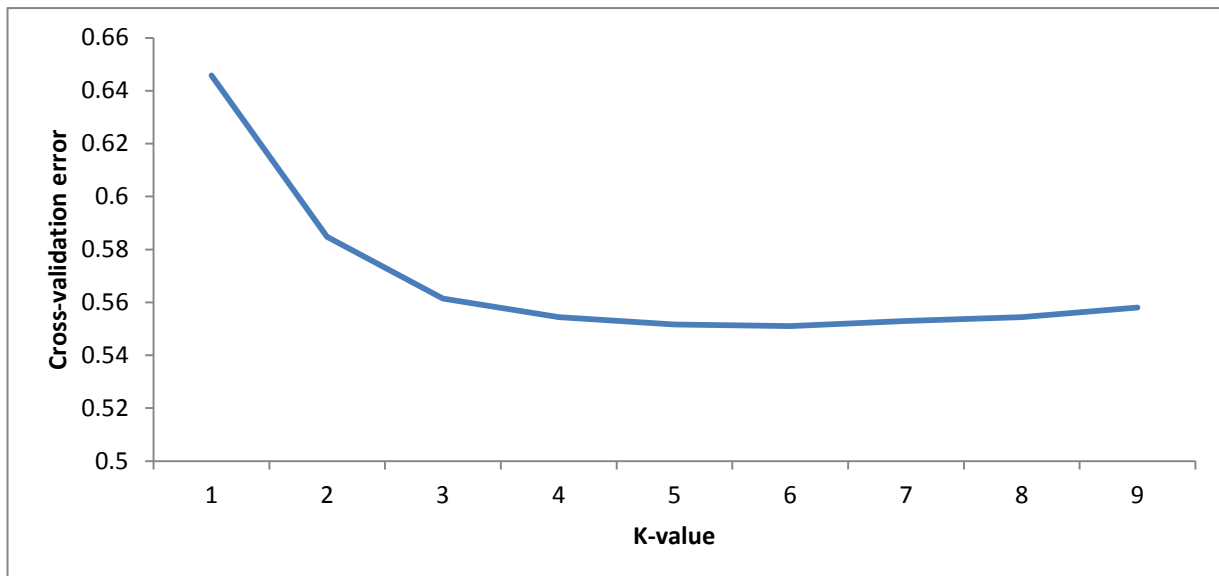


Figure 4.17: Cross-validation plot for combined breeds (Boran, Bonsmara, Hereford)

Cross-validation decreased rapidly until $K=3$ after which the decline took place at a lower rate until $K=6$ was reached. After $K=6$, cross-validation started to increase at a slow rate, indicating that $K=6$ is the smallest value.

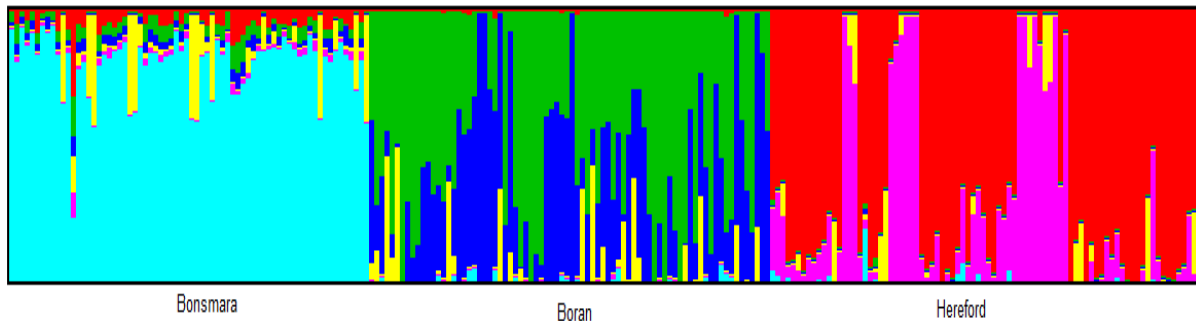


Figure 4.18: Bar plot of the population structure of the combined breeds (Boran, Bonsmara, Hereford)

The combined population (Boran, Bonsmara and Hereford) at $K=6$ was used to generate a bar plot of the three different breeds' population structures using Genesis (Figure 4.18). The three distinct breeds are visible with some admixture visible between all three breeds.

Chapter 5: Discussion

5.1 Introduction

The ultimate goal of most modern beef cattle production systems is to improve the efficiency of production in order to be competitive and economically viable. In order to accomplish this objective, several activities such as animal recording, genetic evaluation and selection are involved. The current performance recording systems along with the advances in the genetic evaluation to derive EBVs have influenced most of the economically important traits in beef cattle. Genetic trends are an important indicator of selection direction and success which aids in the planning of future breeding schemes (Bosso et al., 2009).

This study was requested by the South African Boran society for a phenotypic and genetic characterisation based on the available data. The results can be used to help the Boran society to set breeding objectives for the Boran in South Africa and positioning of the breed in the South African beef industry.

5.2 Phenotypic data

Pedigree data

The South African Boran was introduced to South Africa in 1995 but participation in recording only commenced in 2003. The results from this study clearly show a large variability in pedigree completeness over the past 22 years with an improvement from 2007. The improvement in the pedigree quality can mainly be credited to the improvement in the animal recording through computerisation and the availability of animal recording systems (Bergh, 2010). The accuracy and completeness of pedigrees influence the accuracy of the estimated breeding values (Mrode, 2014). Pedigree completeness is the sum of the percentage of known ancestors over all available generations (Steyn et al., 2012). The trends of the pedigree completeness observed in the Boran breed decreased with subsequent generations which can be attributed to their recent establishment in South Africa (Abin et al., 2016).

Studies conducted to investigate pedigree completeness of beef cattle populations in the world have revealed similar variable degrees of pedigree completeness in a number of breeds. In Italian beef cattle breeds, Chianina showed a pedigree completeness of 62% in the sixth generation and 16.4% in the eighth generation (Bozzi et al., 2006). In a comparison of Irish beef cattle, Simmentals had the lowest pedigree completeness with only 43% at four generations deep (Mc Parland et al., 2007). For Slovak beef cattle breeds, Blonde d'Aquitaine and Simmental had the highest pedigree completeness in the first generation and Limousine had the lowest pedigree completeness across all the studied generations (Kadlecik & Pavlik, 2012). Compared to SA Bonsmara, Boran has a higher completeness in the first generation but lower when comparing the sixth generation (Groeneveld et al., 2009).

Generation interval is an important factor to consider in response to selection (Falconer & Mackay, 1996). For South African Boran, the average generation interval is 5.5 years and is comparable to other South African breeds such as Bonsmara (5.6 years) (Groeneveld et al., 2009) and Brangus (5.17 years) (Steyn et al., 2012). The average generation interval for the Boran population is shorter compared to European breeds such as Charolais (6.17 years), Hereford (6.03 years) and Angus (6.09 years) (Mc Parland et al., 2007). It is however, longer when compared to the US Herefords (4.88 years) (Koch et al., 2004), Marchigiana (4.93 years), Romagnola cattle (5.15 years) (Bozzi et al., 2006) and Blanco Orejinerio (4.7 years) (Martinez et al., 2008). A shorter generation interval will result in a faster rate of genetic change and will thereby affect the rate of genetic progress (Bourdon, 2000; Marquez & Garrick, 2007). The relatively short generation interval of Boran cattle is a favourable characteristic which may result in improvement of genetic progress (Abin et al., 2016).

The estimated generation intervals for the four selection pathways for the Boran breed, where the two sire-offspring pathways (SS and SD) are longer than the dam to son (DS) pathway but shorter than the dam to daughter (DD) pathway, is similar to the reported results for the Bonsmara cattle breed (Groeneveld et al., 2009). Generation interval differences are dependent on the replacement strategy of females, use of proven males for a longer period and selection of breeding males only after progeny testing (Marquez & Garrick, 2007).

The genetic structure of a population at a given time is influenced by the age structure of the parents and the number of breeding males and females in the preceding population that would eventually determine the effective population size (Leroy et al., 2013). For a beef herd to be more profitable, a cow should remain in production for several years to compensate for the culled ones and counterbalance the development and maintenance costs (Day & Nogueira, 2013). However, the main reason for culling a cow earlier is her failure to become pregnant or to give offspring (Van der Westhuizen et al., 2001; BIF, 2010). The age structure of sires and dams can determine the effective population as reproductive lifetime (longevity) increases due to reproductive success (Hamidi Hay & Roberts, 2017). Improved longevity will increase the generation interval and increase accuracy of the predicted breeding value (Roberts et al., 2015). However, this could be realised only when there is accurate and consistent record keeping.

The majority of sires and dams produced offspring between the age of two and five years in the Boran population with dams producing earlier in life than sires. The proportion of sires producing offspring at an older age are greater than dams which indicates that males are used in reproduction longer than females (Roberts et al., 2015). It will therefore, be more profitable if the calving age of the dams is reduced while increasing the proportion of males producing offspring at an earlier age. The calving age of the dams could be reduced by mating heifer's right after puberty (Day & Nogueira, 2013). This will lead to an increase in the number of offspring per dam and ultimately the economic efficiency of the farm. Genetic variation in age at puberty in beef cattle has been reported and efficient utilisation of such variation in selection would potentially influence production efficiency (Philips, 2010).

The distribution of dams by parity influences the rate of turnover of the breeding animals. The rate of turnover is one of the aspects that influence the rate of genetic progress and improvement programmes, since animals with good longevity tend to contribute more offspring to the population (Hamidi Hay & Roberts, 2017). Female production and reproduction is essential as it quantifies the output from the breeding females that were selected to breed future generations and thereby ensures the sustainability of beef cattle production and robustness of the enterprise (Walmsley et al., 2018). The average number of offspring per dam increases by having cows with parity between one and five. The higher numbers of animals with more parity correspond to more offspring being produced and good longevity (Roger et al., 2004).

Inbreeding can be used as a parameter to measure the status of genetic diversity within the Boran population (Northcutt et al., 2004). The accuracy of the rate of inbreeding and relatedness depends on the extent of the pedigree completeness (Kios et al., 2017) and computational methods (Leroy et al., 2013). However, due to Boran cattle's poor recoding of pedigree data has led to an inconsistent trend of inbreeding coefficient and may probably also be an under estimation (Mc Parland et al., 2007). None the less, this trend indicates a low use of related animals. The low inbreeding coefficient implies minimal mating of related individuals which will cause in very slow occurrences of homozygosity, this will have a minimal negative effect on the Boran cattle's performance and fitness due to very low reduction of genetic variation (Kios et al., 2017). Inbred animals are those individuals that are offspring of mating between first cousins (inbreeding coefficient ≥ 0.0625) (Bourdon, 200). This high level of inbreeding will result in the increase of homozygosity occurrence which will lead to increased risk of appearances of undesirable effects within the Boran population (Pryce et al., 2012). A balanced mating policy that favoured best unrelated individuals can be used to correct the possible effects (Bergh, 2010).

It has been shown that continuous improvement in animal recording, genetic evaluation and mating strategies contributes to successful selection and genetic improvement of the beef industry (Eggen, A., 2012). Despite this success, the methods used have promoted an increase in the probability of relatedness and increased level of inbreeding that may compromise long-term selection response and increase the risk of inbreeding depression (Weigel, 2001; Northcutt et al., 2004; Carolino & Gama, 2008). It is therefore, important to obtain insight on the genetic structure of the Boran population to maintain genetic diversity and avoid an increase in inbreeding that would risk genetic diversity and compromise future genetic gain (Makina et al., 2014)

The number of breeding animals at specific times determines the effective population size which is the principal factor that influences the rate of genetic drift and inbreeding in a population over a period of time (Weigel, 2001; Groeneveld, et al., 2009). The decrease observed in the trend of breeding animals after 2013 may be due to older animals being culled and the presence of young animals, as only animals having a service record or those that appear as parents in the birth record were considered in the calculation of breeding animals. Effective population size can be used as a parameter to measure the status of genetic diversity within the Boran population (Biegelmeier et al., 2016) due to its direct relationship with the rate of inbreeding and loss of genetic diversity over time (Caballero & Toro, 2000; Charlesworth, 2009).

The results on the Boran population indicated a decreasing trend for effective population size due to a decrease in the number of breeding animals. Reduction in effective population size may increase the selection response through selection intensity but can also lead to inbreeding depression and the loss of genetic variance that limit selection from new mutations in the long term (Cervantes et al., 2008). An effective population size between 50 and 100 may cause an increase in the rate of genetic progress of 0.5% to 1% per generation which is sufficient to maintain the genetic diversity within the population (Leroy et al., 2013). A drop in the effective population size below this limit would result in a decline in population fitness as a result of mutation and genetic drift (Biegelmeyer et al., 2016). The Boran cattle effective population size decreased over the years (71), however, incomplete pedigree records can influence the effective population size value (Carolino & Gama, 2008; Albrechtsen et al., 2009).

Production data

The genetic improvement of the South African Boran over the past 22 years based on available EBVs has been minimal. It should be noted that Boran is a relatively new breed in South Africa. However, incomplete and poor participation in official recording has contributed to the slow genetic improvement of this breed.

Reproductive traits are of economic importance because cows that calve earlier in life and that have regular calving intervals produce more calves in less time, leading to an increase in the replacement rate and productivity of the farm (Patterson et al., 2016). When observing the descriptive statistics, fertility traits such as age at first calving and inter-calving period have decreased over the years. Heifers will calve their first calf earlier in their life with days between calving also being shorter, leading to improved longevity (Gutiérrez et al., 2002).

The descriptive statistics for production traits over the past 22 years indicate that the average birth weight for Boran cattle has decreased, producing smaller calves at birth. However, the average weaning weight has increased over the years, indicating a fast growth rate (Cortés-Lacruz et al., 2017). The average yearling weight, final weight and mature weight stayed more or less consistent over the past decade. These weights are influenced by factors such as genetics, management and nutrition (Walmsley et al., 2018).

Observation of the EBVs indicated that the Boran population showed an increase in the trend of age at first calving (AFC) of 0.41 to 1.19. This trend indicated that females are calving at a later stage in life which will cause a decrease in the total number of calves produced in a life time resulting in a decrease in productivity (Ahlberg et al., 2016). Selection

for lower age at first calving will result in a decrease in the generation interval and an increase in annual genetic gain (Marquez & Garrick, 2007).

In this study, the genetic trends for the two fertility traits recorded indicated no progress. An increase in the genetic trend for calving interval of the Boran population was observed, probably due to a highly positive genetic correlation between age at first calving (AFC) and calving interval (CI) (Rust & Groeneveld, 2001). The increased calving interval can potentially cause a decrease in the number of calves produced per cow in her life time which will lead to a chain effect of decreased productivity of the herd (Boligon et al., 2016). However, due to limited records available for fertility, it is not possible to draw absolute conclusions regarding fertility traits. Due to the importance of fertility, it will be imperative to include fertility in the breeding objective and selection programmes for South African Boran.

The genetic trend for birth weight indicated a slight increase in birth weight (direct) (-0.11 to 0.16). Increase in birth weight (direct) influences calf survival and is associated with dystocia (Bennett & Gregory, 2001; Hickson et al., 2006), increased culling and decreased fertility rates (Meijering, 1984; Roger et al., 2004). Increase in birth weight is associated with a correlated response when selection for mature weight is practised (Santana et al., 2014). However, Boran cattle's birth weight was high when compared to Red Angus (-1.1) (Ahlberg et al., 2016).

The genetic trend for birth weight indicated a slight decrease in birth weight (maternal) (-0.03 to -0.06). The decrease in birth weight (maternal) refers to the dam's ability to produce calves that are lighter than expected at birth (McHugh et al., 2014). The uterine environment created by the dam restricts the growth of the foetus resulting in smaller birth weight (Walmsley et al., 2018). By using both birth weight (direct) and birth weight (maternal) more accurate information for predicting a calf's birth weight and to control dystocia will be provided (Lykins et al., 2000). The most important maternal effects influencing calf growth from conception until weaning are the uterine environment during pregnancy, the transfer of antibodies through colostrum, the maternal ability of the cow to protect the calf and the milk yield (Pryce et al, 2002).

Weaning weight of the calves is the main source of farm income for the commercial farmer (Miller & Wilton, 1999) and at the genetic level weaning weight depends on both the genetic potential of the calf (direct effect) and the effect of the dam (maternal effect) (Cortes-Lacruz et al., 2017). In this study, the genetic trend for weaning weight (direct) showed an increase (0.62 to 2.13) while weaning weight (maternal) showed a decrease (-0.14 to -0.18). Weaning weight (direct) followed a similar trend as birth weight (direct) due to the positive genetic

correlation that exists between the two traits (Santana et al., 2014). A negative correlation existed between the maternal environment of the dam and the genetic ability of her calf (Miller & Wilton, 1999) due to potential antagonistic effects of genes related to growth and maternal ability (Mota et al., 2016a). Due to the decrease in the trend of weaning weight (maternal), the conclusion can be made that the Boran dams do not produce enough milk because bulls are being selected based on growth and not on maternal characteristics. This can be improved through selecting Boran males based on daughters offspring with higher weaning weights (EBVs).

A high positive genetic correlation exists between weights measured earlier in life such as birth weight or weaning weight, and future weights such as yearling weight (12 months), final weight (18 months) and mature weight (Snelling et al., 2010). The trend for birth weight and weaning weight showed an increase which results in an increase in yearling weight and final weight but the trend for mature weight plateaued. Selection criteria to obtain moderate birth weights and mature weights while maintaining a rapid growth rate are complex and need comprehensive selection (Abin et al., 2016). Improvement in Boran cattle production efficiency is not necessarily related to an increase in genetic trends for all the recorded traits.

The genetic trends for traits recorded for the Boran breed showed some improvement over the past 22 years, although unfavourable changes occurred for traits such as age at first calving, calving interval, birth weight (direct) and weaning weight (maternal). Implementation of a breeding programme will require consistent and accurate measurements of traits for genetic evaluations to provide breeders with accurate EBVs to reach their breeding objectives. The Boran Breeders' Society are making continuous efforts to improve growth rate by targeting different stages of growth weight (weaning, yearling, final weight) as presented by the change in their genetic trends. Selection of individual animals based on the EBVs derived from accurate performance data will aid towards optimum genetic progress in the desirable direction. The current variation in the rate of genetic change observed in this study is probably due to incomplete records. The relatively slow rate of genetic improvement might be attributed to selection emphasis on traits that are difficult to measure and the recent introduction of the Boran breed to South Africa. This can be enhanced with higher participation in animal recording of the desired traits.

The results of the genetic trends of different traits confirmed the importance of animal recording systems for genetic management of Boran cattle as only a limited amount of Boran farmers participated in recording and more is needed for accurate data. It offers the opportunity for monitoring livestock genetic diversity and ensures a sustainable improvement

programme. An animal recording system should be used for the management of all beef cattle in South Africa.

5.3 Genotypic diversity and population structure

Genetic diversity analyses were performed on the South African Boran to give insight into the genetic structure of the breed. Heterozygosity indicates the amount of polymorphism measured for assessing the genetic variability of a population. Observed and expected heterozygosity differs due to non-random mating within the population (Falconer & Mackay, 1996). In this study, the Boran population had a relatively high expected heterozygosity (0.348 after QC and 0.361 after LD-pruning). This relatively high value may be due to long-term natural population adaptation in an environment where admixing of different strains of various populations occurred (Ojango et al., 2011). The Boran population showed a modern MAF value (0.258) after quality control and a slightly higher MAF value (0.276) after LD-pruning. This modern occurrence of MAF may be due to the small population of the Boran (Falconer & Mackay, 1996; Hill, 2014). Therefore, more Boran cattle need to be genotyped in order to obtain a more accurate prediction (Fan et al. 2010).

Effective population size refers to the number of individuals in an idealized population that would give rise to similar rates of inbreeding as observed in the actual breeding population, making it an important parameter to assist in explaining the evolution of different populations (Falconer & Mackay, 1996). The strength of linkage equilibrium in the genome is useful for inferring ancestral effective population size (Hayes et al., 2003; Albrechtsen et al., 2009). The rapidly declined Boran population may be due to a significant bottleneck that had occurred at breed formation, and subdivision of the population that resulted in significantly reduced effective population size (Daetwyler et al., 2010). The reduction in numbers observed in the Boran population over the past 958 years may be due to post-domestication events of human migration (Gautier et al., 2007). The relative small effective population may be due to intense selection, inbreeding and the wide spread use of artificial insemination in South Africa, and also the use of few elite sires (Hayes et al., 2009). For response to selection to occur, the effective population must be above 50 animals per generation (FAO, 1998). The trend for effective population of the South African Boran at this stage is decreasing with every generation which may lead to an effective population smaller than 50 animals per generation resulting in no response to genetic gain. Currently, the Boran cattle's effective population is estimated at 184 animals.

It is important to maintain genetic diversity in order to prevent low performance resulting from inbreeding (Edea et al., 2013). The genetic inbreeding coefficient (F_{IS}) of an individual

indicates whether individuals of the subpopulation are under a non-random mating system or not (Dorji & Daugjinda, 2014). The Boran population showed a negative low inbreeding coefficient (-0.019) which was even lower after LD-pruning (-0.027). This indicates well maintained genetic diversity and limited inbreeding within the Boran population (Williams et al., 2016). However, inbreeding levels should be estimated every five years to determine any unfavourable changes in order to prevent an increase in inbreeding which could result in loss of genetic variation and the occurrence of inbreeding depression as well as an increase of rare lethal disorders (Williams et al., 2016). Information regarding genetic diversity and population structure among cattle breeds is essential for genetic improvement (Groeneveld et al., 2010).

The Boran showed no distinct clusters within the breed which indicates genetic diversity within the breed. However, Boran was compared to the Bonsmara and Hereford based on genetic diversity and population structure. The Principal Component Analyses indicated three distinct populations and showed that the Boran breed is not related to Bonsmara or Hereford, as was expected due to their classification (Hardy et al., 2003; Boligon et al., 2016). The data showed that among indigenous (Boran), locally-developed (Bonsmara) and *Bos taurus* (Hereford) cattle breeds genetic differentiation range is moderate (0.1-0.18) where more genetic differentiation occurs between Bonsmara and Hereford than between Bonsmara and Boran. This is comparable to 15% reported between African and European breeds (Gautier et al., 2007) and 17% reported between the Ethiopian and Hanwoo cattle populations (Edea et al., 2013).

Population structure analysis revealed some signs of admixture and genetic relationship between Boran, Bonsmara and Hereford. However, the analyses also revealed three distinct populations. This indicates that the genetic diversity of breeds may be directly linked to the areas of origin and relatedness geographically due to isolation (Mota, et al., 2016a). This could be the reason for the two main ancestral lines of the Boran due to the unique route of migration into Southern Africa, small population size and recent introduction into South Africa. The three breeds are not related to each other which is in agreement with separate domestication events and divergences (McKay et al., 2008; Decker et al., 2014).

The results obtained in this study provided a reference of the current genetic potential and can serve as a benchmark for formulation of breeding objectives. The different genetic trends indicate the need for proper recording that contributed to limited data available for genetic evaluations and probably hindered genetic improvement. Genetic diversity is relatively high based on genomic analyses. This study can serve as a basis for formulation, selection and revision programmes for South African Boran.

Chapter 6: Conclusion and recommendations

African cattle have evolved over many centuries and today the majority are classified as Zebu. Historical evidence indicates that Boran cattle, also classified as Zebu, have been present in Africa 2000 BC. The largest share of African Zebu cattle is Boran cattle and kept in arid and semi-arid areas in Kenya. Boran cattle are used for multiple purposes such as milk production, meat and draft power. In South Africa the Boran is predominantly used as a beef breed. Boran cattle are known for a high fertility rate, drought resistance, low disease susceptibility, and heat tolerance that all contribute to their ability to adapt to a variety of climates including several climatic regions of South Africa.

The Boran was introduced into South Africa in 1995 and since then the numbers of Boran cattle have increased to 36 048 registered Boran cattle. Despite a relatively recent introduction into South Africa the Boran breeders have been participating in animal recording, focussing on seven different traits of economic importance. Both pedigree and phenotypic records are submitted to SA Studbook for genetic evaluations. Estimated Breeding Values (EBVs) are routinely provided to breeders for use in their selection programs. The Boran has also joined the BGP (Bovine Genomic Project) to generate genotypic data necessary to build a genotypic reference population. Due to the limited scientific research available on the South African Boran, the University of Pretoria was approached by the Boran Breeders Society to perform a phenotypic and genetic characterisation of the South African Boran based on available. The aim of this study was to provide reference data for compiling breeding objectives and further genomic applications.

The results from this study highlighted the lack of complete animal recording. Pedigree recording was complete for the first generation, but as the generations continue there was a dramatic decline in pedigree completeness simply due to incomplete record keeping. This was also observed with the recording of production traits of the Boran with only complete records from the past seven years. Incomplete pedigree and performance data could affect the accuracy of the EBVs, leading to incorrect selection decisions, slow genetic progress and unfavourable genetic trends.

The genetic trends for all traits discussed showed an upwards trend, but may not be positive for all traits. For birth weight it is unfavourable due to larger calves increasing the risk of dystocia. The trends indicate that a plateau has almost been reached for mature weight. Reproduction traits also showed an upwards trend indicating breeding at a later stage in life and longer time between calvings. The overall breeding objective for Boran will require some

consideration to ensure that future genetic trends for traits such as fertility and birth weight move in favourable direction.

Genomics holds potential for increasing accuracy of selection with major advances and technological developments being made in the field of molecular genetics over the past two decades. Genomics holds several advantages such as more accurate selection at early ages for traits that are difficult or expensive to measure such as fertility, disease resistance and feed conversion. These advantages generally shorten the generation interval, resulting in faster genetic progress. Genomic tools also present opportunities to study South African Boran at a genomic level in order to discover their unique genetic structure and to unravel their genetic potential which will contribute to a better understanding of the domestication and breed formation, and the development of new theories of population genetics for improved selection and genetic improvement of production.

Genotypic results indicated low inbreeding and high heterozygosity levels for the South African Boran population. This contributes to the fact that the Boran population has a unique gene pool with low inbreeding, contributing to the preservation of this unique gene pool. Comparison of Boran with Bonsmara and Hereford showed three independent groups. However, the Boran cattle differentiated into two unique population groups which probably contribute to the unique genetic composition of the South African Boran. The Boran has genetic potential to contribute unique characteristics to the South Africa beef industry.

Boran cattle are adapted to South Africa conditions and are an excellent breed for using in an extensive grazing system. However, EBV data indicate that a new breeding objective needs to be considered. This data can be used to make decisions regarding how to design breeding objectives for the Boran breed in order to improve the breed in the future. The limited number of complete phenotypic and pedigree records indicates that more emphasis needs to be placed on improving animal recording which will enhance decision making based on selection and limit inbreeding. Further studies can only be performed once more accurate record keeping has been implemented to evaluate genetic trends. The South African Boran contains a unique set of genes that can potentially not only aid in the improvement of the breed within South Africa, but also in the improvement of crossbreeding. The Boran is taking part in the BGP and adding genotypes will enable the breed to obtain a reference population and reap the benefits of genomic selection in the future.

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Addendum A

Year	N Obs	Variable	Mean	Std Dev	Minimum	Maximum
1995	734	gebdir_m
		gebmat_m
		spndir_m
		spnmat_m
		jaar_m
		mnd18_m
		afc_m	1334.89	60.44304	1266	1396
		icp_m	463.6	84.53875	384	565
		volw_m
1996	507	gebdir_m
		gebmat_m
		spndir_m
		spnmat_m
		jaar_m
		mnd18_m
		afc_m	1298.08	192.1252	1034	1700
		icp_m	484.8	113.3273	354	672
		volw_m
1997	439	gebdir_m	25	.	25	25
		gebmat_m	25	.	25	25
		spndir_m
		spnmat_m
		jaar_m
		mnd18_m
		afc_m	1303.43	185.1796	1015	1539
		icp_m	559.1818	192.6748	345	900
		volw_m
1998	438	gebdir_m	32.75	2.872281	31	37
		gebmat_m	32.75	2.872281	31	37
		spndir_m
		spnmat_m
		jaar_m
		mnd18_m

		afc_m	1161.47	79.34979	1067	1353
		icp_m	477.125	144.7534	318	689
		volw_m
1999	756	gebdir_m	35.5	5.554921	23	40
		gebmat_m	35.5	5.554921	23	40
		spndir_m
		spnmat_m
		jaar_m
		mnd18_m
		afc_m	1324	175.3767	1074	1611
		icp_m	900	.	900	900
		volw_m
2000	1020	gebdir_m	31.22222	5.953524	21	39
		gebmat_m	31.22222	5.953524	21	39
		spndir_m
		spnmat_m
		jaar_m
		mnd18_m
		afc_m	1169.7	139.9199	918	1435
		icp_m	468.8182	58.0445	387	555
		volw_m
2001	1667	gebdir_m	30.58065	4.870142	23	45
		gebmat_m	30.58065	4.870142	23	45
		spndir_m
		spnmat_m
		jaar_m
		mnd18_m
		afc_m	1117.18	88.37719	939	1391
		icp_m	592.0769	180.6001	360	900
		volw_m	340	.	340	340
2002	2264	gebdir_m	27.30303	2.651472	22	32
		gebmat_m	27.30303	2.651472	22	32
		spndir_m
		spnmat_m
		jaar_m
		mnd18_m

		afc_m	1119	136.4777	941	1447
		icp_m	448.2917	145.7134	311	787
		volw_m	408.8889	49.10307	340	485
2003	4072	gebdir_m	29.33824	3.202659	22	44
		gebmat_m	29.33824	3.202659	22	44
		spndir_m
		spnmat_m
		jaar_m
		mnd18_m
		afc_m	1111.12	99.19431	894	1367
		icp_m	434.8571	112.5919	323	742
		volw_m	375.75	49.79027	300	430
2004	3550	gebdir_m	29.34483	3.971865	17	40
		gebmat_m	29.34483	3.971865	17	40
		spndir_m
		spnmat_m
		jaar_m
		mnd18_m
		afc_m	1074.77	170.8874	818	1700
		icp_m	462.8841	92.55103	311	755
		volw_m	426.6	53.06642	330	510
2005	4886	gebdir_m	28.15385	3.803194	20	37
		gebmat_m	28.15385	3.803194	20	37
		spndir_m	195.375	22.26769	170	235
		spnmat_m	195.375	22.26769	170	235
		jaar_m	250	.	250	250
		mnd18_m
		afc_m	1060.09	143.5289	823	1391
		icp_m	434.987	80.8194	286	658
		volw_m	413.5833	53.15711	330	536
2006	10052	gebdir_m	27.95455	3.028294	15	37
		gebmat_m	27.95455	3.028294	15	37
		spndir_m	221.3889	30.3187	160	333
		spnmat_m	221.3889	30.3187	160	333
		jaar_m	252	.	252	252
		mnd18_m	317	.	317	317

		afc_m	1043.34	155.7108	715	1700
		icp_m	459.8261	100.8737	304	900
		volw_m	401.2558	65.26178	270	504
2007	9695	gebdir_m	29.36236	3.669538	19	45
		gebmat_m	29.36236	3.669538	19	45
		spndir_m	218.3913	31.47573	150	290
		spnmat_m	218.3913	31.47573	150	290
		jaar_m	269.5455	74.84292	160	510
		mnd18_m	365.0222	50.74557	250	460
		afc_m	1066.78	177.3659	700	1702
		icp_m	460.1477	124.8271	261	900
		volw_m	403.1316	60.92429	299	589
2008	10333	gebdir_m	28.68	4.310264	15	47
		gebmat_m	28.68	4.310264	15	47
		spndir_m	207.5042	32.14009	140	296
		spnmat_m	207.5042	32.14009	140	296
		jaar_m	278.0741	60.80431	145	436
		mnd18_m	375.6154	66.02671	283	508
		afc_m	1064.03	209.2441	707	1702
		icp_m	457.6968	118.851	275	900
		volw_m	407.4609	55.23164	269	540
2009	10585	gebdir_m	29.42196	5.217416	15	51
		gebmat_m	29.42196	5.217416	15	51
		spndir_m	209.1848	29.70508	140	295
		spnmat_m	209.1848	29.70508	140	295
		jaar_m	240.6667	26.52133	205	310
		mnd18_m	374.375	52.10358	297	469
		afc_m	1049.1	170.8383	462	1702
		icp_m	450.9748	114.7536	277	900
		volw_m	402.8772	54.52978	280	580
2010	12796	gebdir_m	29.15831	4.383693	15	46
		gebmat_m	29.15831	4.383693	15	46
		spndir_m	197.6619	32.45771	126	328
		spnmat_m	197.6619	32.45771	126	328
		jaar_m	277.1635	85.05545	160	490
		mnd18_m	339.675	54.74886	215	431

		afc_m	1044.41	154.5025	566	1702
		icp_m	452.186	109.5899	275	900
		volw_m	408.1496	55.22353	283	566
2011	12337	gebdir_m	29.40705	4.579051	15	53
		gebmat_m	29.40705	4.579051	15	53
		spndir_m	200.2688	29.97089	100	313
		spnmat_m	200.2688	29.97089	100	313
		jaar_m	247.4899	66.55882	168	444
		mnd18_m	312.6	52.96406	198	474
		afc_m	1052.74	169.2414	703	1702
		icp_m	455.0319	111.519	282	900
		volw_m	395.3569	54.92809	265	560
2012	13368	gebdir_m	28.96113	4.513735	15	55
		gebmat_m	28.96113	4.513735	15	55
		spndir_m	201.6782	32.99012	104	395
		spnmat_m	201.6782	32.99012	104	395
		jaar_m	265.9291	61.51412	140	420
		mnd18_m	323.0089	52.07747	150	447
		afc_m	1045.94	169.6306	631	1702
		icp_m	434.3308	82.9073	281	900
		volw_m	388.9795	45.53953	271	540
2013	13922	gebdir_m	29.15556	4.85339	15	65
		gebmat_m	29.15556	4.85339	15	65
		spndir_m	203.0301	32.24297	110	304
		spnmat_m	203.0301	32.24297	110	304
		jaar_m	263.3401	71.1833	140	414
		mnd18_m	303.7788	49.21973	231	467
		afc_m	1020.1	146.7636	634	1702
		icp_m	401.1232	44.62707	284	566
		volw_m	381.8545	48.38338	277	520
2014	12615	gebdir_m	29.28765	5.097963	15	63
		gebmat_m	29.28765	5.097963	15	63
		spndir_m	197.2687	30.14869	112	328
		spnmat_m	197.2687	30.14869	112	328
		jaar_m	243.992	60.63541	125	360
		mnd18_m	260.3263	38.77772	180	375

		afc_m	906.938	114.1633	602	1702
		icp_m	454	.	454	454
		volw_m	361.6471	44.32119	290	450
2015	10492	gebdir_m	28.90452	4.180265	15	65
		gebmat_m	28.90452	4.180265	15	65
		spndir_m	197.1169	33.80065	100	325
		spnmat_m	197.1169	33.80065	100	325
		jaar_m	243.6787	43.96459	146	412
		mnd18_m	294.9202	46.70557	194	429
		afc_m	740.6	22.74423	716	771
		icp_m
		volw_m
2016	8538	gebdir_m	29.03054	4.186759	15	58
		gebmat_m	29.03054	4.186759	15	58
		spndir_m	195.5238	29.01113	106	275
		spnmat_m	195.5238	29.01113	106	275
		jaar_m	249.2778	44.42905	173	390
		mnd18_m
		afc_m
		icp_m
		volw_m