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**The assessment of the genetic improvement of South African composite  
breeds and their respective foundation breeds**

by

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## DECLARATION

I, Sithole Phillipine hereby declare that this thesis, submitted for the MSc (Agric) Animal Science: Animal Breeding and Genetics degree at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at any other University.

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## ABSTRACT

South Africa (SA) has a diverse climate that poses potential challenges for future beef production. Different composite breeds that combine the superior growth and beef-producing potential of the European *Bos taurus* breeds with the adaptive traits of *Bos taurus africanus* and *Bos indicus* breeds have been well established over the past century. Even though composite breeds have been used extensively in SA livestock production, research efforts focusing on these breeds have been sparse. The aim of this study was to utilize phenotypic and genotypic data to characterize the genetic status of three SA composite beef breeds (Braford, Santa Gertrudis, and Simbra) in comparison to their selected founder breeds namely, Brahman and Simmentaler. The phenotypic data for the different breeds consisted of pedigree data from the establishment of the herdbook (1957 – 1997) up to 2020. Based on PopReport analysis pedigree completeness (PIC) between composite breeds over six generations was higher than 90% and across breeds PIC in the six-generation depth varied from 24.90% for the Braford to 88.00% for both the Simmentaler and Brahman breed. The average inbreeding coefficient per year was low across all the breeds ranging from 0.011% (Braford) to 0.054% (Simmentaler). The effective population size ( $N_e$ ) across the breeds varied from 152 in the Santa Gertrudis breed to 750 in the Braford breed respectively. The average genetic change calculated by averaging the estimated breeding values (EBVs) from 2000 to 2020 was investigated for reproduction, growth, and carcass traits. Genetic trends for reproductive trends were favorable in all the breeds varying from -0.088 in days to calving (DC) to +0.020 in scrotal circumference (SC) trait. The Santa Gertrudis breed had a slightly higher birth weight (BW) compared to the Braford and Simbra breeds. Across the breeds, the overall genetic trends for growth traits varied from +0.007 (BW) in the Simmentaler to +0.737 (MCW) in the Simbra breed. Carcass weight (CW) based on real-time ultrasonic records (RTU) across the breeds ranged from 9.80 kg in the Braford breed to 19.12 kg in the Brahman breed in 2020. A total of 5 210 (Illumina® Bovine 7K) and 103 646 (Genomic Profiler™ Bovine 150K SNP) SNPs after quality control (QC) were available for genomic analysis. Results of the study across the breeds indicated that the Simbra breed had the highest level of genetic diversity ( $H_o = 0.427; 0.413$ ) for both panels and the Brahman had the lowest level of genetic diversity ( $H_o = 0.291; 0.016$ ). Principal component analysis (PCA) and model-based clustering algorithms distinguished the breeds according to their ancestral origin with the Santa Gertrudis animals clustered separate from the other breeds. Admixture analysis revealed that the Simbra is a composite breed composed of 58.1% (Simmentaler) and 26.4% (Brahman) genetic composition. The estimated  $N_e$  in the last 12 generations ago across the breeds ranged from 215 (Santa Gertrudis) to 316 (Simmentaler) indicating a higher risk of inbreeding for the Santa Gertrudis if not managed carefully. The results of the study indicated genetic improvement in composite breeds compared to its selected founder breeds over the years, indicating that these breeds have the potential for sustainable beef production in both commercial and non-commercial beef production systems.

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## LIST OF ABBREVIATIONS

ADG	Average Daily Gain
AFC	Age at First Calving
AFLP	Amplified Fragment Length Polymorphism
AFS	Age at First Service
AGBU	Animals Genetics and Breeding Unit
AGR	Average Genetic Relatedness
AI	Artificial insemination
ARC	Agricultural Research Council
BF	Subcutaneous Backfat Thickness
BFAP	Bureau for Food and Agricultural Policy
BGP	Beef Genomics Project
BLUP	Best Linear Unbiased Prediction
BW	Birth Weight
CE	Calving Ease
CI	Calving Interval
CM	Centimetre
CNV	Copy Number Variation
CS	Calving Success
CV error	Cross Validation Error
CW	Carcass Weight
DALRRD	Department of Agriculture Land Reform and Rural Development
DC	Days to Calving
DNA	Deoxyribonucleic Acid
EBV	Estimated Breeding Values

EMA	Eye Muscle Area
FAO	Food and Agricultural Organisation
$F_{GRM}$	Genomic Relationship Matrix-based Inbreeding Coefficient
$F_{ROH}$	Runs of Homozygosity-based Inbreeding Coefficient
$F_{IS}$	Genomic Inbreeding Coefficient
$F_{ped}$	Pedigree based Inbreeding Coefficient
$F_{ST}$	Wright's $F$ statistic
FW	Final Weight
GCTA	Genome-Wide Complex Trait Analysis
GDP	Gross Domestic Product
GEBV	Genomic Estimated Breeding Value
Gen	Generation
GGP	GeneSeek® Genomic Profiler
GRM	Genomic Relationship Matrix
$h^2$	Heritability
$H_E$	Expected Heterozygosity
$H_o$	Observed Heterozygosity
HWE	Hardy-Weinberg Equilibrium
IBD	Identity by Descent
ICAR	International Committee for Animal Recording
ID	Identification
IMF	Intramuscular Fat
INTERGRIS	Integrated Registration and Genetic Information System
Kg	Kilogram
$L$	Generation Interval
LD	Linkage disequilibrium



LMA	Longissimus Muscle Area
LRF	Livestock Registering Federation
MAF	Minor Allele Frequency
MCW	Mature Cow Weight
MD	Dam-to-Daughter
Mm	Millimeter
MOT	Sperm Mortality Trait
MS	Dam-to-Son
$N_e$	Effective Population Size
NGS	Next Generation Sequencing
PCA	Principal Component Analysis
PCR	Polymerase Chain Reaction
PIC	Pedigree Completeness
QC	Quality Control
REA	Rib Eye Area
RF	Rump Fat Thickness
RFA	Rib Fat
$r_g$	Genetic Correlation
ROH	Runs of Homozygosity
RTU	Real-Time Ultrasound
SA	South Africa
SAFA	South African Feedlot Association
SC	Scrotal Circumference
SD	Sire-to-Daughter
SNP	Single Nucleotide Polymorphism
SS	Sire-to-Son

USA

United States of America

WW

Weaning Weight

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## CHAPTER ONE: INTRODUCTION

### 1.1 Introduction

The global human population is predicted to grow to 9.7 billion people by the year 2050, with most of the growth anticipated in low- and middle-income developing countries including South Africa (SA) (United Nations, 2022). Currently, the South African human population is estimated at 60.6 million people (Statistics South Africa, 2022) and this number is expected to increase to 72.5 million by 2050 (United Nations, 2019). This rapid population growth will give rise to an increasing demand for food, particularly, animal protein. As a result, the focus of animal agricultural industries should be to optimise productivity and efficiency within the different production systems to improve food security. The per capita meat consumption in SA currently, is approximately 36.15kg, 12.95kg, 4.98kg, and 2.95kg of chicken, beef, pork, and mutton and lamb, respectively (BFAP, 2022). Despite beef being the second most consumed animal protein, following chicken, it provides important sources of nutrients such as protein, iron, zinc, and vitamin B12 (Bohrer, 2017). The beef production sector plays an important role and contributes greatly to household income, especially in rural communities, and on a larger scale to the national gross domestic product (GDP) and food security (DALRRD, 2021; Oduniyi *et al.*, 2021).

Beef in SA is produced throughout the country, and it occupies the majority of the agricultural land (~68.6%) suitable for grazing (DALRRD, 2021). The beef producing sector consist of a highly developed (commercial farming) and a developing sector (smallholder & subsistence farming) that differs both in marketing opportunities and production capabilities. Commercial feedlots, which rely on formulated feed, produces approximately 75% of the beef consumed in SA, while the other 25% is largely generated extensively by the developing sector based on natural veld (SAFA, 2008; Van Marle-Köster & Visser, 2018). The anticipated climate change in the Southern African region is likely to have an impact on these production systems. Climate change has been extensively reported to have potential constraint on beef production, and the impact thereof is felt through heat stress and drought which affects reproduction, fertility, and the overall production (Scholtz *et al.*, 2013; Chingala *et al.*, 2017). Therefore, in order to mitigate the impact of climate change and meet the demand for animal protein, selection for ideal breeds (i.e., indigenous and composite beef breeds) that withstand these conditions, is essential in improving the efficiency and sustainability of current and future local beef production.

South Africa has three distinct cattle genetic resources that are subdivided into indigenous Sanga cattle (*Bos taurus africanus*), exotic (both *Bos indicus* and European *Bos taurus*), and composite breeds. Indigenous Sanga cattle are important components of livestock production in SA because of their adaptive traits acquired through many years of natural selection (Makina *et al.*, 2016). Sanga cattle are recognized for their ability to produce and reproduce well under adverse environmental conditions that may expose them to suboptimal nutrition, parasite exposure (internal and external), and climatic

extremes (Makina *et al.*, 2016; Gororo *et al.*, 2018). Although exotic breeds are recognized for their higher production potential, they are reportedly to be poorer in adapting to sub-tropical regions and endemic diseases of SA (Van Marle-Köster & Visser, 2021). The potential for breed complementarity necessitated crossbreeding between indigenous Sanga cattle, *Bos indicus* and European *Bos taurus* breeds thereby improving productivity while maintaining good maternal traits and adaptability. This led to the development of composite breeds such as the Bonsmara in 1937 which aimed to improve the overall meat quality by crossing 5/8 blood composition of the Afrikaner with 3/8 blood composition of the Hereford and the Shorthorn breed (Bonsma, 1980; Bosman *et al.*, 2017). Similarly, several other composite breeds such as the Braford, Simbra, and Santa Gertrudis which are now well established in SA, were also produced as a result of crosses between *Bos taurus africanus*, *Bos indicus* and European *Bos taurus* breeds to improve productivity through heterosis and complementarity (Gregory *et al.*, 1993).

Since their development and introduction into the South African beef industry in the early 1900's, composite breeds have played an integral role in local beef production. Despite being faced with diverse geographic and climatic challenges that are characteristic of SA, the proven performance of these breeds has deemed them potential resources to ensure sustainability in future beef production (Theunissen *et al.*, 2013). Composite cattle populations have combined utility through exploitation of both the adaptive traits of the *Bos taurus africanus* and *Bos indicus* breeds as well as the higher productivity of European *Bos taurus* breeds. This foundation breed complementarity enhances the performance of, and selection for, composite offspring within different environmental conditions (Theunissen *et al.*, 2013). Experimental trials carried out in tropical and sub-tropical regions have reported relatively fast growth (Gregory *et al.*, 1993), ease of management (Schoeman, 1999) as well as high carcass quality and high precocity (Martin *et al.*, 2007) for these breeds. Notwithstanding their local relevance and importance, composite breeds have received limited attention in research with regards to their current genetic status (i.e., diversity and inbreeding levels) and genetic progress that has been achieved to date. In addition, the potential for introduced genomics-based technologies has also not been explored for smaller composite breeds of SA (apart from the most populous Bonsmara breed).

In SA, most composite beef breeders are making use of estimated breeding values (EBVs) computed by means of best linear unbiased prediction (BLUP) (Henderson, 1984) methodology, to achieve genetic improvement. The breeders' societies residing over composite breeds, actively participate in animal and performance recording through SA Studbook, Agricultural Research Council (ARC), and Livestock Registering Federation (LRF) (Studbook, 2016; Breedplan, 2022). A number of traits including production, reproduction (fertility), and fitness traits are routinely measured and recorded on the respective data base (Logix Beef, Breedplan, and Integrated Registration and Genetic Information System (INTERGRIS), respectively) for genetic improvement (Van Marle-Köster & Visser, 2018). The availability of large-scale recording schemes for computation of trait specific EBVs



has contributed largely to the genetic progress of these breeds until the discovery of genomics and development of genomic technologies (Miller, 2010; Van Marle-Köster & Visser, 2018).

In SA the establishment of the Beef Genomics Program (BGP) enhanced the application of genomic technologies in beef production (Van Marle-Köster & Visser, 2018). The inception of the BGP has allowed the expansion of genomics-based studies mainly due to the increased number of genotyped animals generated for several of the approximately 30 breeds. The availability of sufficient single nucleotide polymorphism (SNP) genotypes has made it possible to conduct detailed genetic characterization of the multitude of SA beef breeds. SA genomic studies performed thus far have, however, largely focused on the indigenous Sanga cattle breeds (Makina *et al.*, 2016; Zwane *et al.*, 2016; Lashmar, 2020). None of these comprehensive studies have included numerically smaller composite breeds and research attention has favoured the largest and most popular composite breeds such as the Beefmaster and Bonsmara (Bosman *et al.*, 2017; Van Marle-Köster *et al.*, 2021). Consequently, genome-level information and composition of these numerically smaller composite breeds is sparse, and a baseline genomic diversity characterization, in addition to demographic, and phenotypic characterization, will serve as a foundation for downstream genomic endeavours (e.g., implementing genomic selection in the future). Furthermore, knowledge of the genetic diversity and population structure will prove beneficial for breed conservation, utilization, management, and future improvement.

## 1.2 Aim and objectives

The overall aim of this study was to utilize pedigrees, EBV based performance data and SNP based genotypic data to comprehensively characterize the current genetic status of three South African composite breeds (Braford, Santa Gertrudis and Simbra) and two of their selected founder breeds (Brahman and Simmentaler).

In order to accomplish the aim, the following objectives were implemented:

1. To estimate inbreeding levels, generation interval ( $L$ ), effective population size ( $N_e$ ), and pedigree completeness (PIC) of three South African composite breeds (Braford, Santa Gertrudis and Simbra) and two of their selected founder breeds (Brahman and Simmentaler).
2. To determine genetic trends of three South African composite breeds (Braford, Santa Gertrudis and Simbra) and two of their selected founder breeds (Brahman and Simmentaler) using estimated breeding values (EBVs).
3. To determine genomic diversity and population structure of three South African composite breeds (Braford, Santa Gertrudis and Simbra) and two of their selected founder breeds (Brahman and Simmentaler) using single nucleotide polymorphism (SNP).

## CHAPTER TWO: LITERATURE REVIEW

### 2.1 Introduction

Until the recent introduction of genomics-based studies, genetic improvement of composite breeds was mainly based on quantitative research for selection purposes in breeding programs, with limited information of the genetic architecture underlying the selected traits (Zakizadeh *et al.*, 2007; Van Marle-Köster & Visser, 2018). Conventional selection methods utilized statistical methods of best linear unbiased prediction (Henderson, 1984) to generate estimated breeding values (EBVs) which allowed genetic ranking and consequently the accurate selection of superior animals. Phenotypic recording became the preferred tool for selection, however, this approach limited the accuracy of selection for traits that are difficult and/or expensive to measure, sex-limited and lowly heritable (Calus *et al.*, 2013; Wakchaure *et al.*, 2015). In addition, the accuracy of EBVs may be compromised due to incomplete pedigree data (Cortés *et al.*, 2019). Currently, genomics, offers more opportunities for genetic improvement by overcoming the shortcomings of conventional selection methods (Miller, 2010). This chapter will provide a literature overview of composite beef cattle, with specific reference to their development, their role in the South African beef industry, and their participation in genetic evaluation program for breed improvement. This will be followed by a discussion on the potential use of genomic information in the characterization of these breeds.

### 2.2 Composite breeds within the South African context

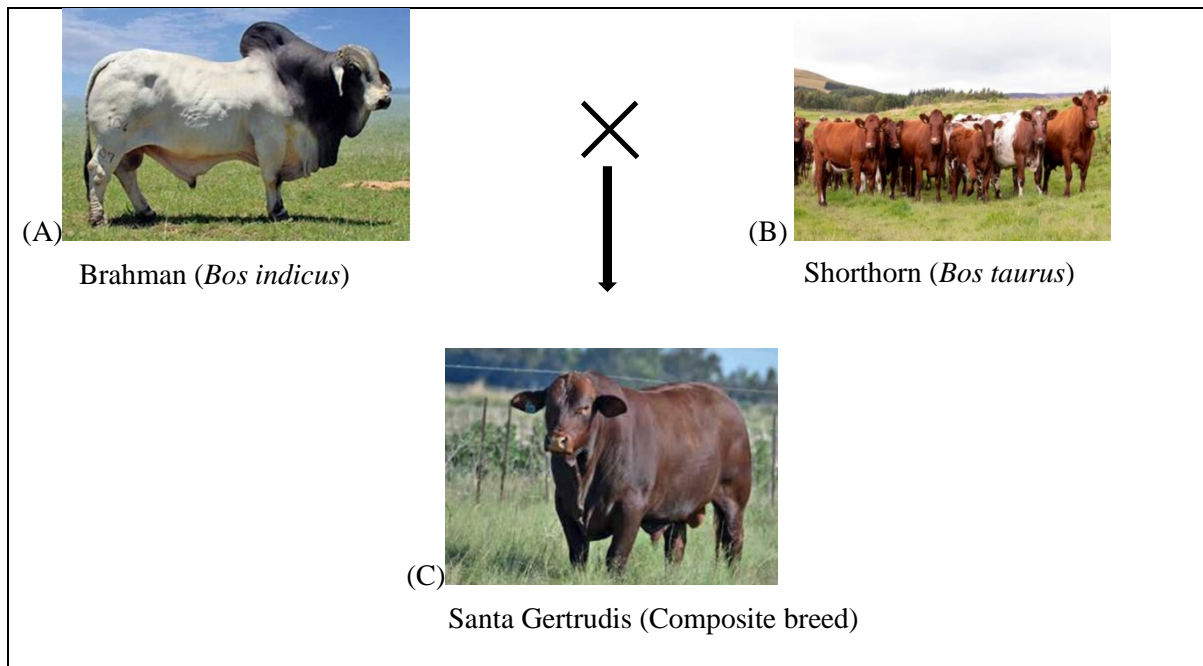
Modern taurine and indicine cattle breeds were domesticated from two distinct wild auroch subspecies namely *Bos primigenius primigenius* and *Bos primigenius namadicus*, respectively. Taurine cattle were domesticated ~10,500 years ago in Eastern Europe whereas indicine cattle were domesticated later ~7,000 years ago in India (Loftus *et al.*, 1994; Bradley *et al.*, 1996). Human trade and migration led to the subsequent spread of these cattle population throughout the world including in Africa. Archaeological evidence suggests that the *Bos taurus* without humps were introduced first into Africa and mated with the wild African aurochs which gave rise to African taurine breeds (Hanotte *et al.*, 2000; Decker *et al.*, 2014; Mwai *et al.*, 2015). The African taurine expanded and dispersed in the North-eastern part of Africa and zebu cattle breeds were introduced later in the African continent (Hanotte *et al.*, 2002). Following this separate domestication that occurred in Africa, interbreeding along with artificial selection for traits of economic importance led to specialised breeds that differ in phenotypic and genotypic characterization respectively (Verdugo *et al.*, 2019).

Currently, in Africa, there are approximately 180 breeds which consist of 150 indigenous breeds and 30 introduced exotic and commercial composite breeds (Mwai *et al.*, 2015; Ouédraogo *et al.*, 2021). In South Africa (SA) there are 30 different breeds that are classified into five categories namely *B. taurus*, *B. indicus*, *Sanga*, *Sanga zebu* types and composite breeds (Felius *et al.*, 2011; Van

Marle-Köster *et al.*, 2013). Composite breeds were developed artificially through crossbreeding animals of indicine or Sanga breeds with those of taurine descent. These composite populations differ based on breed composition depending on the percentage contribution of each foundation breed (Buzanskas *et al.*, 2017) with the most common indicine founder breed used including the Brahman, and taurine founder breeds used including the Hereford, Simmentaler, Angus and Shorthorn. The Santa Gertrudis, Simbra, and Braford are classified as composite breeds developed from these founder breeds and are well established breeds present in both the developing and developed sector of the South African beef production systems.

The Santa Gertrudis breed is a medium sized cattle breed characterized by dark red (cherry red) coat colour with large drooping ears, loose hides, short hair, and folded skin in the dewlap area (and sometimes the underline) (Sangarasivam, 1972; Figure 2.1). The development of the Santa Gertrudis began in the early 1930s with the purpose of breeding a beef breed that exploited breed complementarity for adaptation (to the climatic conditions as well as internal and external parasites) and optimal utilization of tropical range grass of the United States of America (USA) (Cartwright, 1978; Ferraz *et al.*, 2000). This breed was developed as a result of mating a 3/8 Brahman (*Bos indicus*) with a 5/8 Shorthorn (*Bos taurus*) (Mallett, 1959; Sangarasivam, 1972). The Brahman (*Bos indicus*) proportion of the Santa Gertrudis equips the breed with high heat tolerance and parasite resistance, which makes them well suited to tropical environments and the Shorthorn equips the breed with high fertility, ease of calving, excellent mothering qualities, early maturing, and good temperament. Although Santa Gertrudis was mainly produced in the USA, it was later distributed to other parts of the world.

The first Santa Gertrudis animals were introduced in SA during the early 1960s by Taylor Roley from the USA. The SA Santa Gertrudis Breeders Society was developed in 1973 to promote, disseminate and genetically improve the breed (Scholtz, 2010). This breed, due to its outstanding average feed conversion, growth, reproductive and adaptive traits is ranked among the 12 most popular synthetic breeds in the feedlot production sector (Scholtz *et al.*, 2008; Santa Gertrudis Breeders Society of South Africa, 2023).

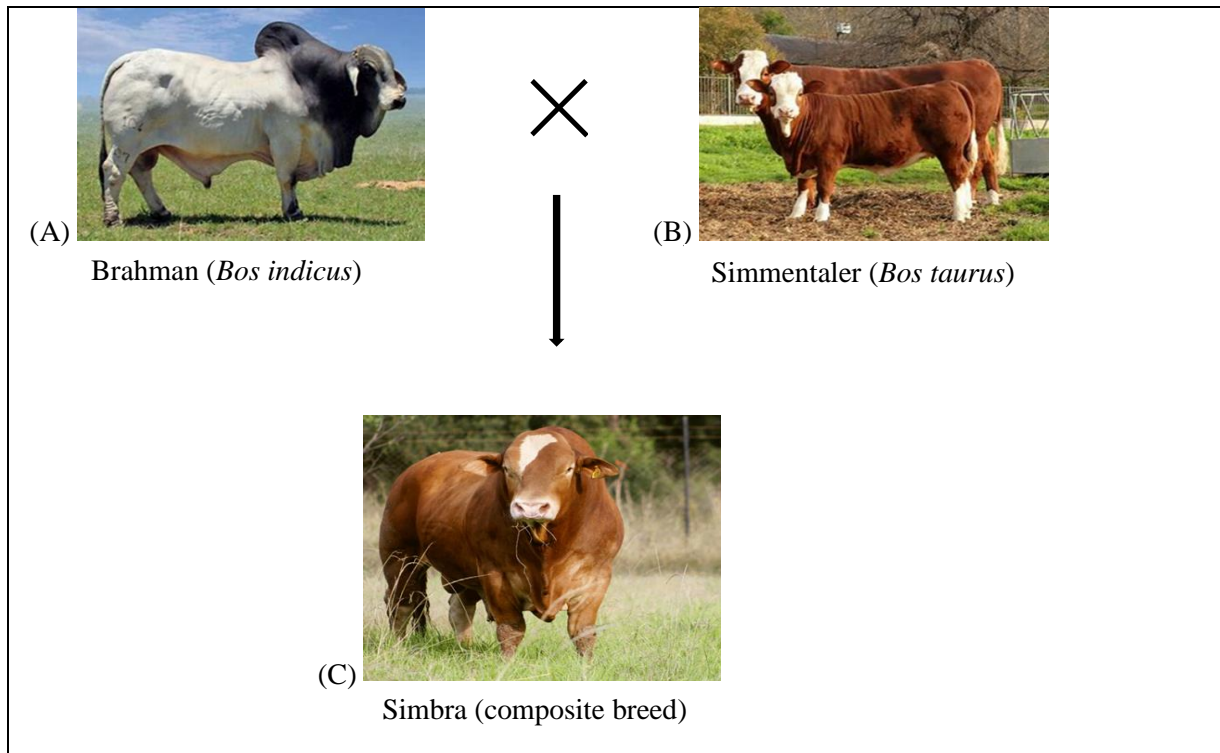


**Figure 2.1** Santa Gertrudis composite breed and founder breeds. Adapted from (A) <https://brahman.co.za/wp-content/uploads/pdf>, (B) [www.beefshorthorn.org](http://www.beefshorthorn.org), (C) <http://www.gyranda.com.au>

The Simbra breed is characterized by a smooth coloured coat that varies between red and black with white markings on the face. The breed is a composite breed developed during the late 1960s in the Gulf Coast of the USA by combining 5/8 Simmentaler (*Bos taurus*) and 3/8 Brahman (*Bos indicus*) as founder breeds (Figure 2.2) (Gouws, 2016). The aim of the experimental crossing between the founder breeds was to create a composite beef breed with both improved growth and adaptive traits. The selection of Brahman cattle was based on their unique attributes, such as toughness, tolerance to heat and insects, outstanding forage abilities, ease of calving, and longevity. The inclusion of the Simmental breed was motivated by its favourable characteristics, including early sexual maturity, docility, rapid growth rates, high fertility, and good carcass qualities (Mukuahima, 2008). The Simbra breed was officially recognized as a breed by the American Simmental Society in 1977, almost two decades after the initial cross and this breed was also distributed to other countries globally.

The Simbra breed was introduced in SA in the late 1990s (Smith, 2010). The SA Simmental Breeders Society registered the first generation of Simbra cattle in 1986, and the breed has grown in terms of popularity since, ranking among the top nine synthetic breeds in the country (Scholtz *et al.*, 2008). More recently the Simbra Breeders' Society has started to accept admixture ratios slightly different from its original composition of up to 3/8 Simmental and 3/4 Brahman ratios depending on the objective of the breeder. In SA, according to Bosmans (1994) findings the breed composition of the SA Simbra breed indicates a higher proportion of the Simmentaler (75%) compared to the Brahman

breed. The choice of the composition is driven by consumer demand for leaner beef and, more importantly, the objective of enhancing weaning weights (WW).

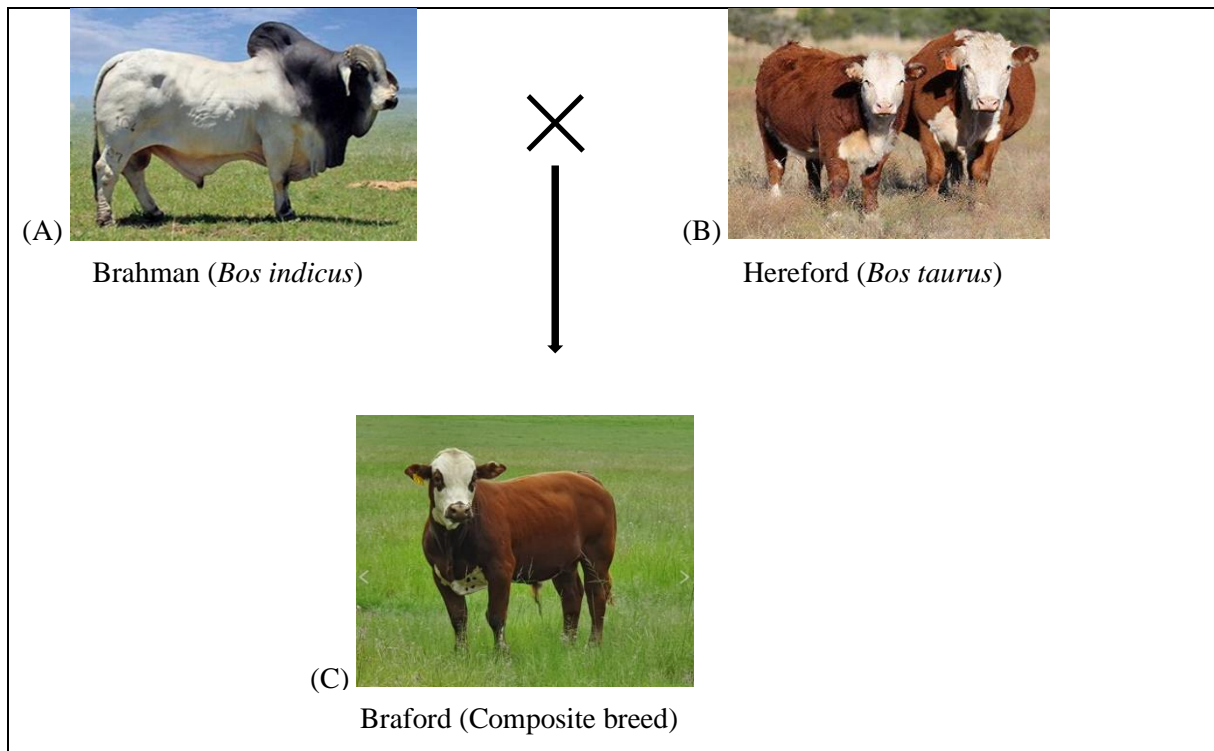


**Figure 2.2** Simbra composite breed and founder breeds. Adapted from (A) <https://brahman.co.za/wp-content/uploads/pdf>, (B) <https://southafrica.co.za/Simmentaler-cattle.html>, (C) <https://simbra.org>

The Braford breed is characterized by a medium to large body frame with a smooth coat that is red with white underbelly, head, and feet (Figure 2.3). This breed's development acknowledges two distinct historical lines: Australian and American Braford, which originated in 1946 and 1947, respectively, with a common purpose of developing a beef breed with improved growth and adaptive traits suitable for the two regions (González *et al.*, 2022). The differentiation between the two lineages lies in the use of Hereford bulls in the American Braford lineage, while Hereford cows were incorporated in the Australian Braford lineage. The founder breeds that were included in the structured crossbreeding resulted in a composite breed consisting of 3/5 Brahman and 3/8 Hereford (Figure 2.3) (Orellana *et al.*, 2009). The Hereford, which was used as the basis for the cross, provided superiority in characteristics such as fertility and meat quality and this was complemented by the longevity and outstanding mothering ability of the Brahman (Scholtz, 2010).

The first Braford cattle in SA were introduced from the USA during the mid-1970s by two cattle breeders namely Flip de Jager from Lady Smith (KwaZulu Natal province) and Naude Bremer from Rosendal (Free State province). The breeders developed Braford by crossbreeding registered Brahman and Hereford breeds. In addition to several imports of pure Braford cattle from the USA,

breeders in SA have been crossbreeding Brahman and Hereford cattle to breed the Braford. In 1997, the South African Braford Breeders' Society was established with the SA Stud Book (Braford Cattle Breeders' Society of South Africa, 2023). The society became the seventh member of the World Braford Confederation.



**Figure 2.3** Braford composite breed and founder breeds. Adapted from (A) <https://brahman.co.za/wp-content/uploads/pdf>, (B) <https://hereford.org/508a-1-jpg-1>, (C) South African Braford Breeders Society, 2023

### 2.3 The importance of crossbreeding

The growing demand for animal products mainly in developing countries requires an urgent improvement in livestock productivity and efficiency. In Southern African countries the use of genomic tools that can potentially increase genetic progress is slow due to the lack of phenotypic records, small population size, and the high cost of genotyping (Lashmar *et al.*, 2019; Mrode *et al.*, 2019). Crossbreeding has been practically applied in breeding programs and it is believed to be one of the methods for breed improvement. Studies have suggested that genetic improvement can be achieved when specialized European, British, and zebu sire lines, which excel in paternal traits, are crossed with indigenous dam lines that excel in maternal traits (lower feed requirements, low birth weights, low mortality, and good maternal abilities) (Schoeman, 1989; Scholtz & Theunissen, 2010). The crossbred offspring (i.e.,  $F_1$ ) of these breeds will maximize productivity through the use of terminal sires to exploit complementarity and heterosis effects.

Heterosis is a major component that increases economically important traits in crossbreeding. Lowly heritable traits such as reproduction, longevity, and maternal ability traits have the greatest benefit of heterosis thus making crossbred dams desirable in crossbreeding systems. The cumulative effects of these traits from heterosis contribute to calf weaning weight per cow and this can lead to an increase in the weight of replacement heifers bred from crossbred cows (Schiermiester *et al.*, 2015). A study by Cundiff *et al.* (1974) provided information on the heterosis effects of reproduction traits using purebred Hereford, Angus and Shorthorn cows compared with crossbred cows of the breeds. Results of the study indicated that the heterosis effect reduced the interval from parturition to first oestrus and the average date of conception. Similarly, maternal heterosis showed positive effects of increased weaning weights of 6.4% greater for crossbred than for straight bred cows. Theunissen *et al.* (2014) reported that crossbred females in rotational crosses involving two or three breeds with British and European sires exhibited higher fitness levels compared to their straight-bred counterparts. This improvement in fitness was accompanied by positive effects on both pre- and post-weaning weights, for both direct and maternal heterosis. Also Cundiff *et al.* (1992) reported that heterosis contributes to the longevity of cows by extending their lifespan by up to 13 years. Furthermore, the study reported a significant increase of 30% in the total calf weight weaned per cow over her lifetime due to heterosis.

Other studies conducted the effects of crossbreeding in different beef cattle breeds and the result indicated consistent improvement in carcass quality, reproduction, and production traits. In a study that compared the production and reproduction traits of straight bred Adaptaur and Belmont Red cows to first generation (F1) cows sired by Boran, Tuli and Brahman bulls, it was found that all F1 crossbreds had higher calving and survival rates at 18 months of age than straight bred cows (Mpofu, 2002). Wang *et al.* (2021) evaluated carcass traits and meat quality in several breeds the Simmental crossbred demonstrated superior meat performance and exhibited low fat meat with a favourable fatty acid composition. Mokolobate *et al.* (2014) demonstrated that properly designed sustainable crossbreeding systems can lead to an increase of up to 21% in the kilograms of calf weaned per large stock unit. This improvement in crossbreeding efficiency enhances cow productivity and contributes to a reduction in the carbon footprint per unit of beef production.

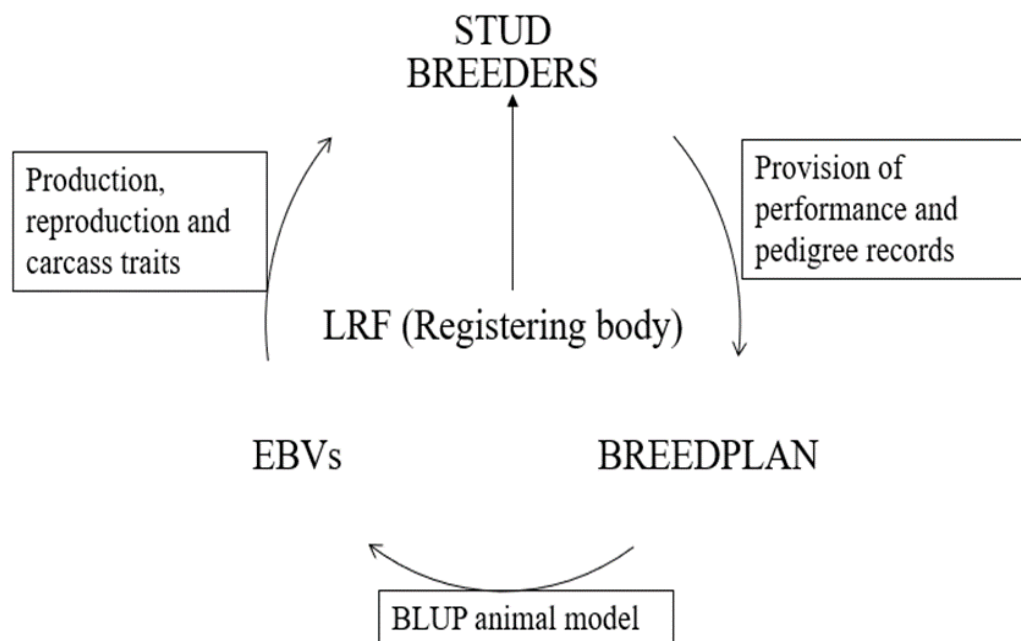
## **2.4 Genetic evaluation and traits of economic importance**

Genetic evaluation for the South African cattle population is primarily conducted by two service providers namely Studbook and Livestock Registering Federation (LRF). These service providers play a crucial role in maintaining and providing information systems to breed societies to assist in improving the genetic merit of beef cattle breeds. Breedplan and Logix are information systems used by breeders to perform genetic evaluation.

Breedplan genetic evaluation system was first established in Australia in 1984 by the Animal Genetics and Breeding Unit (AGBU) (Graser *et al.*, 2005) and is the most widely used service provider globally (Banks & Rickards, 2012). In SA, Breedplan has existed since the mid-nineties and is offered

by the LRF to provide registration and genetic evaluation for stud breeders (Van Marle-Köster & Webb, 2014). Genetic evaluations are performed for the eight breed societies registered under the LRF which are Braford, Brahman, Brangus, Limousin, Simmentaler, Simbra, Santa Gertrudis, and Wagyu breeders' society (Breedplan, 2022).

The Breedplan performs genetic evaluation based on performance and pedigree data collected from the breed societies. The data collected is integrated into a multi-trait BLUP animal model depending on the trait. Traditional EBVs are generated by this model for economically important traits relating to growth, reproduction, and carcass qualities (Breedplan, 2022). The generated EBVs are applied in selection by the breeders in selection programs. However, traits included in the Breedplan genetic evaluation system vary among breed societies based on breeder-specific breeding objectives and the service provider's needs (Breedplan, 2022). To achieve accurate selection, it is important that the recording done by the breeders for traits of economic importance adhere to the International Committee for Animal Recording (ICAR) standard guidelines for animal identification, recording and genetic evaluation of the breeds (ICAR, 2018). Figure 2.4 gives a summary of how genetic evaluation is performed by Breedplan for stud breeders registered with the LRF.



**Figure 2.4** Flowchart of how genetic evaluation is performed by the Breedplan for stud breeders registered with the LRF

The traits included in the Breedplan genetic evaluation system for different breed societies is determined by economic importance, heritability ( $h^2$ ) and genetic correlation ( $r_g$ ) with other traits. Reproduction traits are important components in the beef production system because these traits dictate the reproduction efficiency and genetic progress of an animal. These traits are considered the major



contributors to the profitability of the farm, and they can be subdivided into male and female reproduction traits. The female reproductive traits determine the ability of an animal to continue a normal oestrus cycle following calving and conception as well as establish and maintain pregnancy over the gestation period, while the male reproductive traits focus on evaluating a bull's ability to produce semen that possesses the potential to result in successful pregnancies (Foote, 2003; Berry *et al.*, 2014). The estimation of traditional EBVs for reproduction traits has limitations due to their low heritability (higher environmental influence), difficulty to record and the late expression of these traits in the life of an animal (Johnston & Bunter, 1996). Reproductive traits that are recorded by Breedplan include gestation length (GL), calving ease (CE), days to calving (DC), and scrotal circumference (SC).

Gestation length refers to the difference in days from conception to parturition (Norman *et al.*, 2009). Gestation length is expressed in days and the trait is easily calculated using data from bulls and calves that are conceived by both artificial insemination (AI) and natural mating. Selection for shorter GL is favourable in breeding programs due to the positive economic benefits and its positive genetic association with other traits. Jenkins *et al.* (2016), for example, observed that a shorter GL results in calving ease (CE), while long gestation length results in calves that die within the perinatal period. Similarly, Norman *et al.* (2011) indicated that shorter GL estimates were optimal for CE, birth weight (BW) and days open. Therefore, it is advised that breeders select for shorter GL, for high growth rates and lighter BW, to avoid the effects of calving difficulty.

Calving difficulty (dystocia) has an impact on the cost of beef production because it results in death of dams, loss of calves, an increase in calving interval (CI) as well as an increase in veterinary treatment cost (Mujibi & Crews Jr, 2009). Calving is influenced by many environmental and genetic factors and is largely affected by calf morphology (size of calf at birth) and by dam characteristics (cows birth canal and gestation length) (Van Tassell *et al.*, 2003; Bongiorno *et al.*, 2012). Selection for higher CE is more favourable in breeding programs because of its association with other traits such as low BW. Several studies have indicated that selection for high CE improves paternal stillbirth incidence, as well as growth-related traits such as for BW and average daily gain (ADG) (Barwick *et al.*, 2001; Pausch *et al.*, 2011; Burggraaf & Lineham, 2016).

Days to calving refers to the difference between the days when the dam was first exposed to a bull in a breeding season and the subsequent calving date (Berry *et al.*, 2014). DC EBVs are calculated using only natural or paddock joining excluding data from AI and embryo transfer (Graser *et al.*, 2005). DC estimates are reported in days and can be reported for dams and sires. The DC EBVs generally have low accuracies until a sire has a large number of daughters with DC records. Higher or positive DC are generally more unfavourable because they result in calves with longer numbers of DC, and this impact will be cumulative over the lifetime of those calves (Berry *et al.*, 2014). However, there is a small favourable genetic correlation between the DC and the SC; therefore, it is advised that breeders select for DC traits directly to improve the fertility of female animals.

Scrotal circumference is a useful trait in breeding programs due to the ease of measurement and moderate to high heritability (Moreira *et al.*, 2015). Scrotal circumference is measured in centimetre (cm) using a tape measure position and the trait is measured when bulls are weighed at 400 days to indicate the fertility of young bulls. Several factors contribute to the fertility of bulls, including their plane of nutrition, level of libido, structural soundness, reproductive organ functionality and semen quality (Patterson *et al.*, 2016). These factors collectively, influence the bull's ability to successfully impregnate cows and play a crucial role in overall breeding efficiency.

The estimation of EBVs for SC are important to determine the quality and consistency of spermatozoa producing tissues as well as age at puberty (Nino-Soto & King, 2004). SC trait is strongly and positively correlated to weight, and it is possible to select for growth, female fertility and SC simultaneously. Table 2.1 shows heritability ( $h^2$ ) and genetic correlation ( $r_g$ ) for reproductive traits in composite, taurine and indicine beef cattle breeds.

**Table 2.1** Summary of heritability ( $h^2$ ) and genetic correlation ( $r_g$ ) for reproductive traits in composite, taurine and indicine beef cattle breeds

Traits	Breeds	$h^2$	$r_g$	Reference
CD/ CI	Composite breed	0.01/ 0.04	0.75	Van Der Westhuizen <i>et al.</i> (2000)
DC/ SC	Composite breed	0.07/ 0.35	0.37	Burrow (2001)
DC/ CS	Angus	-	-0.66	Johnston <i>et al.</i> (2001)
SC	Bonsmara	0.46	-	Nephawe <i>et al.</i> (2006)
SC	Composite breed	0.22	-	Mourão <i>et al.</i> (2007)
GL/ CE	Charolais	0.62/ 0.14	-0.38	Mujibi & Crews (2009)
SC/ MOT	Tropical composite breed	0.75/ 0.32	0.70	Corbet <i>et al.</i> (2012)
AFC/ AFS	Santa Gertrudis	0.07/ 0.11	0.99	Morales & Cos (2013)
SC	Composite breed	0.25	-	Santana Jr <i>et al.</i> (2014)
WP/ DC	Santa Gertrudis	0.13	-0.41	Corbet <i>et al.</i> (2017)
DC/ SC	Brahman	0.09/ 0.44	-0.32	Johnston & Moore (2019)

DC = Days to calving, SC = Scrotal circumference, CS = Calving success, WP = Weeks pregnant, GL = Gestation length, CI = Calving interval, CE = Calving ease, MOT = Sperm mortality trait, AFC = Age at first calving, AFS = Age at first service

Growth traits are easy-to-measure traits as a result of their early expression in the life of an animal (Prayaga, 2003). Moreover, these traits possess a moderate to high heritability and have undergone substantial selection intensity and genetic improvement (Table 2.2). These traits are expressed and described by body weights measured at different stages by weighing animals with an electronic scale. Growth traits are measured in kilograms (kg) and these traits include BW measured

within 24 hours of birth and weights measured later in life at 200-, 400- and 600-days and 2 years of age in the Breedplan recording system (Graser *et al.*, 2005).

**Table 2.2** Summary of heritability estimates ( $h^2$ ) for growth traits in composite beef cattle breeds

Traits	Breeds	$h^2$	References
BW	Composite breed	0.26	Pires <i>et al.</i> (2016)
	Brangus	0.21	Neser <i>et al.</i> (2012)
	Simbra	0.10	Smith (2010)
	Bonsmara	0.41	Nephawe (2004)
	Santa Gertrudis bulls	0.38	Aaron <i>et al.</i> (1987)
WW	Simbra	0.67	Smith (2010)
	Bonsmara	0.14	Corbet <i>et al.</i> (2006)
	Brangus	0.23	Neser <i>et al.</i> (2012)
	Bonsmara	0.69	Banda <i>et al.</i> (2014)
YW	Brangus	0.53	Stelzleni <i>et al.</i> (2002)
	Brahman	0.14	Pico (2004)
	Simbra	0.11	Smith (2010)
	Bonsmara	0.26	Corbet <i>et al.</i> (2006)
	Composite breed	0.26	Mourão <i>et al.</i> (2007)
	Brangus	0.53	Stelzleni <i>et al.</i> (2002)
FW	Bonsmara	0.20	Maiwashe <i>et al.</i> (2002)
	Crossbred	0.15	Prayaga & Henshall (2005)
	Brangus	0.29	Neser <i>et al.</i> (2012)
	Simbra	0.10	Smith (2010)
MCW	Bonsmara	0.41	Nephawe (2004)
	Brangus	0.24	Neser <i>et al.</i> (2012)

BW = Birth weight, WW = Weaning weight, YW = Yearling weight, FW = Final weight, MCW = Mature cow weight

The primary focus of selection in most SA cattle breeds has been on growth traits. However, Coleman *et al.* (2021) indicated that selection for higher BW is unfavourable because of its genetic association with dystocia and increase in age at first calving (AFC). Conversely, lower BW is unfavourably correlated with growth and weight traits during later stages in the life of an animal. Therefore, animals with average BW are considered ideal for breeding purposes to avoid any negative impact on farm productivity. In addition, average BW is ideal because of its strong correlations with

reproductive and carcass traits (Caetano *et al.*, 2013; Pires *et al.*, 2016). Table 2.3 shows genetic correlation ( $r_g$ ) for growth traits in composite cattle breeds.

**Table 2.3** Summary of genetic correlation ( $r_g$ ) for growth traits in composite beef cattle breeds

Traits	Breeds	$r_g$	References
YW/ FW	Brahman	0.21	Pico (2004)
WW/ YW	Simbra	0.45	Smith (2010)
WW/ FW	Brangus	0.99	Neser <i>et al.</i> (2012)
BW/ WW	Bonmara	0.25	Banda <i>et al.</i> (2014)
BW/ WW	Composite breed	0.42	Pires <i>et al.</i> (2016)

BW = Birth weight, WW = Weaning weight, YW = Yearling weight, FW = Final weight, MCW = Mature cow weight.

Carcass traits are important to producers due to the rising demand for good quality beef. The genetic progress of carcass traits is possible to achieve due to its moderate to high heritability estimates (Table 2.4), however, limitations are the recordings available, mainly because carcass traits are performed by visual assessment of body scores after slaughter (Crews Jr & Kemp, 2002).

**Table 2.4** Summary of heritability ( $h^2$ ) and genetic correlation ( $r_g$ ) for carcass traits in composite cattle breeds

Traits	Breeds	$h^2$	$r_g$	References
RF	Brangus	0.14	-	Johnson <i>et al.</i> (1993)
EMA/ RF	Santa Gertrudis	0.18/ 0.14	-0.11	Meyer (1999)
LMA/ CW	Brangus	0.39/ 0.59	0.61	Moser <i>et al.</i> (1998)
EMA/ RF	Hereford	0.41/ 0.64	0.21	Reverter <i>et al.</i> (2000)
RF/ IMF	Crossbred	0.24/ 0.33	-	Newman <i>et al.</i> (2002)
IMF/ LMA	Brangus	0.16/ 0.31	0.25	Stelzleni <i>et al.</i> (2002)
REA/ BF	Angus	0.32/ 0.34	0.20	Seroba <i>et al.</i> (2011)
CW/ REA	Crossbred	0.40/ 0.24	0.30	Miar <i>et al.</i> (2014)
BF/ IMF	Hereford	0.29/ 0.44	0.44	Su <i>et al.</i> (2017)

BF = Subcutaneous backfat thickness, LMA = Longissimus muscle area, RF = Rump fat thickness, IMF = Intramuscular fat, CW = Carcass weight, EMA = Eye muscle area, REA = Rib eye area

Breedplan in SA measures carcass traits based on real-time ultrasound (RTU) scanning of live animals. RTU scanning is a cost-effective method used to estimate the body composition of beef cattle. This technology is highly reliable and enables the rapid and cost-effective estimation of carcass characteristics in young animals (Crews Jr & Kemp, 2001; Yokoo *et al.*, 2010). The RTU carcass traits

that are commonly recorded include carcass weight (CW), subcutaneous backfat thickness (BF), intramuscular fat (IMF), eye muscle area (EMA), and rump fat (RF) (Table 2.5). The EBVs for these traits are measured using different units and they are commonly measured simultaneously with 400- or 600-day weight. Table 2.5 describes the points of measurement for the prediction of carcass EBVs in cattle breeds.

**Table 2.5** Description of real-time ultrasonic carcass traits measured by the Breedplan genetic evaluation system in composite beef cattle breeds

<b>RTU measurements</b>	<b>Description</b>
BF (mm)	Measured as the subcutaneous adipose depth (fat) layer over the <i>longissimus dorsi</i> muscle positioned between the 12th and 13th rib
IMF (%)	Measured at the 12th and 13th rib
CW (kg)	Measured immediately after slaughter
EMA (cm <sup>2</sup> )	Measured, at the <i>longissimus thoracicus et lumborum</i> area at the 12th and 13th rib
RF (mm)	Measured between the hook and pin bones at the P8 site.

BF = Subcutaneous backfat thickness, IMF = Percentage intramuscular fat, CW = Carcass weight, EMA = Eye muscle area, RF = Rump fat

The acceptability of beef meat and the yield grade are determined by many characteristics such as its weight, colour, flavour, juiciness, and tenderness (Gupta *et al.*, 2013; Stewart *et al.*, 2021). Carcass weight (CW) is one of the important factors that define its value and is essential to determine the price of saleable meat in the beef market (Warriss, 1990). Tenderness can vary between young and older animals. Meat from young animals tends to be more tender, whereas meat from older animals tends to have increased connective tissue between the muscle fibers, resulting in lower tenderness (Araujo, 2003). Juiciness also impacts meat palatability and is closely related to fat deposition, particularly marbling. These characteristics are influenced by the same factors that affect the yield grade.

## 2.5 Genomic characterization of beef cattle breeds

Genetic improvement programs such as the BLUP animal model, reproductive technologies, and multi-trait selection indices have been used to select animals with desirable traits, for example, animals with high meat production, fertility for population longevity, docility for ease of handling, and climate resilience (Tixier-Boichard *et al.*, 2015; Zhao *et al.*, 2015). Although high genetic progress has been achieved for traits of economic importance this has intensified artificial selection for increased productivity at the expense of genetic diversity. Several studies have reported that these programs result in the excessive use of few elite genotypes, and this increases the allelic frequency of desirable traits and it drives the selected alleles in the genomic region to reach fixation which will ultimately reduce genetic diversity (Nomura *et al.*, 2001; Makanjuola *et al.*, 2020). Preserving and managing the genetic

diversity of farm animals is highly critical to facilitate long-term genetic improvement which is crucial to meet the current production needs by allowing effective responses to selection for changing breeding goals, market drivers and environmental conditions (Notter, 1999; Groeneveld *et al.*, 2010).

Various methods have been proposed to assess the genetic diversity of a population to preserve its gene pool and preserve its valuable genetic resources (Engelsma *et al.*, 2010). Traditionally, performing pedigree analyses based on pedigree data has been the primary approach toward the characterization of the genetic diversity of populations over generations. Pedigree data offers a cost-effective tool used to assess genetic diversity and is based on mendelian sampling probabilities which state that full sibs are always identical (Woolliams & Oldenbroek, 2018; Kasarda *et al.*, 2019). The use of pedigree data has been extensively applied in studies on various cattle breeds (Table 2.6), providing insights into the population's history and allowing for the detection of different events of selection that have influenced changes in allelic frequencies. Table 2.6 presents different parameters used to study genetic diversity based on pedigree data, further enhancing the understanding of population genetics.

**Table 2.6** Summary of studies to estimate genetic diversity parameters based on pedigree data

<b>Breeds</b>	<b><i>F</i> (%)</b>	<b><i>AGR</i> (%)</b>	<b><i>N<sub>e</sub></i></b>	<b>References</b>
Braford	0.002	0.004	462.96	González <i>et al.</i> (2022)
Simmentaler	0.10	-	127	Mc Parland <i>et al.</i> (2007)
Brangus	1.39	-	166.7	Steyn <i>et al.</i> (2012)
Bonsmara	0.26	-	54.57	Sölkner <i>et al.</i> (1998)
Brahman	0.86	0.64	65.6	Vásquez-Loaiza <i>et al.</i> (2021)
Simmentaler	1.49	0.99	48.03	De Araujo Neto <i>et al.</i> (2020)
Hereford	0.06	-	64	Mc Parland <i>et al.</i> (2007)
Pinzgauer	-	-	232	Sölkner <i>et al.</i> (1998)

*F* = Pedigree-based inbreeding coefficient, *AGR* = Average genetic relatedness, *N<sub>e</sub>* = Effective population size

The quality and completeness (depth) of pedigree data has a significant impact on the accurate estimation of pedigree-based population parameters. The likelihood of finding a common ancestor that may lead to inbreeding depression relies on the completeness level of the pedigree data (Hidalgo *et al.*, 2021; Ablondi *et al.*, 2022). However, for many cattle populations in developing countries there is lack of pedigree records as a result of either the absence or inaccuracy of record keeping (Woolliams & Oldenbroek, 2018; Eusebi *et al.*, 2019). Even for registered breeds obtaining ancestry information is challenging since one or more pedigree paths may involve foreign herd records and early ancestry information may not be stored electronically. Therefore, incomplete pedigree-based data will make it difficult to accurately estimate genetic diversity and modern genomic methods for the detection of

genetic diversity in the DNA may overcome limitations associated with incomplete pedigree information and pedigree errors (Zanella *et al.*, 2018; Kasarda *et al.*, 2019; Biscarini *et al.*, 2020).

In recent years molecular markers are used in several studies to genetically characterize cattle breeds (Campos *et al.*, 2017; Kawaguchi *et al.*, 2022). The polymerase chain reaction (PCR) based microsatellites and single nucleotide polymorphism (SNP) are the most frequently used molecular markers to perform genetic diversity (Yaro *et al.*, 2017). Microsatellites were the preferred DNA markers used to perform population genetic diversity studies because of their high polymorphism, ease of interpretation and reproducibility (Cañón *et al.*, 2001; Hoshino *et al.*, 2012). These markers were also used for assessing genetic diversity, parentage verification, determination of the genetic structure within populations, estimation of phylogenetic relationships, and admixture among populations (Kios *et al.*, 2012; Gororo *et al.*, 2018; Van Der Westhuizen *et al.*, 2020). However, because they are time-consuming, expensive to develop, and their genotyping and allele scoring is labour intensive, they have been mostly replaced by SNP markers (Vignal *et al.*, 2002; Yadav *et al.*, 2017; Yaro *et al.*, 2017).

The rapid development of next-generation sequencing (NGS) has facilitated the identification of SNPs throughout the entire genome of species. It is estimated that three to eight biallelic SNPs are as informative as one microsatellite markers (Weir *et al.*, 2006). The widespread adoption of SNPs over microsatellites can be attributed to their numerous advantages, including abundance, robustness, suitability for high-throughput technologies, cost-effectiveness, standardization between laboratories, low genotyping error rate, relatively stable inheritance patterns, and low mutation rates (Fan *et al.*, 2010; Fernández *et al.*, 2013). Currently, a variety of commercial SNP genotyping panels with variable densities are used to characterise genetic diversity in cattle breeds (Eggen, 2012; Nicolazzi *et al.*, 2015). Furthermore, these markers have been applied in parentage verification, selection signatures and diversity of copy number variants (CNV) in beef cattle (Makina *et al.*, 2015; Wang *et al.*, 2015; Sanarana *et al.*, 2021). Table 2.7 summarises some of the most used commercial genotyping panels in cattle genomics studies including genetic diversity studies.

**Table 2.7** Single nucleotide polymorphism genotyping panels used for genomic studies in beef breeds

SNP genotyping panel	Species	No of SNPs	References
<b>Affymetrix®</b>			
Axiom® Genome wide BOS1	<i>Bos taurus, Bos indicus</i>	648 875	(Thermo Fisher Scientific, 2023)
<b>Illumina®</b>			
Bovine LD			
- Version 1		6 909	
- Version 1.1	<i>Bos taurus</i>	6 912	
- Version 2		7 931	Illumina (2023)
Bovine SNP 50K			Matukumalli <i>et al.</i> (2009)
- Version 1	<i>Bos taurus</i>	54 001	
- Version 2	<i>Bos taurus</i>	54 609	
- Version 3	<i>Bos taurus</i>	53 812	
Bovine HD SNP 777K	<i>Bos taurus, Bos indicus, Bos taurus africanus</i>	777 962	
<b>Geneseek®</b>			
GGP Bovine LD v3		26 151	
GGP-indicus	<i>Bos indicus</i>	35 090	
GGP HD Bovine indicus	<i>Bos indicus</i>	76 879	Illumina (2016)
GGP Bovine 100K	<i>Bos indicus</i>	95 256	
GGP Bovine 150K	<i>Bos taurus</i>	139 480	

No = Number, LD = Low density, HD = High density

Van Der Nest *et al.* (2021) evaluated breed ancestry and signatures of selection for the Simbra crossbreed and its founder breed using Illumina® Bovine LD SNP 7K. A high genetic diversity was found in the Simbra breed compared to its founder breeds (Simmentaler and Brahman breeds). Lashmar *et al.* (2018) used the Illumina® Bovine SNP 150K to investigate genetic diversity and autozygosity and the results indicated low levels of inbreeding. On the other hand, Van Marle-Köster *et al.* (2021) performed a whole genome SNP characterization of different livestock population using the GGP 150K SNP panel. The results indicated low levels of inbreeding in the Bonsmara composite breed compared to its founder breed Hereford. Blackburn *et al.* (2014) evaluated genetic diversity of the Braford by utilizing the a customised 60K SNP genotyping panel. The results of the aforementioned study indicated a low level of genetic differentiation and a high level of genetic admixture between the Braford breed and its founder breeds (Brahman and Hereford). In addition, Table 2.8 provides a compilation of several studies that have employed SNP markers to investigate genetic diversity in composite beef cattle breeds.



**Table 2.8** Summary of a selection of genetic diversity studies based on different SNP markers in composite cattle breeds

Breed	SNP genotyping panel	References
Santa Gertrudis, Beefmaster	Bovine SNP 50K	Bovine HapMap Consortium <i>et al.</i> (2009)
Braford	Bovine SNP 60K	Blackburn <i>et al.</i> (2014)
Bonsmara	Bovine SNP 50K	Makina <i>et al.</i> (2014)
Pinzqau	Bovine SNP 50K	Kukučková <i>et al.</i> (2017)
Bonsmara	GGP-HD 80K	Bosman <i>et al.</i> (2017)
Drakensberger	GGP SNP 150k	Lashmar <i>et al.</i> (2018)
Bonsmara	Bovine SNP 50K	Pierce <i>et al.</i> (2018)
Brangus	Bovine HD SNP 777K	Paim <i>et al.</i> (2020)
Simbra	Bovine LD 7K	Van Der Nest <i>et al.</i> (2021)
Bonsmara	GGP SNP 150K	Van Marle-Köster <i>et al.</i> (2021)

SNP = Single nucleotide polymorphism, LD = Low density, HD = High density, GGP = GeneSeek® Genomic Profiler

### 2.5.1 Genetic diversity parameters

SNP markers have proven to be useful to assess the genetic diversity within and among populations based on genotypic data. Assessing the genetic diversity is an important tool for the development of breeding and conservation programs, as well as the implementation of sustainable management programs (Allendorf *et al.*, 2010). In beef production the forces of selection (i.e., natural and artificial selection), increases in inbreeding and population bottlenecks have been reported to be the main reason behind the loss of genetic diversity (Kim *et al.*, 2018; Bolaji *et al.*, 2021). As a result, maintaining genetic diversity is critical because it enables a population to respond positively to selection hence allelic variations are vital for long-term survival. Saravanan *et al.* (2022) indicated that genetic diversity can be measured in three ways (between breeds, within breeds and interrelationships between population) using basic descriptive statistics for each marker for the entire population. To study genetic diversity, various parameters can be quantified to characterise the population structure including minor allele frequency (MAF), heterozygosity values ( $H_E$  and  $H_O$ ), inbreeding coefficients ( $F_{IS}$ ) and effective population size ( $N_e$ ) (Eusebi *et al.*, 2019).

Minor allele frequency (MAF) describes the frequency of the least occurring allele at a given locus within a population (Qwabe, 2011; FAO, 2021). MAF calculates the number of alleles segregating within a given population which makes it crucial when selecting for genetic variants for genotyping and/or sequencing. Preferably the inclusion of genetic variants is based on higher MAF values below a set threshold (usually 1-5%) and this may introduce ascertainment bias because low MAF values are overlooked (FAO; 2021). The exclusion of low/ rare variants in a genotyping panel may underestimate

MAF values and this have an impact on the accurate estimation of genetic diversity, linkage disequilibrium (LD) and  $N_e$  (Helyar *et al.*, 2011; O'Brien *et al.*, 2014; Makina *et al.*, 2015). The accurate estimation of MAF is essential because a high frequency of rare alleles may reflect an increase in the probability of fixed alleles and an increase in the probability of homozygous genotypes while low frequencies of rare alleles reflect high genetic diversity, population expansion, and population subdivision (Linck & Battey, 2019).

Lower mean population-wide MAF was found for SA indigenous cattle breeds for example the Nguni (0.17) compared to exotic breeds for example the Angus (0.21) in a study by Qwabe *et al.* (2013) using the Illumina® Bovine 50K SNP panel. In the same study higher MAF values were observed in Angus x Nguni crossbred (0.19) compared to purebred Nguni (0.17). Van Marle-Köster *et al.* (2021) utilised the GGP Bovine 150K SNP genotyping panel and the results indicated higher MAF average in a composite Beefmaster breed (0.316) compared to its founder breed Brahman (0.21) reported by Boichard *et al.* (2012). The low observed MAF estimates in Sanga and *Bos indicus* breeds in the studies have mostly been ascribed to ascertainment bias. The proportion of polymorphic markers has been reported to be lower in non-discovery breeds such as the Brahman when compared to taurine breeds e.g., Angus breed, this is because ancestral haplotypes were not included in the construction of mostly commercially available genotyping panels (Porto-Neto *et al.*, 2013; Lashmar *et al.*, 2021). Therefore, the use of these panels is expected to be optimally useful for taurine and crossbred breeds carrying taurine haplotypes.

Allelic frequencies within a population are used to estimate genetic diversity. Expected heterozygosity ( $H_E$ ) versus observed heterozygosity ( $H_O$ ) are the two commonly used parameters for estimating the allelic frequency within a population.  $H_E$  represents the probability that two randomly and independently selected alleles from a population will differ at a specific locus (Nei, 1973). It is estimated with the formula:  $H_E = 1 - \sum p^2$ , where  $P_i$  is the frequency of alleles at any locus. In a population a high  $H_E$  reflects that a population is genetically diverse and therefore, it can easily adapt to environmental changes as well as respond to natural and artificial selection (Eusebi *et al.*, 2019) while low  $H_E$  reflects inbreeding, genetic drift and population isolation resulting in the loss of genetic diversity (Ojango *et al.*, 2011).

On the other hand, observed heterozygosity ( $H_O$ ) is a parameter used to measure the frequency of heterozygotes in a population. In real populations allelic frequency is affected by selection, mutation, population bottleneck and population size hence  $H_O$  will vary from  $H_E$  (Eusebi *et al.*, 2019). Essentially, if  $H_O < H_E$ , it explains high inbreeding within the population whereas  $H_O > H_E$  accounts for recent population outbreeding or admixture (Mburu & Hanotte, 2005).

Many previous studies have reported SNP-based heterozygosity in cattle populations, for example, Porto-Neto *et al.* (2014) utilised the Illumina® 777K SNP panel to study the genetic diversity of *Bos taurus*, *Bos indicus*, and composite breeds. Results of the aforementioned study indicated higher genetic diversity in the Santa Gertrudis breed ( $H_E = 0.33$ ) and lower genetic diversity in the Brahman

(0.26) and Shorthorn breeds (0.25). Van Der Nest *et al.* (2021) performed a study that aimed to assess the genetic diversity, population structure, and admixture patterns using the Illumina® Bovine LD 7K SNP panel. The results indicated a slightly higher genetic diversity in the Simbra breed ( $H_E = 0.427$ ) compared to Brahman ( $H_E = 0.295$ ) and Simmentaler breeds ( $H_E = 0.417$ ). In another study that investigated the genetic diversity and population structure of six South African cattle breeds using the Illumina® Bovine 50K SNP panel, a high genetic diversity was observed in the SA Bonsmara composite breed ( $H_E = 0.29$ ) compared to its founder breed the Afrikaner breed ( $H_E = 0.24$ ) (Makina *et al.*, 2014). The increased genetic diversity in composite breeds is a result of the heterosis effect that positively contributes to increased genetic diversity (Wakchaure *et al.*, 2015).

The inbreeding coefficient ( $F$ ) represents the probability that two alleles within an individual are identical-by-descent (IBD) relative to the founder population, assuming that alleles between individuals are unrelated (Wright, 1922; Marras *et al.*, 2015). This parameter is commonly used to estimate the rate of increase in inbreeding which occurs when genetic relatives mate and produce offspring. Increases in the rate of inbreeding is as a result of intensive selection applied in populations, small population size and the use of reproductive technologies (Nomura *et al.*, 2001; Fernández *et al.*, 2011). Several studies have reported that increases in inbreeding is associated with the loss of genetic diversity and increases in deleterious alleles such as embryonic lethal mutations consequently affecting the overall fitness and performance of the population (González-Recio *et al.*, 2007; Mastrangelo *et al.*, 2016).  $F_{ped}$  has been traditionally estimated based on formulae described by Wright, (1922) as follows:

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

Where  $F_t$  and  $F_{t-1}$  are average inbreeding of the offspring and their parents respectively

In most cases pedigree data is unavailable and inaccurate, especially in local breeds or populations. With the availability of SNPs genotyping panel  $F$  can be accurately estimated from genomic data in the absence of pedigree information (Zhang *et al.*, 2015; Mastrangelo *et al.*, 2016). Genomic inbreeding coefficient measures based on genome-wide SNPs is based on different methods such as Wright's  $F_{IS}$ , marker to marker genomic relationship matrix ( $F_{GRM}$ ), and runs of homozygosity ( $F_{ROH}$ ) (Vanraden, 1992; Zhang *et al.*, 2015). The genomic inbreeding coefficient based on Wright  $F_{IS}$  is a commonly used method to estimate  $F$  and describes the proportion of the total inbreeding within a population relative to the subpopulation (Wright, 1969; Lenstra *et al.*, 2012). Therefore, Wright's  $F_{IS}$  is indicative of excess homozygosity in a population. A negative  $F_{IS}$  may arise from crossbreeding and a positive  $F_{IS}$  may be the results of genetic subdivision (Lenstra *et al.*, 2012). The genomic inbreeding based on Wrights  $F_{IS}$  is estimated for genotyped animals based on the formula described by (Wright, 1969) as follows:

$$F_{IS} = 1 - \frac{H_{obs}}{H_{exp}}$$

Where Hobs is observed heterozygosity, Hexp is expected heterozygosity.

A study by Makina *et al.* (2014) investigated genetic diversity between indigenous SA Sanga breeds with taurine breeds using Illumina® Bovine 50K SNP panel. The Bonsmara breed indicated low levels of genomic inbreeding coefficient ( $F_{IS} = -0.017$ ) than its founder breed the Afrikaner breed ( $F_{IS} = -0.004$ ). Van Marle-Köster *et al.* (2021) also found low levels of inbreeding in the Bonsmara ( $F_{IS} = -0.001$ ) compared to the Hereford breed ( $F_{IS} = 0.002$ ). The low genomic inbreeding coefficient obtained in composite breeds corresponded with the results obtained by Blackburn *et al.* (2014) and Van Der Nest *et al.* (2021) and this can be ascribed the composite nature of these breeds that results in increased heterozygosity (Wakchaure *et al.*, 2015).

Effective population size ( $N_e$ ) measures the genetic diversity and the rate of inbreeding level in a population (Bolaji *et al.*, 2021). In beef cattle breeds,  $N_e$  gives an indication of the population size of individuals that contributes to the genetic composition of subsequent generations and the evolutionary forces that shape the genome of complex traits (Wright, 1931; Bolaji *et al.*, 2021). Normally,  $N_e$  is typically lower than the total population size, as not all individuals in a population contribute equally to reproduction. In beef cattle breeds, several factors such as AI, population subdivision, selective breeding, and the use of popular sires can reduce  $N_e$  (Gholizadeh *et al.*, 2008; Bolaji *et al.*, 2021). Maintaining a sufficient  $N_e$  is important for preserving genetic diversity and ensuring the viability of beef cattle breeds.

Different methods including demographics, pedigree-based data, and molecular markers can be used to measure  $N_e$  in populations (Li & Kim, 2015; Bolaji *et al.*, 2021). Pedigree based data has been the preferred method to measure  $N_e$  based on the change in the probability of IBD. This method estimates  $N_e$  based on a formula described by (Wright, 1969) as follows:

$$N_e = 1/(2*\Delta F)$$

Where:

$\Delta F$  = increase in inbreeding coefficient

Nevertheless, traditional pedigree-based methods rely on the availability of accurate and complete pedigree records spanning over multiple generations which is often lacking for most breeds in developing countries. To address the challenge related to incomplete pedigree data the use of marker-based approach based on SNP markers has been proposed (Bolaji *et al.*, 2021). SNP based methods estimate  $N_e$  from the information on linkage disequilibrium (LD) and recombination distance between adjacent SNPs. The persistence of LD over short recombination distances suggests limited historical recombination events, which can be indicative of a smaller  $N_e$  in the distant past. On the other hand, LD observed over a long recombination distance can provide insights into the more recent  $N_e$ , referring to the  $N_e$  in more recent generations. LD over long distances indicates the preservation of genetic associations between distant loci, suggesting a lack of recombination and a relatively recent decrease

in population size. The SNeP package (Barbato *et al.*, 2015) is a software package that is used to estimate  $N_e$  trends across generation using SNP data and is calculated based on the following equation:

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

Where:  $N_{T(t)}$  represents the effective population size  $t$  generations ago, which is calculated using the formula  $t = (2f(c_t))^{-1}$  (Hayes *et al.*, 2003),  $c_t$  denotes the recombination rate estimated for a specific physical distance between SNPs using the Sved and Feldman approximation (Sved & Feldman, 1973),  $r^2_{adj}$  represents LD value adjusted for sample size, and  $\alpha$  is a correction factor accounting for the occurrence of mutations.

SNP-based  $N_e$  has previously been investigated in cattle breeds, for example, Makina *et al.* (2015) estimated  $N_e$  for the South African Sanga cattle, exotic and indigenous SA composite breeds. The results of the study observed high  $N_e$  estimates at more recent generation for the Sanga breeds (Nguni = 95; Drakensberger = 87) and composite breed (Bonsmara = 77) and low  $N_e$  estimate for the taurine breeds (Holstein and Angus). The study concluded that the low  $N_e$  observed for taurine breeds is as a result of intense selection and the use of relatively few elite sires. Villa-Angulo *et al.* (2009) estimated  $N_e$  for US Angus (taurine) and observed a rapid decline in  $N_e$  over the last 100 generations, indicating a reduction in genetic diversity. Biegelmeyer *et al.* (2016) observed higher estimates of  $N_e$  for the composite breed (Braford = 220) as compared to one of its founder breed Hereford ( $N_e = 153.6$ ).

### 2.5.2 Methods for estimation of population structure

The population structure of beef cattle breeds plays a significant role due to the need to understand the genetic composition of a population. This understanding is essential for providing informed breeding advice to breeders and farmers. It also enables the development of effective crossbreeding strategies that maximize heterosis while also addressing concerns related to inbreeding and its negative impacts. SNP data can be utilized to assess and describe population structure based on different methods such as principal component analysis (PCA) and admixture model-based clustering method.

Principle component analysis (PCA) is a method used to differentiate ancestries in order to genetically identify relationships between animals (Anderson *et al.*, 2010). The purpose of PCA is to analyse multivariate data containing information from numerous alleles and loci and condense it into a smaller set of probability-based variables known as principal components (PC) (Patterson *et al.*, 2006; Lenstra *et al.*, 2012). The PCA retains important information and visualise the pattern of similarities of the principal components as points on a graph (Patterson *et al.*, 2006). The clustering algorithm is commonly used to assign individuals to their population of origin and animals that originated from the same ancestral or geographical regions tend to cluster together which indicates close relatedness between the individuals. The differentiation between populations using PCA is calculated with the use

of an arithmetical formula which divides from genomic relationship matrix (GRM) based on a formula described by Vanraden (2008) as follows:

$$G = \frac{(M - 2P)(M - 2P)}{2 \sum p_i(1 - p_i)}$$

Where: G is the relationship matrix, M is a matrix of allele A,  $p_i$  is the frequency of allele A of the  $i^{\text{TH}}$  SNP, P is a matrix with rows containing  $p_i$ .

Various studies have investigated the population structure in composite beef cattle breeds using PCA. For example, a study by Blackburn *et al.* (2014) where a PCA was constructed for the Braford composite breed revealed that the Hereford was clustered furthest from the Brahman and Nellore indicating that there is no genetic relationship between the Hereford and the two breeds. The study indicated that the clustering between the breeds is ascribed to a separate domestication that occurred between the taurine and indicine breeds. The Braford was clustered between the Hereford and Brahman which is expected because it is a composite breed originating from these foundation breeds. Van Der Nest *et al.* (2021) produced a PCA where the composite breed Simbra was clustered in between the two parental breeds (Simmentaler & Brahman). Paim *et al.* (2020) revealed divergence between Angus and Brahman whereas Brangus was intermediate for the first principal component analysis.

Admixture software developed by Anderson *et al.* (2010) is another method used to determine genetic differentiation between populations. This method involves estimating allele frequencies and ancestry proportions, thus providing insights into the historical evolutionary forces that have influenced the genome's structure of a population. A maximum likelihood approach is used which incorporates genotypes with SNP markers to calculate probability-based quantities ancestry coefficient. The ancestry coefficients are subdivided into predefined K clusters which allow for determining the proportion of an individual's genome that originated from distinct ancestral pools (Anderson *et al.*, 2010; Lenstra *et al.*, 2012). To determine the optimal K value, a cross-validation error (CV) estimates are employed, selecting the value that yields the lowest error. The lowest CV value obtained from the analysis is visualized through an admixture plot, which illustrates the ancestral populations contributing to each breed.

In a study to assess the genetic structure of various beef breeds, at  $K = 3$  the Beefmaster and Santa Gertrudis breed revealed signatures of admixture from indicine and taurine breeds (Bovine HapMap Consortium *et al.*, 2009). Admixture analysis in a study by Makina *et al.* (2014) revealed shared ancestry between the Bonsmara and Nguni breeds and limited ancestry with its founder breed the Afrikaner at  $K = 6$ . The Bonsmara was developed in an area (Eastern part of Southern Africa) where Nguni breeds migrated, and this could explain the high genetic link between the breeds than the Afrikaner that migrated in the Western part of Southern Africa. In a study to investigate the genetic composition of the Brangus breed Paim *et al.* (2020) revealed that the Brangus, is a composite breed

with an admixture genome from the Angus and the Brahman breed. The study further indicated that intensive selection for production traits such as IMF and ADG resulted in the proportion of these founder breeds deviating from the original breed composition defined by 3/8 Angus and 5/8 Brahman breeds.

## **2.7 Conclusion**

Service providers such as the LRF perform genetic evaluation for stud breeders providing EBVs for on farm selection. Consequently, these service providers incorporate genomic data which is useful for performing genetic diversity. Because pedigree analysis that is traditionally used to estimate genetic diversity limits the accurate estimation of inbreeding in cattle breeds, preventing the effective management of genetic diversity, molecular markers are used to avoid over or under estimation of genetic diversity. According to studies conducted, the different commercial SNP genotyping panels have proven to be useful for characterization of genetic diversity in composite breeds. SNPs allow for a more accurate assessment of genetic diversity than information provided by pedigree analyses.

## CHAPTER THREE: MATERIALS AND METHODS

### 3.1 Introduction

In this study, phenotypic and genotypic data were used to characterise three South African composite breeds (Braford, Santa Gertrudis, and Simbra) and two of their selected founder breeds (Brahman and Simmentaler). Estimated breeding values (EBVs) based performance data were used to visualise genetic trends for traits of economic importance relating to growth and production (birth, weaning, yearling, final and mature cow weight), reproduction (calving data and scrotal size), and carcass characteristics (carcass weight, eye muscle area, rib fat, rump fat, ribeye area and intramuscular fat). Pedigrees and single nucleotide polymorphism (SNP) genotypic data were used to study population structure and genomic diversity of these breeds. Pedigrees, performance data based on EBVs, and genotypic data were obtained from the Livestock Registering Federation (LRF) with the consent of the individual breed societies. For data utilization ethics approval (NAS338/2021) was granted by the Ethics Committee of the Faculty of Natural and Agricultural Sciences at the University of Pretoria.

### 3.2 Materials

#### Phenotypic data

Pedigree data of the three composite breeds (Braford, Santa Gertrudis and Simbra) and two of their selected founder breeds (Brahman and Simmentaler) were used for the study to analyse their population structure. For each breed, pedigree data was available from the establishment of the herdbook (1957 – 1997) up to the year 2020. The year of the formation for each breed society and the corresponding number of animals available with pedigree data are presented in Table 3.1.

**Table 3.1** The year of formation of each breed society and the number of animals with pedigree records available per breed

Breeds	Formation of breed society in South Africa	Number of animals with pedigree files
Braford	1997	50 206
Santa Gertrudis	1974	346 671
Simbra	1986	318 252
Brahman	1957	813 778
Simmentaler	1964	663 106

The performance data consisted of EBVs of different traits of economic importance. The EBVs were calculated by means of a best linear unbiased prediction (BLUP) animal model implemented



through Breedplan, based on both pedigree and performance data and provided by the LRF. The traits to be investigated were selected based on the following criteria 1) traits that had non-zero records and 2) sufficient data was available for the trait (a minimum of at least 1000 records). The EBVs for the traits included in the analysis were related to growth and production (birth, weaning, yearling, final and mature cow weight), reproduction (calving data and scrotal size), and carcass characteristics (carcass weight, eye muscle area, rib fat, rump fat, ribeye area and intramuscular fat). No calving EBV estimates were available for the Santa Gertrudis and Braford. Except for carcass weight (CW), the remaining carcass traits were excluded for the Braford breed due to insufficient data. The number of EBV records per trait for each breed are presented in Table 3.2.

**Table 3.2** Number of animals with estimated breeding values (EBVs) available for traits of economic importance for a period between 2000 to 2020 in composite breeds and their selected founder breeds

Trait (EBV)	Braford	Santa Gertrudis	Simbra	Brahman	Simmentaler
Birth weight (kg)	36 834	113 497	225 118	302 460	247 898
Weaning weight (kg)	35 648	115 116	226 907	303 649	248 328
Yearling weight (kg)	34 787	114 258	225 087	303 495	248 139
Final weight (kg)	35 455	114 696	226 060	302 959	248 536
Mature cow weight (kg)	31 298	110 624	217 710	299 395	248 000
Scrotal circumference (cm)	4 073	86 303	116 554	264 674	56 179
Days to calving (days)	0	0	43 889	36 734	67 667
Carcass weight (kg)	25 957	104 427	215 190	294 991	242 211
Eye muscle area (cm <sup>2</sup> )	0	77 526	66 642	56 612	76 869
Rib fat (mm)	169	13 522	96 977	88 921	85 674
Rump fat (mm)	170	11 461	98 633	91 290	90 732
Ribeye area (cm)	44	3 421	74 708	62 556	103 385
Intramuscular fat (%)	0	9 388	48 352	27 058	0

### Genotypic data

The genotypic data for the breeds were generated using different SNP genotyping panels including the Illumina<sup>®</sup> Bovine 7K SNP genotyping panel that contains 7931 SNPs (mean inter-SNP distance of <3 SNP/kb), and the GeneSeek<sup>®</sup> Genomic Profiler<sup>™</sup> (GGP) Bovine 150K SNP genotyping panel that contains 139 480 SNPs (mean inter-SNP distance of 19 SNP/kb). No genomic data was available for the Braford breed and, therefore, the breed was excluded from this part of the analysis. Table 3.3 summarizes the number of animals with available genomic data for each SNP genotyping panel.

**Table 3.3** Number of SNP-genotyped animals available per genotyping panel for composite breeds and their selected founder breeds

SNP genotyping panel	Santa Gertrudis	Simbra	Brahman	Simmentaler
Illumina® Bovine (7K) LD v.2	69	261	182	172
GeneSeek® Genomic Profiler™ Bovine 150K	35	22	92	11

### 3.3 Methods

#### 3.3.1 Pedigree-based parameters

The population structure of the SA composite and founder breeds was analysed using the web-based PopReport software application developed in Germany by the Friedrich-Loeffler-Institut (FLI) of Farm Animal Genetics (Groeneveld *et al.*, 2009). Prior to computation, pedigree files consisting of the sire identification (ID), dam ID, animal ID, birth date, and gender of the animals were prepared as input files using Excel and uploaded separately into PopReport software following the removal of 1) duplicate animals and 2) sex inconsistencies. Pedigree completeness (PIC), generation interval ( $L$ ), inbreeding coefficient ( $F$ ), and effective population sizes ( $N_e$ ) were the key parameters analysed and were calculated as summarized in Table 3.4:

**Table 3.4** Formulas used to analyse pedigree-based population parameters for composite breeds and their selected founder breeds in PopReport software

Parameters	Formula	Description	References
PIC	$I_{dk} = \frac{1}{d} \sum_{i=1}^d ai$	Describers' pedigree depth over generations	Groeneveld <i>et al.</i> (2009)
$L$	$L = \frac{Lss+Lsd+Lds+Ldd}{4}$	Describes the average age of the parents at birth of their selected offspring	Falconer & Mackay, (1996)
$F$	$\Delta F = \frac{(Ft-Ft-1)}{(1-Ft-1)}$	Measures the probability that two individuals chosen at random in a population possess identical alleles as a result of a common ancestor	Falconer & Mackay, (1996)
$N_e$	$N_e = 1/2\Delta F$	Estimates the number of individuals in a population that contributed genetically to the offspring of the next generation	Falconer & Mackay, (1996)

PIC = pedigree completeness,  $L$  = generation interval,  $F$  = inbreeding coefficient,  $N_e$  = effective population size

### 3.3.2 Estimated breeding value (EBV) based genetic trends

The data containing the EBV's were provided by the LRF. R studios version 4.1.3 (Team, 2013) was used to calculate averages for each trait per year. EBVs for each breed within the datasets were retrieved and averaged for each trait per year. The averaged EBVs for growth and production, reproduction and real time ultrasonic (RTU) carcass traits were used to compile genetic trends and MS Excel (2013) was used to visualize the trends with line graphs.

### 3.3.3 Genomic diversity parameters

#### 3.3.3.1 Quality control (QC)

Raw data in the form of Illumina<sup>®</sup> final reports (.txt files) were acquired from the LRF. SNPConvert version 2.7 software (Nicolazzi *et al.*, 2016) was used to convert the raw data to PLINK version 1.9 software (Purcell *et al.*, 2007) input files (.MAP and .PED) and, subsequently, binary files (.BIM, .BED and .FAM). PLINK version 1.9 software was used to extract common SNPs and a total of 7421 for the Illumina<sup>®</sup> Bovine 7K and 119 338 for the GGP Bovine 150K SNP genotyping panels were identified as common SNPs. The --merge command in PLINK (Purcell *et al.*, 2007) was used to merge the separate datasets after filtering duplicated SNPs and those located on mitochondrial and sex chromosomes (X and Y). Physical positions were standardized and mapped according to the UMD3.1 bovine reference genome (Nicolazzi *et al.*, 2016). The genotypes of the two datasets underwent quality control by applying predefined thresholds for QC parameters, as specified in PLINK (Purcell *et al.*, 2007), as outlined in Table 3.5. Animals with low genotyping call rates were removed, as well as SNPs with low genotyping call rates, low mean minor allele frequency (MAF), and deviations from Hardy-Weinberg Equilibrium (HWE).

**Table 3.5** PLINK command and threshold values applied for genetic diversity in composite breeds and their selected founder breeds

Parameter	Command	Threshold
Duplicates	--list-duplicate-vars	-
Sex chromosomes	--chr-1-29	-
Sample call rate	--mind	0.10
SNP call rate	--geno	0.10
MAF	--maf	0.01
HWE	--hwe	0.0001

A total of 651 animals remained in the merged dataset after sample-based QC. Twenty-seven animals were removed from the Brahman breed due to poor sample call rate (<90%). After marker-

based QC 3.44%, 2.57%, 9.07%, and 2.87% of SNPs were removed for the Brahman, Simmentaler, Simbra, and Santa Gertrudis populations, respectively. The number of SNPs excluded for the analysis for Santa Gertrudis, Simbra, and Brahman populations were based on marker-based call rate of <90% while MAF and HWE contributed to the removal of most SNPs in the Simmentaler and merged population. Table 3.6 presents the number of SNPs that were retained for downstream analysis in the dataset of animals genotyped with the Illumina® Bovine 7K SNP genotyping panel.

**Table 3.6** Results following sample and marker-based quality control for composite breeds and their selected founder breeds genotyped with low density Illumina® Bovine 7K SNP genotyping panel

<b>Population</b>	<b>Sample&lt;90% call rate</b>	<b>SNP&lt;90% call Rate</b>	<b>MAF &lt;1%</b>	<b>SNP&lt;HWE (p&lt;0.0001)</b>	<b>Polymorphic loci (%)</b>	<b>SNPs remaining for analysis (%)</b>
Santa Gertrudis	4	122	125	8	7 296	7 166
Simbra	4	37	123	31	7 298	7 230
Brahman	27	100	496	77	6 925	6 748
Simmentaler	0	7	194	12	7 227	7 208
Merged	33	53	109	2 049	7 312	5 210

< = less than

A total of 152 animals remained in the merged dataset after sample-based QC. Five animals were removed from the Simmentaler breed due to poor sample call rate (<90%). After marker-based QC 13.15%, 6.00%, 12.18% and 8.71% and of SNPs were removed in for the Santa Gertrudis, Simbra, Brahman and Simmentaler populations, respectively. The major contributor to the removal of SNPs in the population studied was based on marker-based call rate <90% and MAF except for the merged dataset. Table 3.7 presents the number of SNPs that were retained for downstream analysis in the dataset of animals genotyped with the GGP Bovine 150K SNP.

**Table 3.7** Results following sample and marker-based quality control for composite breeds and their selected founder breeds genotyped with high density GGP Bovine 150K SNP genotyping panel

<b>Population</b>	<b>Sample&lt;90% call rate</b>	<b>SNP&lt;90% call Rate</b>	<b>MAF 1%</b>	<b>SNP&lt;HWE (p&lt;0.0001)</b>	<b>Polymorphic loci (%)</b>	<b>SNPs remaining for analysis (%)</b>
Santa Gertrudis	0	937	6 184	36	113 154	112 181
Simbra	2	21 324	11 280	0	108 058	86 948
Brahman	1	3 584	16 792	349	102 546	98 826
Simmentaler	5	2 654	7 730	6	111 608	108 948
Merged	8	2 717	2 690	10285	116 648	103 646

< = less than

### 3.3.3.2 Summary statistics

Minor allele frequency (MAF) statistics were calculated before QC and any related MAF filtering and were estimated for each population using the `--freq` command in PLINK (Purcell *et al.*, 2007). After QC, within-breed genetic diversity parameters were calculated per population using PLINK (Purcell *et al.*, 2007). The mean observed ( $H_o$ ) and expected heterozygosity ( $H_e$ ), as well as the average inbreeding ( $F_{IS}$ ), were estimated for each population using the `--het` command in PLINK (Purcell *et al.*, 2007). This was calculated as the difference between the number of non-missing genotypes and the number of non-missing genotypes, expressed as a proportion of non-missing genotypes using the following formula:

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

Where  $O(HOM)$  represents the observed number of homozygous genotypes and  $N(NM)$  represents the number of non-missing genotypes.

### 3.3.3.3 Principal component analysis (PCA)

PCA was performed on the Illumina<sup>®</sup> Bovine 7K pruned dataset based on 4743 SNP markers. Genome-wide Complex Trait Analysis (GCTA) version 1.24 software (Yang *et al.*, 2011) was used to investigate genetic relatedness per population. A genomic relationship matrix (GRM) was first created, followed by the estimation of eigenvalues and eigenvectors for the first three principal components (PCA). The eigenvectors values were then used to plot principal one and two against each other in Microsoft Excel (2013), to visualize clustering within populations.

### 3.3.3.4 Admixture

The Admixture version 1.2 software (Alexander *et al.*, 2009) was employed to infer ancestral contributions for each breed and visualize the population structure. Using the `--cv` command, that enables a cross-validation procedure to be conducted, various K values, ranging from 2 to 14 were run using the Illumina<sup>®</sup> Bovine 7K SNP dataset. During the cross-validation, the software calculated the cross-validation error for each K value, allowing for the identification of the K value that yielded the lowest error. This value was considered the optimal number of inferred clusters representing ancestral populations. To determine the ancestral population of each breed based on the ideal K value in each cluster, the Genesis version 0.2.3 software (Buchmann & Hazelhurst, 2014) was used to facilitate the inference of ancestral populations and the visualization of breed-specific population structures in a bar plot.

### 3.3.3.5 Effective population size ( $N_e$ )

The recent and past effective population sizes ( $N_e$ ) was estimated for animals genotyped with the Illumina<sup>®</sup> Bovine 7K SNP genotyping panel. These estimations were conducted using the SNeP

package software (Barbato *et al.*, 2015) which calculates  $N_e$  based on linkage disequilibrium (LD) information. SNeP package software (Barbato *et al.*, 2015) predicts  $N_e$  from the equation derived by Corbin *et al.* (2012) as follows:

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

Where:  $N_{T(t)}$  represents the effective population size  $t$  generations ago, which is calculated using the formula  $t = (2f(c_t))^{-1}$  (Hayes *et al.*, 2003),  $c_t$  denotes the recombination rate estimated for a specific physical distance between SNPs using the Sved and Feldman approximation (Sved & Feldman, 1973),  $r^2_{adj}$  represents LD value adjusted for sample size, and  $\alpha$  is a correction factor accounting for the occurrence of mutations.

## CHAPTER FOUR: RESULTS

### 4.1 Introduction

In this chapter the results are reported on the genetic structure based on pedigree data. Genetic trends are reported for EBVs on traits of economic importance for the different breeds followed by the results of the genomic characterization.

#### 4.1.1 Pedigree-based population parameters

##### 4.1.1.1 Trends for pedigree completeness (PIC)

Table 4.1 presents pedigree completeness (PIC) for the three composite breeds and two of their selected founder breeds. PIC improved overtime for the studied breeds from the 6<sup>th</sup> generation to 1<sup>st</sup> generation depth. Average PIC between the three composite breeds in the 1<sup>st</sup> generation, was high in the Simbra breed (96.20%) and low in the Braford breed (90.00%). Across the breeds, the Simmentaler and Brahman founder breeds had the highest PIC of up to 88% and the Braford composite breed had the least PIC of 24.90% in the 6<sup>th</sup> generation depth.

**Table 4.1** Estimated average pedigree completeness (%) for a pedigree depth of one to six generation depth for composite breeds and their selected founder breeds

Breed	Gen1(%)	Gen2(%)	Gen3(%)	Gen4(%)	Gen5(%)	Gen6(%)
Braford	90.00	60.80	45.00	35.40	29.20	24.90
Santa Gertrudis	93.40	85.20	80.40	77.20	74.50	71.90
Simbra	96.20	85.90	77.10	69.10	61.80	54.80
Brahman	95.70	94.80	93.70	92.30	90.50	88.00
Simmentaler	98.70	95.70	93.70	92.20	90.70	88.00

Gen = generation

##### 4.1.1.2 Generation interval (*L*)

Table 4.2 presents generation interval (*L*) for the three composite breeds and two of their selected founder breeds. The results indicated that *L* varied between the breeds and of the three composite breeds the longest *L* for both sire- and dam-to-offspring selection pathways was observed in the Braford and Simbra breed respectively. Across the breeds, the longest *L* was observed in the Brahman population for both sire- and dam-to-offspring selection pathways. The shortest *L* estimates were observed in the Braford population for the sire-to-son selection pathway (4.9 yrs) while the Simbra population (5.3 yrs) had the shortest *L* for dams-to-son selection pathway. The male intervals were longer than the female intervals for the Brahman (6.5 yrs) and Santa Gertrudis (6.1 yrs) population,

respectively. Overall, the Brahman population had the longest  $L$  as compared to all the breeds studied (6.3 yrs).

**Table 4.2** Generation interval (years) estimated across four selection pathways, male, female, and breed population for composite breeds and their selected founder breeds

Breed	SS	SD	MS	MD	Male	Female	Breed-wide
Braford	4.9	5.1	5.5	5.5	5.1	5.5	5.4
Santa Gertrudis	5.4	6.2	5.5	5.5	6.1	5.5	5.9
Simbra	5.1	5.2	5.3	5.5	5.2	5.5	5.4
Brahman	6.8	6.5	6.0	6.1	6.5	6.1	6.3
Simmentaler	5.4	5.2	5.7	5.5	5.2	5.5	5.3

SS = Sire-to-Son, SD = Sire-to-Daughter, MS = Dam-to-Son, MD = Dam-to-Daughter, Breed-wide = population

#### 4.1.1.3 Inbreeding and average genetic relatedness

The average inbreeding coefficient ( $F$ ) and average genetic relatedness ( $AGR$ ) per year and generation for the three composite breeds and two of their selected founder breeds are summarised in Table 4.3. The average levels of  $F$  varied with different magnitude in the studied breeds with the highest  $F$  per year observed in the Santa Gertrudis breed (0.054%) and the lowest in the Braford breed (0.011%). Of the three composite breeds the Santa Gertrudis (0.014% & 0.084%) observed higher values of  $AGR$  per year and generation while the Braford breed observed lower values (-0.05% & -0.297%). Across the breeds the Simmentaler breed observed higher values of  $AGR$  per year (0.016%) followed by the Santa Gertrudis breed (0.084%) respectively. The lowest  $AGR$  per year and generation was observed in the Braford breed (-0.05% & -0.297%).

**Table 4.3** Estimated average rate coefficient of inbreeding and average genetic relatedness per year and generation for composite breeds and their selected founder breeds

Breed	( $AGR$ ) per year (%)	( $AGR$ ) per gen (%)	$F$ per year (%)	$F$ per gen (%)
Braford	-0.05	-0.297	0.011	0.067
Santa Gertrudis	0.014	0.084	0.054	0.330
Simbra	0.006	0.035	0.031	0.189
Brahman	0.005	0.037	0.017	0.121
Simmentaler	0.016	0.080	0.044	0.224

$F$  = Inbreeding Coefficient;  $AGR$  = coefficient of average genetic relatedness, gen = generation



#### 4.1.1.4 Effective population size ( $N_e$ )

The estimated effective population size ( $N_e$ ) computed based on the increase in inbreeding for the three composite breeds and two of their selected founder breeds, are summarized in Table 4.4. The results indicate that between the three composite breeds the Braford breed had the highest  $N_e$  value of 750, followed by the Simbra population with an  $N_e$  value of 265. The Brahman founder breed had a higher value of  $N_e$  compared to some of the composite breeds (Simbra and Santa Gertrudis). Overall, the Santa Gertrudis breed exhibited the lowest estimate across all breeds, with a value of 152 animals.

**Table 4.4** Estimated effective population size ( $N_e$ ) for composite breeds and their selected founder breeds

Breed	No of breeding animals	$N_e$
Braford	17 382	750
Santa Gertrudis	155 920	152
Simbra	129 269	265
Brahman	535 889	412
Simmentaler	270 171	223

$N_e$ : Effective population size, No = number

#### 4.1.2 Genetic trends based on estimated breeding values (EBV's)

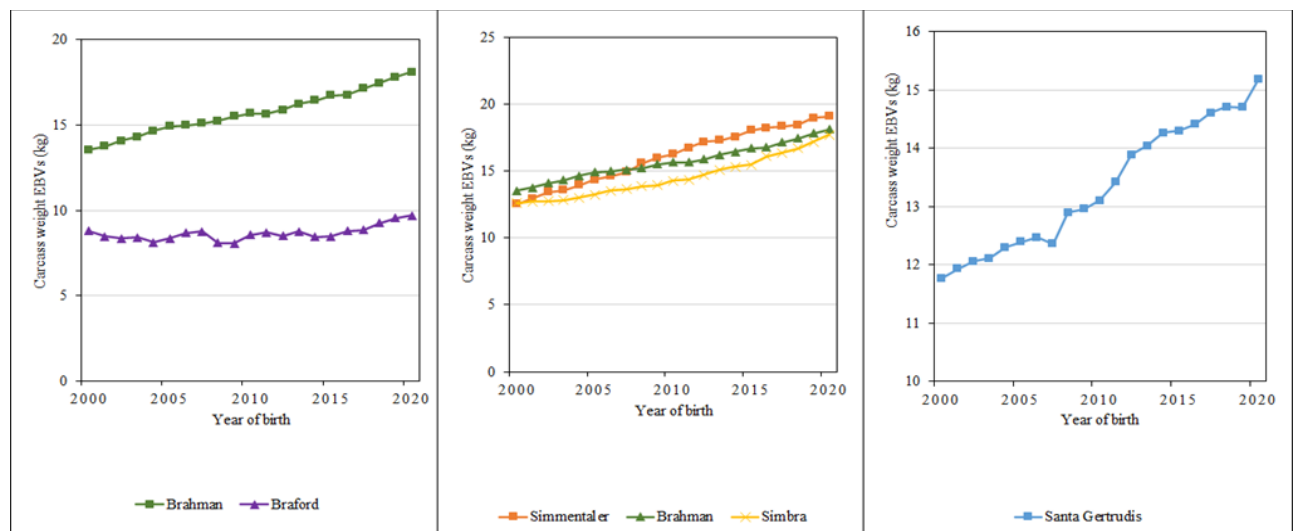
The average annual genetic change for growth and reproductive trait EBV means are presented in Table 4.5. Genetic improvement was achieved for all the breeds in terms of traits of economic importance. Growth traits between composite breeds followed the same increasing trend over the past 20 years. BW was slightly higher in the Santa Gertrudis (+0.017 kg/yr) breed compared to the two composite breeds (Braford and Simbra = 0.015 kg/yr). The average genetic change for growth traits across the breeds varied from +0.007 kg/yr (BW) in the Simmentaler breed to +0.737 kg/yr (MCW) in the Simbra breed. The average genetic change for reproductive traits varied from -0.088 days/yr (DC) to 0.020 cm/yr (SC) in the Simbra breed.

**Table 4.5** Estimated average annual genetic change in EBVs of traits measured for composite breeds and their selected founder breeds between 2000 and 2020

Traits	Braford	Santa Gertrudis	Simbra	Brahman	Simmentaler
Birth weight kg/yr	+0.015	+0.017	+0.015	+0.026	+0.007
Weaning weight kg/yr	+0.030	+0.190	+0.278	+0.232	+0.319
Yearling weight kg/yr	+0.056	+0.220	+0.432	+0.350	+0.534
Final weight kg/yr	+0.133	+0.342	+0.532	+0.450	+0.610
Mature cow weight kg/yr	+0.189	+0.436	+0.737	+0.460	+0.605
Scrotal circumference cm/yr	+0.002	+0.017	+0.020	+0.013	+0.006
Days to calving days/yr	-	-	-0.088	-0.065	-0.067

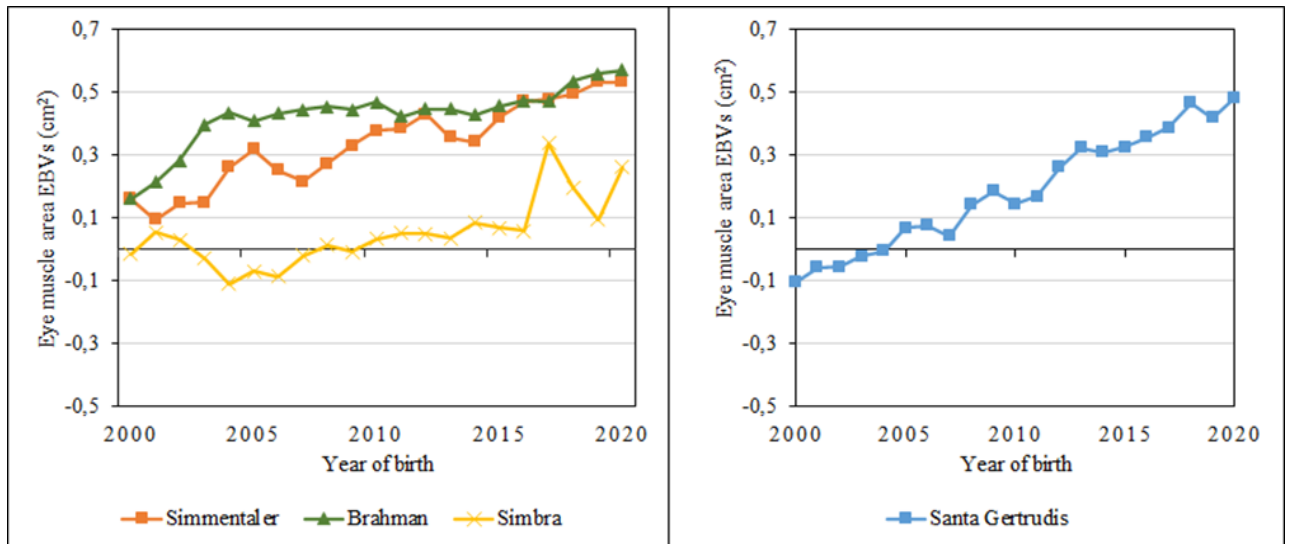
Yr = Year

Annual average estimated EBVs for ultrasonic real time (RTU) carcass traits in composite breeds and their selected founder breeds are presented in Figure (Fig) 4.1 to 4.6. Generally, there was an increase in carcass weight (CW) genetic trends over the years in all the breeds. Genetic improvement between composite breeds was achieved in the Simbra breed followed by the Santa Gertrudis breed. The Simmentaler founder breed observed the highest improvements in genetic merits of CW from 12.50kg in 2000 to 19.12kg in 2020 compared to the Simbra composite breed (Fig 4.1). Similarly, there was genetic improvement in genetic merit of CW in the Brahman breed over the past 20 years compared to the Braford breed that remained nearly constant (~9 kg) (Fig 4.1). The Santa Gertrudis observed a slow improvement in CW over the years from 11.83 kg in 2000 to 15.98 kg in 2020 (Fig 4.1).



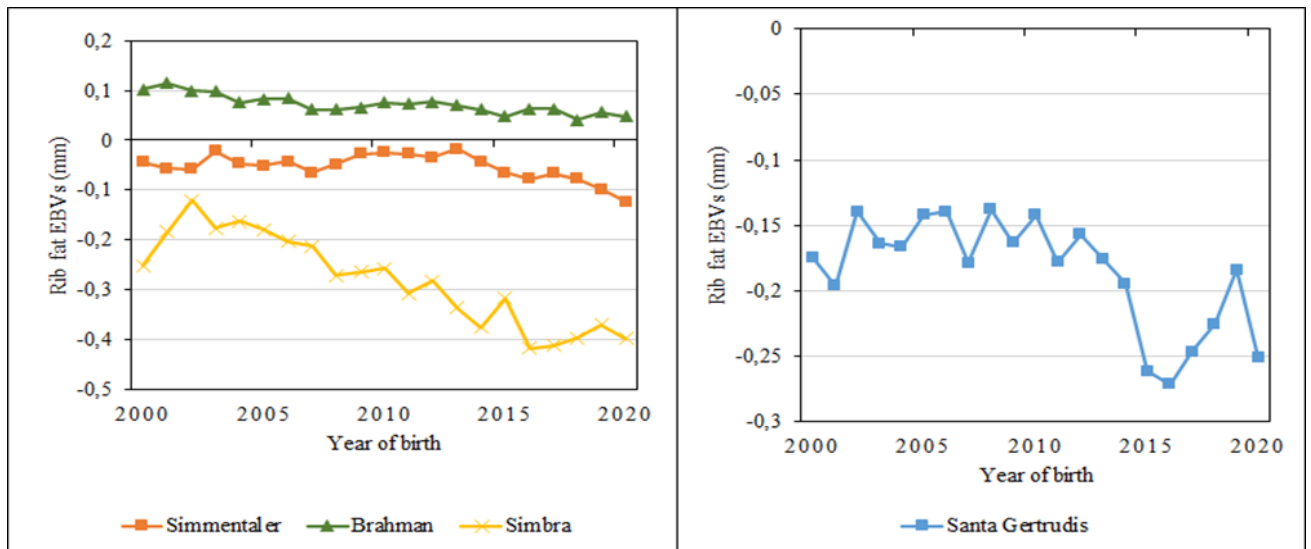
**Figure 4.1** Annual genetic trends for carcass weight EBVs for composite breeds and their selected founder breeds

Fluctuations in eye muscle area (EMA) genetic trends were evident in the Simbra breed while the genetic trends in the Santa Gertrudis breed increased from  $-0.10 \text{ cm}^2$  to  $0.48 \text{ cm}^2$  in the past 20 years (Fig 4.2). The trends for EMA for the Simmentaler and Brahman breed increased over the years compared to the Simbra breed. Genetic trends for the Brahman breed increased from  $0.19 \text{ cm}^2$  in 2000 to  $0.57 \text{ cm}^2$  in 2020 (Fig 4.2).



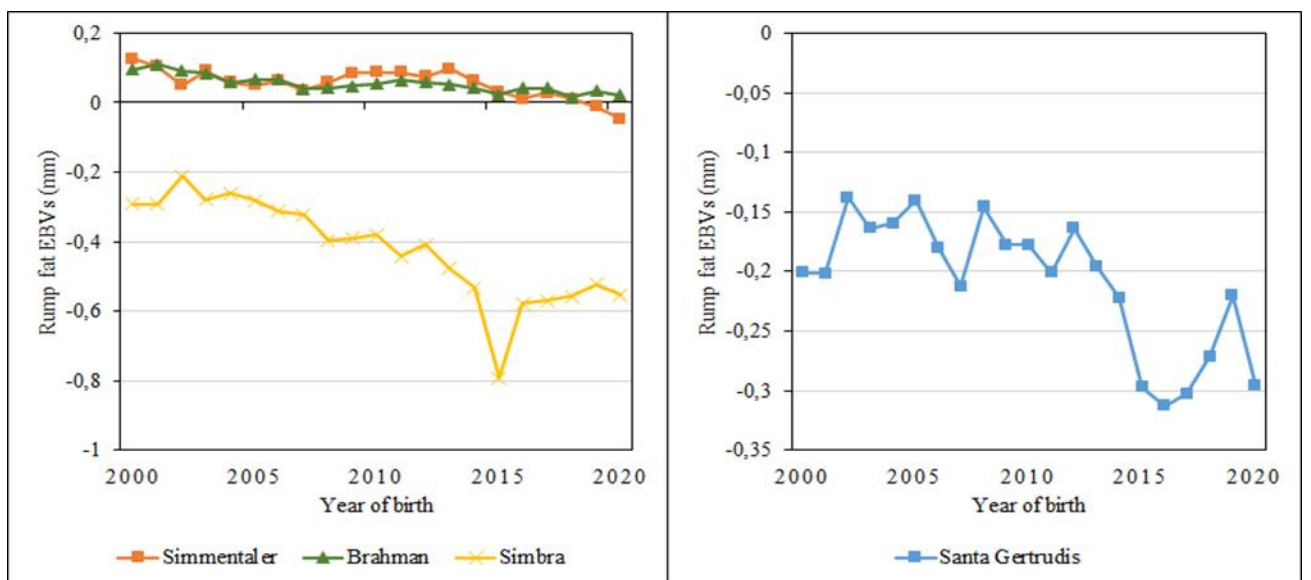
**Figure 4.2** Annual genetic trends for eye muscle area EBVs for composite breeds and their selected founder breeds

The trends of average EBVs for rib fat (RFA) have decreased for all four breeds (Fig 4.3). However, the Simbra breed observed major decrease compared to its founder breeds and in 2020 the RFA was  $0.40 \text{ mm}$  (Fig 4.3). In contrast, genetic trends for the Santa Gertrudis fluctuated over the years with the lowest RFA of  $-0.27 \text{ mm}$  in 2016 and the highest RFA of  $-0.18 \text{ mm}$  in 2008 (Fig 4.3).



**Figure 4.3** Annual genetic trends for rib fat EBVs for composite breeds and their selected founder breeds

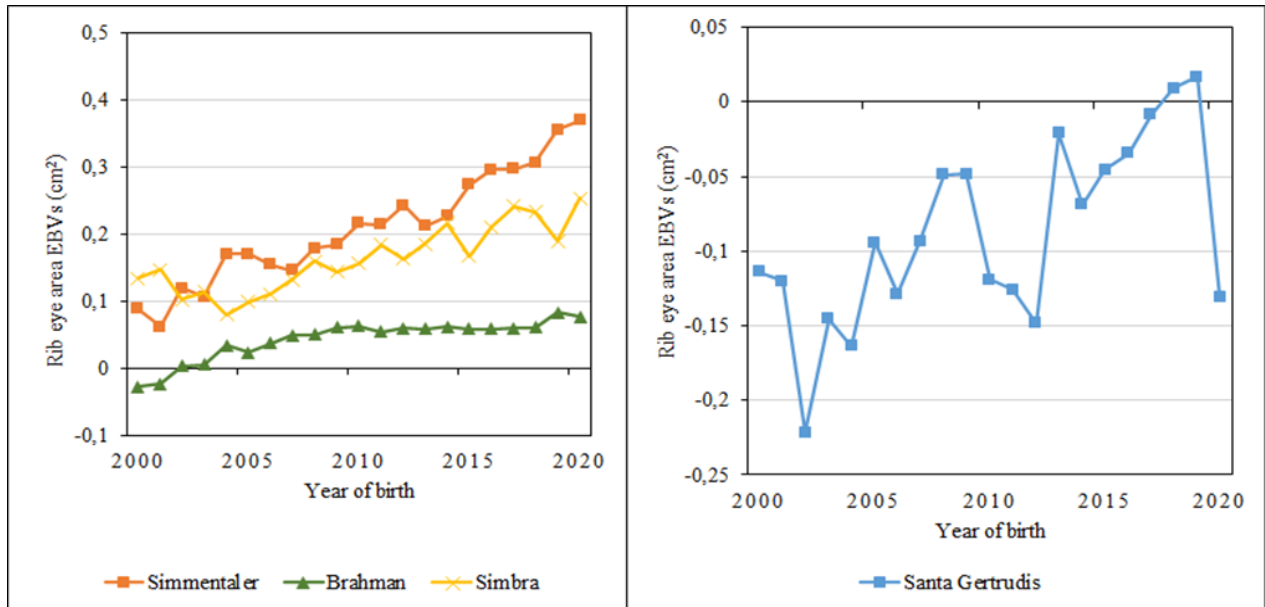
Genetic trends for average EBVs for rump fat (RF) have decreased for all four breeds. A minimum decrease was observed in the Brahman and Simmental er breed respectively compared to the Simbra breed (Fig 4.4). However, the decrease in RF was major in the Santa Gertrudis breed and in 2020 RF was -0.30 mm (Fig 4.4).



**Figure 4.4** Annual genetic trends for rump fat EBVs for composite breeds and their selected founder breeds

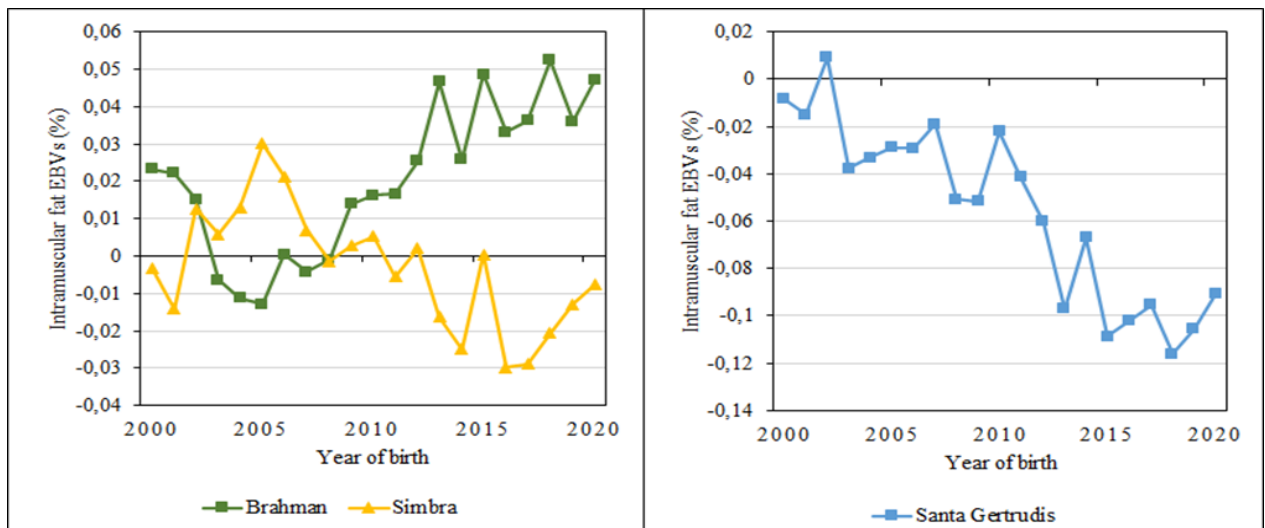
Genetic trends for ribeye area (REA) EBVs between the Santa Gertrudis and Simbra composite breeds fluctuated over the past 20 years. The trends for REA in the Simbra breed were higher than REA trends found in the Brahman breed however lower than in the Simmental er. Genetic trends in the

Simmentaler breed increased over the years from 0.06 cm<sup>2</sup> in 2001 to 0.37 cm<sup>2</sup> in 2020 (Fig 4.5) while genetic trends for REA remained nearly constant in the Brahman breed (~0.05 cm<sup>2</sup>) (Fig 4.5).



**Figure 4.5** Annual genetic trends for rib eye area EBVs for composite breeds and their selected founder breeds

Genetic trends for intramuscular fat (IMF) EBVs fluctuated over the past 20 years in all the breeds (Fig 4.6). The trends for IMF in the Brahman breed fluctuated at an increasing trend compared to the Simbra that fluctuated at a decreasing trend.



**Figure 4.6** Annual genetic trends for intramuscular fat EBVs for composite breeds and their selected founder breeds

### 4.1.3 Genomic diversity parameters

#### 4.1.3.1 Summary statistics

The summary statistics of within-population genetic diversity, calculated based on the lower-density panel, are summarized in Table 4.6. Based on this genotyping panel, the average MAF values between composite breeds were high in the Simbra population (0.332) and low in the Santa Gertrudis population (0.322). Across the breeds, the Brahman population had the lowest MAF value of 0.182. The mean  $H_O$  ranged from 0.319 in the Brahman breed to 0.432 in the Simbra breed. The mean  $H_O$  was higher than the mean  $H_E$  in the Santa Gertrudis, Simbra, and Simmentaler breeds. The results of  $F_{IS}$  in the breeds validated the loss or gain heterozygosity rates with the Brahman and the merged population indicating a positive  $F_{IS}$  of 0.018 and 0.067 respectively.

**Table 4.6** Genetic diversity parameters for composite breeds and their selected founder breeds genotyped with Illumina® Bovine LD 7K SNP genotyping panel

Population	Average MAF	Average $H_E$	Average $H_O$	Average $F_{IS}$
Santa Gertrudis	0.322	0.422	0.426	-0.009
Simbra	0.332	0.426	0.432	-0.013
Brahman	0.182	0.325	0.319	0.018
Simmentaler	0.307	0.406	0.408	-0.002
Merged dataset	0.303	0.406	0.379	0.067

MAF = Minor Allele Frequency  $H_O$  = Observed homozygosity,  $H_E$  = Expected homozygosity,  $F_{IS}$  = Inbreeding coefficient

For the higher-density genotyping panel (i.e., 150K), the Santa Gertrudis breed had a slightly higher level of MAF (0.265), compared to the Simbra breed (0.264). Similar to the lower-density panel, the Brahman had the lowest MAF (0.150) (Table 4.7). Of the two composite breeds the average  $H_O$  was the highest in the Simbra breed and lowest in the Santa Gertrudis breed. Across all breeds the mean  $H_O$  observed similar trends to the lower-density panel and ranged from 0.299 in the Brahman to 0.413 in the Simbra breed. The mean  $H_O$  was higher than the mean  $H_E$  in the Santa Gertrudis, Simbra, and Simmentaler compared to the Brahman breed ( $H_O < H_E$ ). The results of  $F_{IS}$  in the breeds validated the loss or gain heterozygosity rates with the Brahman and the merged population indicating a positive  $F_{IS}$  of 0.018 and 0.067 respectively.

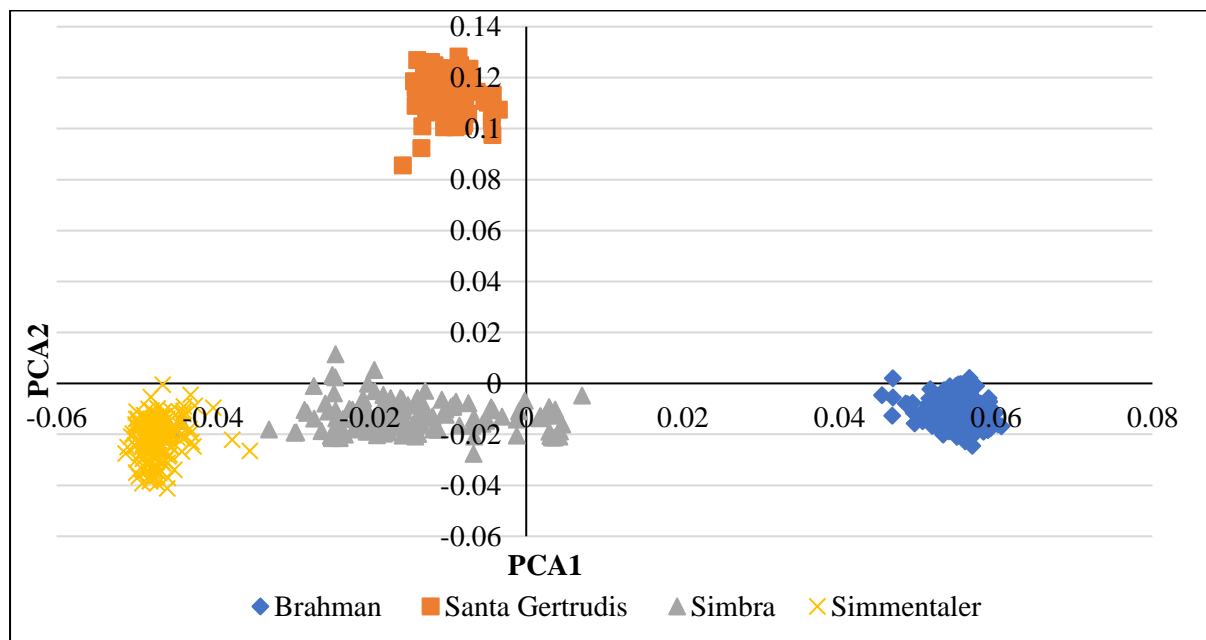
**Table 4.7** Genetic diversity parameters for composite breeds and their selected founder breeds genotyped with GGP 150K SNP genotyping panel

Population	Average MAF	Average $H_E$	Average $H_O$	Average $F_{IS}$
Santa Gertrudis	0.265	0.382	0.398	-0.041
Simbra	0.264	0.366	0.413	-0.128
Brahman	0.150	0.304	0.299	0.016
Simmentaler	0.261	0.380	0.397	-0.044
Merged dataset	0.216	0.332	0.294	0.115

MAF = Minor Allele Frequency,  $H_O$  = Observed homozygosity,  $H_E$  = Expected homozygosity,  $F_{IS}$  = Inbreeding coefficient

#### 4.1.3.2 Principal Component Analysis (PCA)

The first (PCA1) and second principal components (PCA2) explained 12.27% and 2.45% of the total variation and it separated the breeds into three distinct clusters as shown in Figure 4.7. PCA1 and PCA2 were plotted against each other as illustrated in Figure 4.7. The Simbra population formed a separate cluster with both founder breeds (i.e., the Simmentaler, and Brahman) clustering on either side (in closer proximity to the Simmentaler). The Santa Gertrudis was clustered separately from the other breeds.



**Figure 4.7** Genetic relationships between composite breeds and their selected founder breeds showing PCA1 and PCA2

### 4.1.3.3 Genetic differentiation among breeds

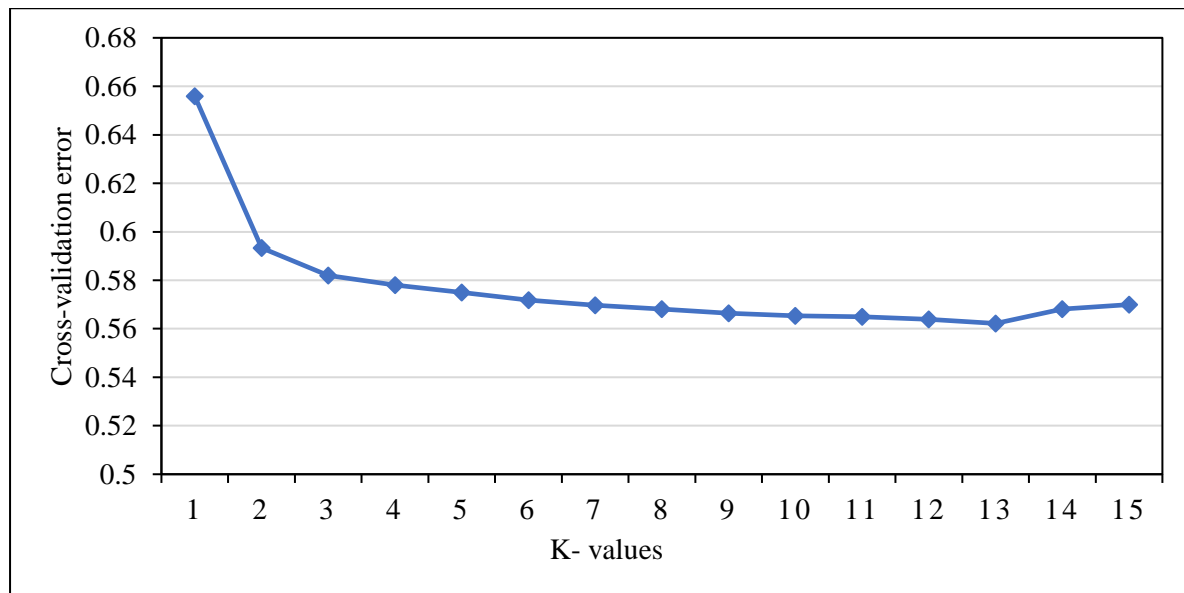
Pairwise  $F_{ST}$  values between each pair of cattle populations are summarized in Table 4.8. As expected, the highest genetic differentiation was observed between the Simmentaler (*Bos taurus*) and Brahman (*Bos indicus*) populations ( $F_{ST} = 0.208$ ). The Santa Gertrudis and Brahman indicated moderate level of genetic differentiation ( $F_{ST} = 1.38$ ) whereas the Simbra and Simmentaler indicated low level of genetic differentiation ( $F_{ST} = 0.041$ ).

**Table 4.8** Wrights fixation index ( $F_{ST}$ ) pair-wise between composite breeds and their founder breeds

Population	Santa Gertrudis	Simbra	Brahman	Simmentaler
Santa Gertrudis	***			
Simbra	0.062	***		
Brahman	0.167	0.147	***	
Simmentaler	0.106	0.041	0.241	***

### 4.1.3.4 Population structure

The K-values indicated the appropriate number of inferred populations as thirteen (CV error = 0.563) and the results are indicated in Figure 4.8.

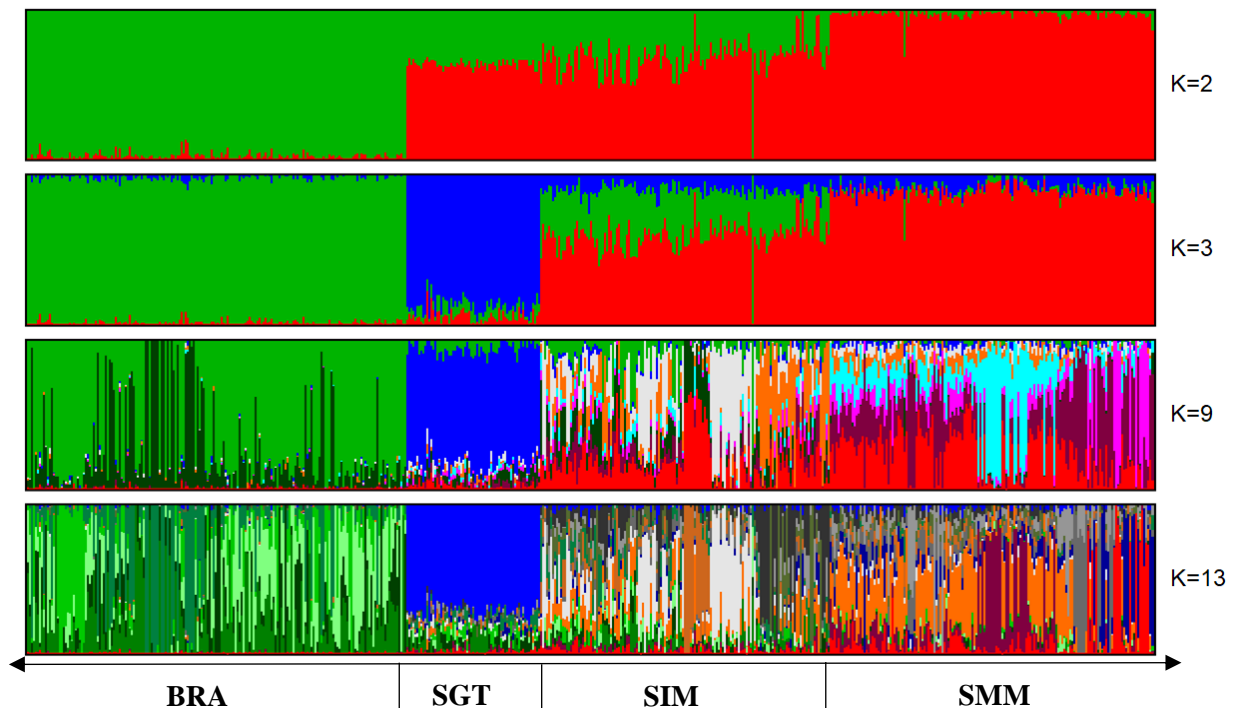


**Figure 4.8** A cross-validation error plot for composite and their selected founder breeds indicating the appropriate K-values

Admixture based clustering from  $K = 2$  to  $K = 13$  for composite breeds and their selected founder breeds are presented in Figure 4.9. From  $K = 2$  to  $K = 13$  the Santa Gertrudis and the Simbra composite breeds indicated that they don't share ancestry. Interestingly, at  $K = 2$  samples were clustered



according to ancestral origins (*Bos taurus* and *Bos indicus*) and breed development (composite breed). The Brahman was separated from the population indicating distinct ancestral backgrounds. Similarly, at  $K = 2$  the Simbra population indicated admixture between the first (Brahman) and third (Simmentaler) ancestral populations. At  $K = 3$  a composite breed; Santa Gertrudis became visible in cluster 2. The Santa Gertrudis was mostly pure and shared small proportion of a common ancestor with the Brahman, Simmentaler and Simbra breed. When thirteen ancestral populations were incorporated different ancestries for subpopulations for the Simbra, Brahman, and Simmentaler population were illustrated in the admixture plot.



**Figure 4.9** Model based admixture plot showing ancestral population for composite breeds and their selected founder breed (BRA = Brahman, SGT = Santa Gertrudis, SIM = Simbra, SMM = Simmentaler)

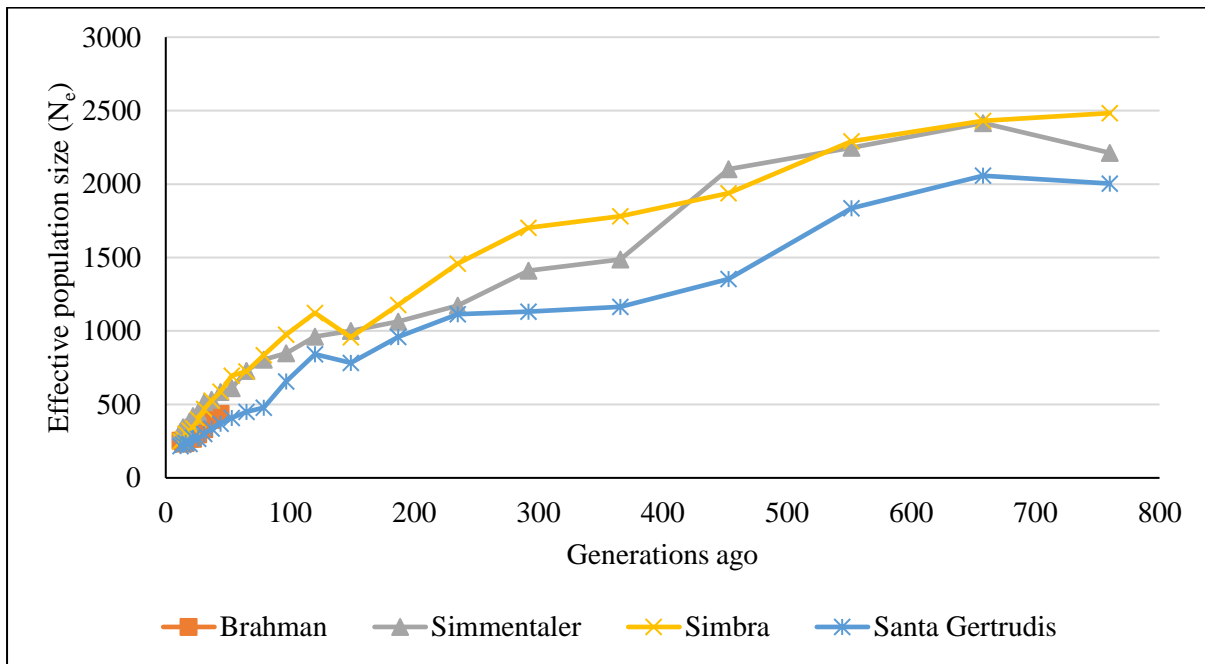
Table 4.9 presents the proportion of the four populations belonging to each of the 13 clusters. At least 49.70% was assigned to cluster 10, while 43.20% of Simbra and 27.70% were in cluster 10 and 6, respectively. The results also indicate that 22.40% of the Santa Gertrudis is assigned within cluster 13.

**Table 4.9** Proportion of membership of the analyzed breeds in each of the thirteen clusters in the admixture program

<b>Predefined Population</b>	<b>Inferred clusters</b>												
	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>7</b>	<b>8</b>	<b>9</b>	<b>10</b>	<b>11</b>	<b>12</b>	<b>13</b>
Santa Gertrudis	0.041	0.158	0.022	0.011	0.012	0.037	0.018	0.011	0.014	0.030	0.022	0.011	0.224
Simbra	0.027	0.014	0.223	0.027	0.002	0.069	0.107	0.165	0.074	0.029	0.432	0.040	0.108
Brahman	0.242	0.003	0.002	0.001	0.001	0.238	0.005	0.002	0.003	0.497	0.009	0.002	0.004
Simmentaler	0.009	0.016	0.019	0.121	0.121	0.277	0.009	0.028	0.155	0.034	0.141	0.147	0.037

#### 4.1.3.5 Effective population size ( $N_e$ )

The effective population size ( $N_e$ ) computed based on the information of LD estimates from the recent generation to 800 generations ago is presented in Figure 4.10. Composite breeds and their selected founder breeds showed a decline in the  $N_e$  values over time. Between composite breeds, the trends in  $N_e$  over 800 generations ago were higher in the Simbra population ( $N_e = 2483$ ) and lower in the Santa Gertrudis population ( $N_e = 2003$ ). Over 12 generations ago,  $N_e$  values across all the breeds ranged from 316 for Simmentaler breed to 216 for the Santa Gertrudis.



**Figure 4.10** Trends in effective population size ( $N_e$ ) over 800 generations ago for composite breeds and their selected founder breeds

## CHAPTER FIVE: DISCUSSION

### 5.1 Introduction

Productivity and efficiency in beef production can be improved through the accurate selection of superior animals to increase genetic gain (Hill, 2016). The establishment of breed societies has provided a foundation to provide data for genetic evaluation, enabling precise selection of animals for inclusion in breeding programs as well as the assessment of their genetic diversity. Genetic diversity is of utmost importance to allow breeds to be relevant and competitive in the changing climatic conditions and agro-production environments, enabling them to adapt to changing climatic conditions and market demands (Groeneveld *et al.*, 2010; Bolaji *et al.*, 2021). While pedigree analysis was traditionally employed to assess genetic diversity over time, they have been replaced by single nucleotide polymorphism (SNPs). Single nucleotide polymorphism being widely distributed throughout the genome, offer more comprehensive information for evaluating genetic diversity and it addresses limitations encountered with pedigree analysis (Eusebi *et al.*, 2019). The present study is the first to investigate population structure, genetic trends, and genetic diversity of South African composite beef cattle breeds and their selected founder breeds based on both phenotypic and genotypic data.

#### 5.1.1 Pedigree-based parameters

Pedigree information plays an important role in breeding programs because it influences genetic evaluations and, subsequently, the genetic improvement of a breed (Banos *et al.*, 2001; Cassell *et al.*, 2003). A large proportion of missing pedigree information affects the accuracy of estimated breeding values (EBVs), which may result in inaccurate selection of animals included in a breeding program. The current study observed an improvement in the quality and integrity/depth of pedigree completeness (PIC) in all the breeds across generations and this may be attributed to higher breed participation in animal recording systems over time (Abin *et al.*, 2016). In the first generational depth PIC between composite breeds was high in the Simbra (96.20%) breed and low in the Braford breed (90.00%). Across the breed PIC in the six-generational depth varied from 24.90% in the Braford breed to 88.00% in both the Brahman and Simmentaler breeds. The Brahman and Simmentaler breeds were imported earlier into South Africa (SA) around 1957 and 1964, respectively, and this longer history of animal recording compared to the Braford that was introduced much later (1997) may have contributed to these observations.

Previous studies have investigated PIC in beef cattle breeds and have revealed similar variability across generations, with increasing trends towards more recent generations. At four-generational depth, Fabbri *et al.* (2019) reported a PIC of 74.00% versus 15.00% for the Italian Mucca Pisana and Sardo Bruna breeds. Furthermore, Bernardes *et al.* (2016) analysed the PIC of the Brazilian Tabapua breed up to sixteen-generation depth and the results reported a 47.99% PIC in the six most

recent generations. In a South African study on indigenous breeds, the Tuli breed had the highest PIC of 68.30%, whereas the Boran had the lowest PIC of 13.80% for six-generation pedigree depth (Abin *et al.*, 2016).

The generational interval ( $L$ ) has a significant impact on the rate of genetic gain in beef production (Falconer & Mackay, 1996). In this study, the estimation of  $L$  for four gametic pathways varied between composite breeds and their selected founder breeds. A longer  $L$  observed in the dam-offspring pathway compared to the sire-offspring pathway in the Braford, Simbra, and Simmentaler breed are comparable to previous results for the Italian Chianina, Marchigiana and Ramagnola breeds (Bozzi *et al.*, 2006), Brazilian Brahman breed (Cavani *et al.*, 2018), and Italian Sardo Bruno breed (Fabbri *et al.*, 2019). In contrast, the longer sire-offspring pathway, compared to dam-offspring pathway, obtained in the Brahman breed was comparable to previous trends observed for the Mexican Simmentaler (Utrera *et al.*, 2018), Brazilian Marchigiana (Santana Jr *et al.*, 2012) and Swedish Brown Swiss breed (Worede *et al.*, 2013), respectively.

The estimation of  $L$  between composite breeds was high in the Santa Gertrudis breed (5.9 years (yrs)) compared to the two composite breeds the Braford and Simbra breeds (5.4 yrs). However, when all the breeds were considered the estimation of  $L$  ranged from 5.3 yrs in the Braford breed to 6.3 yrs in the Brahman breed. The average  $L$  values observed in the studied populations are within the range of values reported for other beef breeds such as Colombian Costeño con Cuernos (5.4 yrs; Martínez *et al.*, 2008), SA Bonsmara (5.6 yrs; Groeneveld *et al.*, 2009), and SA Boran breed (6.3 yrs; Abin *et al.*, 2016). The average  $L$  for the breeds studied were shorter compared to Brazilian zebu breeds (Nelore, Gir and Guzarat) (8 yrs; Faria *et al.*, 2009), and Italian Pontremolese breed (12.51 yrs; Fabbri *et al.*, 2019). However, the averages obtained here were longer when compared to the Brazilian Brahman (4.4 yrs; Cavani *et al.*, 2018), Spanish Sayaguesa (3.75 yrs; Gutiérrez *et al.*, 2003) and Colombian Blanco Orejinegro breeds (4.58 yrs; Ocampo Gallego *et al.*, 2020). The high average  $L$  values calculated across the breeds (~6 yrs) may be attributed to early replacement of females and the intensive selection of reproductive animals that excel in specific traits for longer periods in breeding programs (Marquez & Garrick, 2007; Malhado *et al.*, 2013). Therefore, much effort is needed to decrease  $L$  across all breeds because higher  $L$  values lead to lower genetic progress and lower genetic gains in terms of selection of desirable traits (Carolino *et al.*, 2020). Pryce & Daetwyler (2011) indicated that selection based on genomic enhanced breeding values (GEBV) is a promising tool for shortening  $L$  while increasing genetic progress in traits of economic interest; however, inbreeding should be monitored simultaneously.

Controlling the rate of inbreeding is one of the first step in breeding programs because it negatively affects performance and reduces genetic diversity (García-Atance *et al.*, 2023). In this study, the rate of average  $F$  per year ranged from 0.011% in the Braford breed to 0.054% in the Santa Gertrudis breed. The results for  $F$  per year in all the five studied breeds were low compared to previously reported values, for example, 2.33% for Colombian Blanco Orejinegro (Ocampo Gallego *et al.*, 2020), 1.83%

for SA Afrikaner (Pienaar *et al.*, 2015) and 1.90% to 6.24% for various Brazilian zebu cattle breeds (Santana Jr *et al.*, 2016). Additionally, the range of 0.067 to 0.330 for average  $F$  per generation were also low compared to the reported range of 0.14% to 0.47% in SA indigenous Sanga breeds (Abin *et al.*, 2016) and 3.53% to 4.59% in Berrenda Spanish cattle breeds (González-Cano *et al.*, 2022). Similarly, the coefficient of average genetic relatedness ( $AGR$ ) obtained in the current study were low as compared to 8.82% in Portuguese Mertolenga (Carolino *et al.*, 2020), 5.12% in Mexican Romosinuano breed (Núñez-Domínguez *et al.*, 2020) and 0.44% in the SA Afrikaner cattle breed (Pienaar *et al.*, 2015). The lower average rate of  $F$  and  $AGR$  was below the recommended threshold of 0.5 to 1% in all the breeds suggesting that there was sufficient introduction of new genetic material/exchange of bulls between herds and, hence, controlled and minimized mating of close relatives (González-Cano *et al.*, 2022).

Boichard *et al.* (1997) indicated that the level of inbreeding within a breed is strongly associated and dependent on PIC. Incorrect and incomplete pedigree records remain the major contributor to increased levels of inbreeding, especially for breeds that are reared under extensive production systems. The beef breeds included in this study are farmed under extensive conditions where natural and uncontrolled mating is practiced (i.e., with minimal use of reproductive technologies e.g., AI); this complicates the correct assignment of the paternity to offspring (Visser *et al.*, 2011; Kios *et al.*, 2012). The availability of marker-based parentage verification methods, based on either microsatellites or SNPs, can be utilized by breeders to avoid consanguineous mating and to ensure accurate parentage. A number of laboratories or DNA testing facilities in SA are available to perform parentage verification and this will assist to alleviate problems related to inbreeding (Van Marle-Köster & Visser, 2018; Van Marle-Köster & Visser, 2021).

Effective population size ( $N_e$ ) is a crucial parameter to estimate genetic diversity since it directly influences the inbreeding level in a population (Adepoju, 2022). The Food and Agriculture Organization (FAO) (1998) proposed a threshold value of 50 to 100 animals per herd to prevent the loss of genetic diversity (Meuwissen & Woolliams, 1994) and a threshold of 25 to 255 animals to maintain fitness. The breeds included in the study had greater values than the FAO-recommended values.  $N_e$  values between composite breeds varied from 152 in the Santa Gertrudis breed to 750 in the Braford breed. Across the breeds the Brahman had the second highest  $N_e$  value of 412. The higher values for  $N_e$  observed in these breeds indicated that genetic diversity is maintained at a reasonable level, and this may be attributed to the lower use of AI bulls in beef breeding programs (Mukuahima, 2008). In addition, the higher  $N_e$  values in the studied breeds may indicate less intensive selection for production traits (compared to larger and more advanced breeds) and extensive control of mating between closely related animals (Mastrangelo *et al.*, 2017). However, insufficient pedigree data poses a common challenge when estimating  $N_e$ , particularly for extensively reared breeds. According to Boichard *et al.* (1997) low PIC could result in overestimation of  $N_e$  and in this study the Braford recorded the poorest PIC as depicted in Table 4.4. Therefore, future assessment of genetic diversity using more complete

pedigree information in this breed may address biases introduced due to incomplete pedigree information.

Nonetheless, the  $N_e$  recorded for breeds in the study were well within the range of 380 reported in Italian Maremmana cattle breed (Fioretti *et al.*, 2020), 167 for SA Brangus cattle breed (Steyn *et al.*, 2012), 168 for SA Afrikaner breed (Pienaar *et al.*, 2015) and 169.92 in the Spanish Berrenda en Colorado cattle breed (González-Cano *et al.*, 2022). The  $N_e$  values were higher than the 92.28 observed for Spanish Berrenda en Negro cattle breed (González-Cano *et al.*, 2022), 38.83 in the Portuguese Mertolenga breed (Carolino *et al.*, 2020) and a range of 122 to 138 for Italian cattle breeds (Bozzi *et al.*, 2006). These values were, however, lower than the estimated  $N_e$  in populations such as the Danish ( $N_e = 1\ 667$ ) and French ( $N_e = 2\ 459$ ) Limousines (Bouquet *et al.*, 2011) and Slovakian beef cattle ( $N_e = 809.4$ ) (Pavlík *et al.*, 2014).

### 5.1.2 Genetic trends based on EBVs

Over the past three decades, the BLUP animal model has been the global approach to predict estimated breeding values (EBVs), and this has aided in selection decisions (Crump *et al.*, 1994; Ramatsoma *et al.*, 2014). In this study, EBVs were averaged by year of birth to investigate genetic trends. Genetic trends are important to ensure that past and current selection decisions advance in the direction of an established breeding objectives for traits of economic importance (Larios-Sarabia *et al.*, 2022). This will allow breeders to evaluate genetic progress over time and whether breeding objectives need redefining in order to maximise genetic change.

In this study, the estimates of annual genetic change of the two reproductive traits indicated genetic improvement. Increases in genetic merit for days to calving (DC) were slightly negative, however, favourable for the Simbra composite breed (-0.088 days/yr) and its founder breeds; Brahman (-0.065 days/yr) and Simmentaler (-0.067 days/yr) respectively. Similarly, negative but favourable annual genetic change of -0.11 days/yr have previously been reported for DC in the Brazilian Nellore breed Boligon *et al.* (2016). On the contrary, Schmidt *et al.* (2019) have reported a positive and unfavourable DC of 0.16 days/yr in Brazilian Nellore breeds. The negative genetic changes in the DC values observed in the breeds included in this study are desirable and the results indicate reproductive improvement as sires will service more females on heat at the start of a breeding program (Forni & Albuquerque, 2005). Consequently, this has the potential to enhance the pregnancy rate and increase the lifetime production of calves per cow, which would lead to higher level of productivity within the herd (Boligon *et al.*, 2016).

Positive genetic change in scrotal circumference (SC) was observed for all breeds and ranged from +0.006 cm/yr in the Simmentaler breed to +0.020 cm/yr in the Simbra breed. These estimates were within the range of +0.035 to 0.050 cm/yr observed for the Brazilian Brahman (De Oliveira Bessa *et al.*, 2021) and 0.025 cm/yr to 0.034 cm/yr for Brazilian Nellore beef cattle (Moreira *et al.*, 2015). Higher genetic gains of 0.101 cm/yr to 0.202 were reported in Brazilian Guzerat (Mota *et al.*, 2019; and

Grupioni *et al.*, 2015) and SA Drakensberger cattle (+0.317; Abin *et al.*, 2016). Although the estimates for SC in this study were relatively lower compared to previous studies, the positive SC values still hold significance in terms of enhancing fertility traits. SC is closely associated to the quality and quantity of spermatozoa in bulls, as well as the age at which heifers reach puberty (Van Melis *et al.*, 2010; Terakado *et al.*, 2015). Therefore, these positive SC values have positive implications for improving fertility traits in the studied population.

The annual genetic change for birth weight (BW) for composite breeds varied from +0.015 in the Braford and Simbra breed to +0.017 kg/yr in the Santa Gertrudis breed. Across all breeds, composite breeds had higher values of BW compared to the two selected founder breeds Brahman breed (+0.026 kg/yr) and Simmentaler breed (+0.007 kg/yr). A relatively higher genetic gain (+0.16 kg) has also been reported by Lochner (2018) for BW in SA Boran cattle. In a multi-breed Canadian cattle population, Sullivan *et al.* (1999) furthermore reported a range of +0.049 kg/yr to +0.226 kg/yr for BW. On the contrary, Assan (2012) reported a negative trend for BW (-1.0 kg/yr) in indigenous Tuli cattle of Zimbabwe. The genetic changes in BW reported in the study were positive, however, small. Therefore, it is essential that these values should be monitored because an increase in BW is highly associated with calving difficulties, increase in age at first calving (AFC) and decrease in fertility (Hickson *et al.*, 2006; Gutiérrez *et al.*, 2007).

Reducing the estimates of BW in a breeding program is often a challenging task due to the strong positive correlation observed between BW and other traits such as weaning weight (WW) yearling weight (YW) (12 months), final weight (FW) (18 months) and mature cow weight (MCW) (Snelling *et al.*, 2010). In this study, genetic trends for BW and WW simultaneously increased with future weights (YW, FW, and MCW). It has been shown that selection for rapid increase in growth traits have an unfavourable genetic association with both BW and MCW because of its high cost implications (Abin *et al.*, 2016). Moderate selection for BW and MCW must be applied in the breeding programs. However, selection criteria for these traits must account for genetic correlation between the traits to accomplish the objective as lighter calf's results in low BW, calving ease (CE) and increases calf survival (Hickson *et al.*, 2006; Bennett *et al.*, 2021).

Comparably, Abin *et al.* (2016) reported an annual genetic change for BW of 0.037 kg/yr in SA indigenous breeds, with the corresponding WW, YW, and FW of about 0.549 kg/yr, 0.734 kg/yr and 0.077 kg/yr in the Afrikaner breed, for example. Chud *et al.* (2014) reported a linear increase of 0.073 kg/yr and 0.846 kg/yr per year in BW and WW for Nellore beef cattle in Brazil. Abreu (2017) investigated genetic trends of Brazilian *Bos indicus* breeds and reported estimates of annual genetic change in growth traits of approximately 0.010 kg/yr, 0.077 kg/yr, 0.130 kg/yr and 0.180 kg/yr for BW, WW, YW and FW, respectively.

Genetic trends for carcass weight (CW) indicated genetic progress, which may be attributed to increased growth traits (Campion *et al.*, 2009). The genetic trends for eye muscle area (EMA) indicated a positive trend for all the breeds included in this study. An increase in EMA is desirable because it



results in animals with high carcass yield (Magnabosco *et al.*, 2006). Rump fat (RF) and rib fat (RFA) indicated decreasing trends while rib eye area (REA) indicated a positive trend for the Simbra breed and its founder breeds. According to Goodall & Schmutz (2007), selection for REA results in increased lean tissue growth, which may result in a premium carcass thereby increasing the profitability of the herd. Intramuscular fat (IMF) indicated a positive trend for the Brahman and negative trends for the Simbra and Santa Gertrudis. A decrease in IMF is associated with lean meat, which results in less juicy, less tender and less tasty meat and the overall acceptability (Park *et al.*, 2018).

In this study, there was variation in the rate of genetic change for traits recorded. Overall, genetic trends for the traits recorded in the different breeds were favourable over the past two decades (2000 to 2020). The relatively slower rate of genetic improvement in some traits could potentially be attributed to missing or incomplete performance data, which may have limited the accuracy and completeness of the genetic evaluations. Of the breeds included in this study, the Braford breed was the most recently introduced to South Africa and, therefore, limited participation in performance recording may have played a role in the slower genetic improvement achieved in comparison to other breeds.

### 5.1.3 Genomic diversity

A multitude of SNP genotyping panels are commercially available, varying in both marker density and breed representation (Nicolazzi *et al.*, 2015; Lashmar *et al.*, 2021). Most of the studies in SA have applied these genotyping panels to investigate genetic diversity, especially for indigenous Sanga cattle breeds (Makina *et al.*, 2014, Lashmar *et al.*, 2018). This is the first study to investigate genetic diversity and population structure of numerically smaller SA composite breeds and their selected founder breeds. The results of genome-wide SNP characterization will provide knowledge of the genome-level diversity and genetic architecture of these breeds.

The successful application (and, therefore, utility) of a genotyping panel will greatly depend on the polymorphic content and, therefore, the level of informativeness of the SNPs included thereon; the majority of genotyping panels currently available were constructed from SNP selected in either taurine or indicine breeds (Dash *et al.*, 2018; Lashmar *et al.*, 2021). The minor allele frequency (MAF) of a SNP is a good parameter to determine whether the marker is in fact segregating within a given populations and, hence, whether the marker is informative to that given population. If a SNP is monomorphic (i.e., there is only one allele present in the population), it is not useful to most genomic applications, especially not genomic diversity.

In this study, the average MAF values for animals genotyped with the Illumina® Bovine 7K SNP genotyping panel varied from 0.184 in the Brahman breed to 0.332 in the Simbra breed. The average MAF values obtained were almost similar to the average MAF in ten different cattle breeds by He *et al.* (2018) and in Ethiopian and Asian cattle breeds by Edea *et al.* (2015), which varied between 0.188 and 0.320. The average MAF value for the animals genotyped with GGP Bovine 150K SNP genotyping panel ranged from 0.150 (Brahman) to 0.265 (Santa Gertrudis). The average MAF values

were similar to the MAF values obtained in indigenous SA beef cattle (Nguni: 0.249 to Drakensberger: 0.274) by Van Marle-Köster *et al.* (2021). The higher MAF values obtained for both the Illumina<sup>®</sup> Bovine 7K and GGP Bovine 150K SNP genotyping panel for composite (Simbra and Santa Gertrudis) and European taurine breed (Simmentaler) were supported by a study by Matukumalli *et al.* (2009) based on the Illumina<sup>®</sup> Bovine 50K SNP genotyping panel. On the contrary, Porto-Nerto *et al.* (2014) reported higher MAF values in indicine and composite breeds compared to their taurine counterparts using the Illumina<sup>®</sup> Bovine HD 777K SNP genotyping panel.

The relatively lower MAF values observed for indicine breeds (Brahman) with both the genotyping panels may be attributed to ascertainment bias (Qwabe *et al.*, 2013; Lashmar *et al.*, 2018). Furthermore, the Brahman is a non-discovery breed hence its low MAF value may be attributed to the exclusion of this breed from the initial development of the commercial SNP genotyping panel. The Illumina<sup>®</sup> Bovine 7K and GGP Bovine 150K SNP genotyping panels were primarily based on European taurine breeds with a small proportion of indicine breeds and excluding African breeds (Matukumalli *et al.*, 2009; Lachance & Tishkoff, 2013). Considering that the SNP genotyping panel included in the current study were designed using a large reference of European taurine breeds such as the Simmentaler and Shorthorn, it was expected that the genotyping panel in this study will favour European taurine and composite breeds carrying the European taurine haplotypes.

The estimate for observed heterozygosity ( $H_o$ ) for the animals genotyped with the Illumina<sup>®</sup> Bovine 7K SNP genotyping panel indicated moderate levels of genetic diversity ranging from 0.268 (Brahman) to 0.427 (Simbra). The estimates obtained were similar to the average heterozygosity estimates ranging from 0.363 to 0.415 in Ethiopian and Korean Hanwoo breeds (Edea *et al.*, 2013) and 0.280 to 0.420 in African and Asian cattle breeds (Edea *et al.*, 2015). However, the results were higher than the previously reported heterozygosity ranges of 0.186 to 0.214 in indicine breeds (Lin *et al.*, 2010) and 0.211 to 0.250 in Bangladeshi zebu breeds (Bhuiyan *et al.*, 2021). Across the populations genotyped with the GGP Bovine 150K SNP genotyping panel, the Simbra breed ( $H_o=0.413$ ) indicated the highest level of genetic diversity, and the results are supported by several studies that reported a higher genetic diversity in composite breeds than their founder breeds (Van der Nest *et al.*, 2020; Van Marle-Köster *et al.* 2021). The highest level of genetic diversity in the current study for the composite breed (Simbra) in both the genotyping panel may be attributed to the fact that this breed is a crossbred and crossbreeding between two different populations results in higher heterozygosity and increased productivity due to the heterosis effect (Iversen *et al.*, 2019).

The observed  $F_{IS}$  in the Brahman population genotyped with the Illumina<sup>®</sup> Bovine 7K and GGP Bovine 150K SNP panels were 0.015 and 0.018, respectively, indicating some inbreeding for this breed. The low genetic diversity in the Brahman breed was supported by the  $F_{IS}$  values obtained in the Brahman population examined by Van Der Nest *et al.* (2020) and Van Der Westhuizen *et al.* (2020). It is suggested that the high inbreeding in the Brahman is most likely a result of long-term artificial selection for improved production for certain traits (Albertí *et al.*, 2008; Van Der Nest *et al.*, 2020) and the

underrepresentation of this breed in the Illumina® Bovine 7K and GGP Bovine 150K SNP genotyping panel. Makina *et al.* (2014) indicated that the high inbreeding observed in breeding programs could be attributed to the utilization of a limited number of elite sires. The high genetic diversity in the composite breed (Simbra) in the current study indicates that crossbreeding remains an important approach for expanding the genetic diversity and holds potential for improving production and environmental adaptability.

The PCA results in the current study were consistent with the model-based admixture inferences and separated the breeds into ancestral origin and breed development. As seen for both the admixture results and in the PCA, there was a clear distinction between the Santa Gertrudis and Simbra breed. Similarly at  $K = 2$  and PCA a clear distinction was observed between the Simmentaler and Brahman breed indicating that the two breeds are unrelated ( $F_{ST} = 0.208$ ). The largest genetic divergence between the two breeds can be explained by the two independent domestication events that gave rise to two subspecies i.e., *Bos taurus* and *Bos indicus* breeds and this is supported by the results found in previous studies (Bradley *et al.*, 1996; Machugh *et al.*, 1997). As expected, the Simbra breed appeared as an admixture breed sharing ancestries with the Brahman and Simmentaler breeds. However, the Simbra breed deviated from its original genetic composition of 5/8 Simmentaler (*Bos taurus*) and 3/8 Brahman (*Bos indicus*). The proportions of Simmentaler and Brahman in the Simbra breed were 58.1% and 26.4% respectively. Van Der Nest *et al.* (2021) obtained higher proportions which revealed that the SA Simbra is composed of 64.8% of Simmentaler and 35.2% of the Brahman breed. The deviation of ancestral proportions in the Simbra breed indicates that intensive selection for production traits (leaner carcass) had more influence on the increased taurine composition in the Simbra breed (Bonsma, 1994; Hay *et al.*, 2022).

The Santa Gertrudis formed a separate cluster with the other breeds in the PCA and from  $K = 3$  to  $K = 13$  maintained its purity throughout the admixture. Consistent with the  $F_{ST}$  (0.106) results the Santa Gertrudis had close genetic relatedness with the Simmentaler. The proportion of Simmentaler (25.70%) in the Santa Gertrudis breed can be attributed to a common ancestral background between the Shornhorn (founder breed to Santa Gertrudis breed) and Simmentaler that is traced back to *Bos taurus* in Europe. However, the Santa Gertrudis demonstrated limited shared ancestry with the Brahman (22.10%), and this was expected because the breed is not developed from the local SA Brahman breed. The low proportion of the Brahman in the Santa Gertrudis breed found in the present study is contrasting to the proportions found in the Santa Gertrudis in a study by Bovine HapMap Consortium *et al.* (2009), however, it was supported by Crum *et al.* (2021) who utilized RFmix to estimate the ancestral proportion of the Santa Gertrudis. The lower proportion found in the Brahman breed may be attributed to a strong selection for performance traits which results in selective advantage for taurine breeds thus reducing the Brahman contents.

The estimation of  $N_e$  in the present study observed a decline in  $N_e$  in all studied populations from 800 generations until 12 generations ago indicating historical processes of domestication, breed

formation and population subdivision (Daetwyler *et al.*, 2010; Deng *et al.*, 2019). In the recent 12 generations ago,  $N_e$  values for the breeds in the current study ranged from 216 in the Santa Gertrudis breed to 316 in the Simmentaler breed. The  $N_e$  values in the current study were higher than the FAO-recommended values (50-100) and this indicates that intensive selection and inbreeding is carefully managed in the breeding herds of these breeds (Sudrajad *et al.*, 2017). The trends of  $N_e$  in the studied breeds were comparable with  $N_e$  values of 300 reported in Hanwoo cattle breeds in 4 generations ago (Li & Kim, 2015) and 352 in Hanwoo Korean cattle for the past 10 generations ago (Lee *et al.*, 2011). However, the values of  $N_e$  were higher than  $N_e$  of 56 animals in the last 50 generations ago for South African Nguni cattle population (Dlamini *et al.*, 2022). Similarly, Chhotaray *et al.* (2021) reported lower  $N_e$  of 40 animals over 5 generations ago in Vrindavani crossbred.

The high  $N_e$  values obtained for the breeds in the current study indicate that intense selection and mating of closely related animals is under control in the breeding programs of these breeds (Mastrangelo *et al.*, 2017). However, the  $N_e$  of 216 in the Santa Gertrudis indicates a risk of inbreeding in the future and mating practices (i.e., the choice of bulls, predominantly) should be monitored for this breed.

## CHAPTER SIX: CONCLUSION AND RECOMMENDATIONS

### 6.1 Conclusion

Since the development of composite breeds included in the study, they have been participating in performance recording submitting phenotypic data and pedigree information to service providers (Currently Livestock Registering Federation) for genetic evaluations. In the 2015/2016 year, the LRF in collaboration with the University of Pretoria and Studbook participated in the Beef Genomic Program (BGP) to generate SNP genotyping data. Research efforts focusing on numerically smaller composite beef breeds (i.e., excluding the popular SA Bonsmara and Beefmaster breeds) have been lacking. Assessing the genetic improvement of livestock is crucial for evaluating the impact of selection practices over time and it can also provide valuable insights that can aid in the development of optimal breeding and management strategies.

In this study, three sources of information namely pedigree, performance (based on EBVs) and genomic data were used to assess the genetic status of composite beef cattle breeds and their selected founder breeds. Herdbook information contributed significantly to monitoring population structure and for keeping of performance records for traits of economic importance. There was improvement in pedigree completeness (PIC) from the 6<sup>th</sup> generation to 1<sup>st</sup> generation depth across the breeds, indicating improvements in animal recording. However, the trends in PIC were quite complete for breeds imported early into South Africa (SA). The levels of inbreeding were low whereas, the effective population size ( $N_e$ ) was high among the studied population. These levels are not alarming and not in the range of critical levels indicating the absence of strong intensive selection. The genetic trends for fertility traits and carcass weight (CW) indicated genetic improvement except for some breeds due to lack of performance records. The genetic trends for growth traits were all positive and birth weight (BW) was of low magnitude indicating that they are in the right direction for genetic improvement.

Genomic analysis based on the Illumina<sup>®</sup> Bovine LD 7K and GGP Bovine SNP 150K SNP data revealed high genetic diversity within and among composite breeds. Principal component analysis (PCA) and model-based clustering clearly differentiated the breeds according to their historical origin and breed development. Genetic distinctiveness was observed between taurine and indicine breeds. The Santa Gertrudis formed a tight cluster and separated from the other breeds. The findings of the PCA and admixture in the Simbra breed were consistent with other SA studies conducted indicating that the Simbra composite breed has a higher proportion of the Simmentaler breed than the Brahman founder breed. The study also found that there is a decreasing trend of  $N_e$  over the past 800 generations. The high genetic diversity retained in the current study indicate that composite breeds have the potential for sustainable beef production in both commercial and non-commercial beef production systems. This study serves as a reference for future characterisation of the SA composite breeds included in the study.

## 6.2 Recommendations

In this study, low PIC was observed for some breeds, and this may influence the estimation (through either over- or underestimation) of parameters such as inbreeding and  $N_e$ . To improve the accuracy of pedigree-based analyses, breeders are urged to retain proper pedigree records going forward and to participate more in performance recording. Even though the current breeding programs' strategies to avoid inbreeding are effective for long-term maintenance of genetic diversity, the minimization of mating closely related animals and the introduction of new genetic material is required to increase genetic diversity. The slightly positive genetic trends for BW should be maintained to avoid calving difficulties. The breeds included in the study suggest that analysis based on the Illumina<sup>®</sup> Bovine LD 7K SNP genotyping provided sufficient information to assess genetic diversity, however, genomic data for a larger sample size and higher-density SNPs (e.g., whole-genome sequencing) are required for higher-resolution and unbiased comparison. Furthermore, adding more genotypes will result in a training population for the breeds which could be applied in the current genetic evaluation for the estimation of genomic enhanced breeding values (GEBV) for genomic selection.

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