Co-variance component estimation for South African Hereford, Charolais and Angus cattle for application in genetic evaluations

by

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Declaration

I, the undersigned, 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

This study developed (co)variance components and heritability estimates for growth traits in South African Angus, Charolais, and Hereford cattle, well-established breeds farmed locally for over a century. Genetic parameters are required for genetic evaluations. In this study genetic parameters were estimated for the specific populations by using single- and multi-trait models based on available data over 10-year (2012-2022) and 20-year (2002-2022) periods. Key traits analysed included birth weight, weaning weight, yearling weight, and 18-month weight, Average Daily Gain (ADG), hip height, body length and scrotal circumference. This study developed single and multi-trait models for (co)variance estimations. The single-trait models for Angus birth weight exhibited higher direct heritability estimates (0.41 to 0.49) compared to weaning weight (0.02 to 0.26), yearling weight (0.05 to 0.43), and 18-month weight (0.25 to 0.44) for the Angus breed. The Charolais exhibited similar results, and the Hereford estimates varied across the traits with large variability, birth weight (0.001 – 0.29), weaning weight (0.03 – 0.19), yearling weight (0.07 – 0.25) and 18-month weights (0.01 – 0.56). Single-trait models indicate the role of environmental effects such as inclusion of Sire by Herd (SXH) effects in breed models which raises residual variance, and the Permanent Environment (PE) effect which impacted traits from birth to 18 months, therefore they must be evaluated for inclusion. For Angus, multi-trait heritability estimates were (0.50 ± 0.02, 0.43 ± 0.02) for birth weight, (0.31 ± 0.24, 0.27 ± 0.02) for weaning weight, (0.50 ± 0.04, 0.36 ± 0.03) for yearling weight, and (0.35 ± 0.06, 0.39 ± 0.03) for 18-month weight in the 2012-2022 and 2002-2022 datasets, respectively. Charolais estimates showed birth weight heritability estimates of (0.36 ± 0.04, 0.42 ± 0.03), weaning weight at (0.19 ± 0.03, 0.20 ± 0.03), yearling weight at (0.07 ± 0.02, 0.13 ± 0.03) and 18-month weight at (0.10 ± 0.04, 0.17 ± 0.04) for the same periods. For Hereford (2012-2022 data only), heritability for birth weight was 0.32 ± 0.03, weaning weight 0.20 ± 0.03, yearling weight 0.32 ± 0.06, and 18-month weight 0.46 ± 0.08. Post-wean growth test traits heritability estimates were estimated on the larger data set of 2002-2022. Angus demonstrated moderate to high heritability for ADG (0.19 ± 0.05) and scrotal circumference (0.37 ± 0.07). Charolais exhibited moderate heritability for average daily gain (0.39 ± 0.30) and scrotal circumference (0.57 ± 0.28), and Hereford cattle showed moderate heritability for average daily gain (0.31 ± 0.10) but lower estimates for scrotal circumference (0.21 ± 0.10). The study emphasizes dataset limitations and recommends complete recording and genomic-based parentage testing to improve the accuracy of variance components and estimated breeding values for breeders.

Table of contents

List of figures

Chapter 2: Literature review

Chapter 3: Materials and Methods

Chapter 4: Results

List of tables

Chapter 2: Literature review

Chapter 3: Materials and Methods

Chapter 4: Results

List of abbreviations

ADG	Average Daily Gain
AFC	Age at First Calving
AI	Artificial Insemination
ANOVA	Analysis of Variance
ASREML	Average information Sparse Restricted Maximum Likelihood
BGP	Beef Genomics Program
BLP	Best Linear Prediction
BLUP	Best Linear Unbiased Prediction
BP	Best prediction
CG	Contemporary Groups
DFREML	Derivative-Free REML
EBVs	Estimated breeding values
GBLUP	Genomic BLUP
GEBVs	Genomically Enhanced Breeding Values
GRM	Genomic Relationship Matrix
ICP	Inter-calving Period
LD	Linkage Disequilibrium
LMM	Linear Mixed Models
LRF	Livestock Registering Federation
MAS	Marker Assisted Selection
ML	Maximum Likelihood
MME	Mixed Model Equations
MSI	Missing Sire Information
NRM	Numerator Relationship Matrix
PE	Permanent Environment
PEST	Parameter Estimation

QTL	Quantitative Trait Loci
REML	Restricted Maximum Likelihood
RTU	Real-time Ultrasound
SA	South Africa(n)
SD	Standard Deviation
SNP	Single Nucleotide Polymorphism
SP	Studbook Proper
SXH	Sire by Herd effect
TIA	Technology Innovation Agency
VCE	Variance Component Estimation

Chapter 1: Introduction

1.1 Introduction

Hereford, Charolais and Angus are classified as European Taurine beef cattle breeds and have been farmed in South Africa (SA) for more than 100 years (Angus Society of South Africa, 2023; SA Charolais Breeder's Society, 2023; The Hereford Cattle Breeders' Society of South Africa, 2023). These breeds originate from Europe and have been subjected to selection under SA climatic conditions and production systems and are well established in the beef cattle sector. The number of registered stud breeding animals vary from 18 480 for the Angus breed, 5 620 for the Charolais and 5 109 for the Hereford breed in South Africa (SA Stud Book, 2022).

The establishment of a National Beef Recording and Improvement Scheme in the late 1950s created the foundation for performance recording for the majority of SA beef breeds (Hunlun *et al*., 2007). Due to the ease of recording of weight traits and their relatively high heritability estimates, selection focus was primarily on growth during the 1970's and 1980's. Selection programs were data-driven, focused on production traits such as body weight, and significant progress was seen for most cattle breeds engaging in performance recording (Bullock & Pollack, 2009). During the late nineties, animal breeders recognised the value of goal driven breeding objectives, which resulted in an approach where traits of low heritability and difficult to measure were also considered in selection (Garrick & Golden, 2009). Goal-driven breeding objectives were adopted to balance selection pressure on traits between those important for production and those important for longevity and reproduction, as well as traits relating to environmental impact (Garrick & Golden, 2009). In setting appropriate breeding objectives, breeders need to participate in animal recording to record performance traits for inclusion in selection. In addition, accurate pedigrees are needed and with performance records form the basis for all genetic evaluations. By leveraging this data, farmers can make well-informed management decisions, such as those related to breeding, to produce healthy, safe, and sustainable food that is both valuable and profitable (ICAR, 2024).

The introduction of BLUP technology in the early 90's led to the adoption of a more balanced selection approach to include fertility traits such as inter-calving period and scrotal circumference as well as efficiency traits recorded during central growth tests (Bergh, 2010; Scholtz, 2010). The introduction of Estimated Breeding Values (EBVs) resulted in an increase in recording by breeders as they realized the benefit and potential for genetic progress (Bergh, 2010). Genetic evaluations have become routine for most progressive breeds in SA and breeders routinely use EBV's and selection indices in selection programs. The Beef Genomic Program (BGP), a three-year program (2015-2017) funded by the Technology Innovation Agency (TIA) provided opportunity for participating breeds to genotype founder animals and build reference populations for genomic selection (Maiwashe, 2019). The SA Charolais and Hereford breeds took part in the BGP and have reference populations and receive Genomically Enhanced Breeding Values (GEBVs) for application in selection programs (Maiwashe, 2019).

The estimation of (co)variance components remains an essential step in the estimation of EBVs (Koots *et al*., 1994; Hofer, 1998; Getabalew *et al*., 2019). Heritability estimates are trait and population specific due to differences among environments, allele segregation in a population, and variation in additive and non-additive factors which can affect the estimations (Visscher *et al*., 2008; Preston & Willis, 2013; Getabalew *et al*., 2019). Heritability estimates for different traits are important in selection programs and essential for accurate EBV estimation and allow comparison of traits recorded in different environments across populations (Visscher *et al*., 2008).

Animal models used in prediction of breeding values include single or multi-trait models. Henderson (1970) focused on single trait animal models as this is what was computationally possible at the time (Pollak *et al*., 1984). As computational power increased multi-trait models were developed. Multi-trait models are favoured as selection is often based on several traits of economic importance which are phenotypically and genotypically correlated. A multi-trait model analysis accounts for the relationship between traits and results in a more accurate evaluation (Pollak *et al*., 1984; Mrode & Thompson, 2005; Guo *et al*., 2014). Single trait analysis also has the disadvantage of potentially resulting in biased values, for example if yearling weight is analysed under a single trait model it will be biased as it does not include information on the animals weaning weight which was the basis of selection (Mrode & Thompson, 2005). Multi-trait models are especially useful for traits of low heritability and those which have a low number of phenotypic records as it can increase the accuracy if evaluated with a trait of high heritability (Guo *et al*., 2014). A disadvantage of multi-trait model analyses is the high computing requirements but with the advances in technology and increased computing power this has becomes less of a concern (Mrode & Thompson, 2005; Weller & Ezra, 2016).

The goal of genetic evaluation is to transform selection into a powerful tool for producers to enhance their livestock. Over time, selection has evolved from relying on phenotypic observations of individual animals to utilizing genetic predictions based on the analysis of millions of records from both national and international sources across various breeds (Garrick & Golden, 2008). This shift has been made possible by advancements in computing technology and statistical methodologies, significantly boosting selection accuracy (Bullock & Pollak, 2009; Meuwissen *et al.*, 2016). The importance of genetic evaluations cannot be overstated, as they allow for the identification and propagation of superior genetic traits, ultimately leading to more efficient, productive, and profitable livestock operations. By integrating these evaluations, producers can make informed decisions that enhance the genetic quality of their herds, ensuring long-term sustainability and competitiveness in the beef industry (Bullock & Pollak, 2009; Scholtz, 2010; Miglior *et al*., 2017).

1.2 Aim and Objectives

Heritability, a key parameter in animal breeding, quantifies the proportion of phenotypic variation attributable to additive genetic factors. Accurate estimation of variance components is essential for understanding the genetic architecture of traits and for predicting genetic progress. Given the dynamic nature of populations, influenced by factors such as selection, inbreeding, and environmental changes, heritability estimates can fluctuate over time (Visscher *et.al*.,2008). Therefore, periodic re-estimation is crucial to capture these shifts and ensure the precision of genetic evaluations. By separating phenotypic variance into its genetic and environmental components, variance component analysis provides invaluable insights into the potential for genetic improvement and informs optimal breeding strategies.

The aim of this study was to estimate (co)variance components for birth weight, weaning weight, 12-month and 18-month weights as well as average daily gain, hip height, body length and scrotal circumference for South African Hereford, Charolais and Angus beef cattle breeds for application in South African genetic evaluations.

The following objectives were set to achieve the aim:

1. Data editing and file preparation
2. To determine fixed and random effects for inclusion in models for genetic prediction of pre-wean and post-wean growth (birth weight, weaning weight, 12-month weight, 18-month weights, average daily gain, hip height, body length and scrotal circumference.
3. To estimate (co)variance components for pre-wean and post-wean growth (birth weight, weaning weight, 12-month weight, 18-month weights, average daily gain, hip height, body length and scrotal circumference.
4. To perform a single-trait and multi-trait analyses of variance components for the three breeds.
5. To estimate breeding values and genetic trends for all above-mentioned traits for the South African Angus beef cattle breed.

Chapter 2: Literature review

2.1 Literature review

2.1.1. Introduction

Selective breeding for desirable traits in beef cattle is essential for efficient beef production and accurate estimation of the genetic potential of breeding stock supports this process. This literature review explores covariance component estimations for three prominent beef cattle breeds: South African (SA) Angus, Hereford, and Charolais. This review will focus on how these estimations contribute to genetic evaluations, specifically focusing on Estimated Breeding Values (EBVs). EBVs are critical selection tools, providing breeders with a reliable prediction of an animal's genetic merit for a particular trait. The review will delve into the importance of covariance components in calculating EBVs and their impact on genetic improvement programs for these three breeds.

2.1.2. Brief overview of the SA beef cattle industry

The SA beef industry is a fast-growing industry and is second in size to the poultry industry (Ngxumeshe *et al.*, 2020), with a per capita consumption of 17.1 kg versus 36.2 kg respectively (DALRRD, 2023). The industry is characterized by notable diversity in breed types, environments, market demands, and production (DALRRD, 2022). The overall gross value of beef production is contingent upon the volume of slaughtered cattle and the market prices obtained by producers. Between 2011/12 and 2017/18, the gross value of beef production in South Africa surged from R19.3 billion to R37 billion, marking a notable increase of 173% over this interval. However, in 2018/19, there was a marginal downturn of 7% attributed to the Foot and Mouth Disease outbreak, which led to an international ban on South African beef imports (DALRRD, 2022). Subsequently, the gross value rebounded, continuing to rise through 2020/21. This decade-long upsurge can be largely attributed to heightened beef consumption trends observed in recent years. On average, the annual gross value of beef production during this period stood at R30.2 billion (DALRRD, 2022).

South Africa has around 12.2 million cattle in the formal sector with around 50 000 producers. Up to 65 to 70% of beef production in South Africa comes from commercial feedlots. All three breeds under study, the Angus, Charolais and Hereford are listed among the 12 most important breeds in feedlot production. Table 2.1 shows the proportion of breed types present in the feedlot system obtained from an agricultural report DALRRD (2022).

Table 2.1 The proportion of breed types slaughtered in feedlots

Breed type	Proportion slaughtered
Sanga types	29%
Zebu types	11%
British types	26%
European types	27%
Dairy/other	7%

South Africa produces 1.06 million tons of beef per year of which 32 million kg is exported, and 4.3 million kg of beef is also imported annually, the per capita consumption is 17.45 kg/year (DALRRD, 2022). The seed stock industry is crucial for genetic advancement in livestock, as it serves as the foundation for breeding superior animals. In South Africa, the genetic enhancement of seed stock herds benefits the entire population, provided the industry engages in national recording and improvement programs. Seed stock producers focus on breeding animals with desirable traits, which are then distributed throughout the broader animal population according to the gene flow pyramid (Figure 2.1). Stud breeders must remain aware of the market demands to better design breeding programs and policies that benefit the commercial cattle breeder (Hunlun *et al.*, 2007; Van Marle-Köster & Visser, 2018) This ensures that superior genetic material permeates the entire livestock population, leading to overall genetic improvement and enhanced productivity (Scholtz, 2012; DALRRD, 2022). In Figure 2.1 the different proportions of beef cattle farmers in South Africa can be seen obtained from DALLRD (2022).

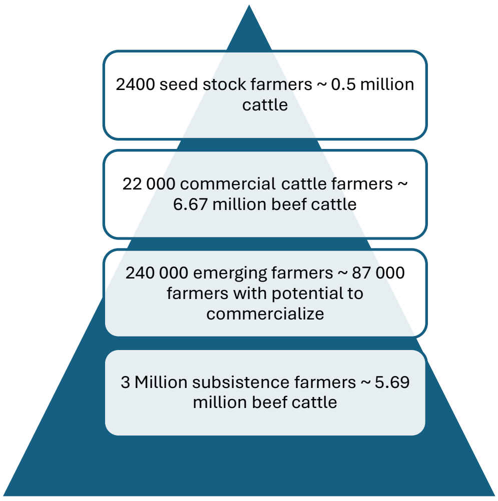


Figure 2.1 Gene flow pyramid for beef and dual-purpose cattle in South Africa

Although British and European breeds comprise only 25% of the seed stock industry as seen in Table 2.2 (DALRRD, 2022), they dominate the feedlot sector, with 53% of cattle in feedlots originating from these breeds. This indicates their effective use as sire lines in crossbreeding with Sanga types as dam lines to fulfil the needs of the commercial sector as seen in DALRRD (2022). Taurine breeds such as the Hereford, Angus, and Charolais are used as sire lines in crossbreeding with Sanga dam lines, and therefore important for the diverse SA climate and commercial cow-calf production sector.

Table 2.2 The contribution of the different breed categories to the different beef producing sectors

Breed category	Emerging	Commercial	Seed stock
Sanga, Sanga derived	41.0%	28.7%	41.8%
Zebu, Zebu derived	19.2%	11.6%	32.9%
British breeds	1.8%	26.2%	9.2%
European breeds	3.0%	26.8%	16.1%
Other	35.0%	6.7%	-

Performance recording, tracing back to the mid-20th century, is typically managed by breed associations, government bodies, or private entities. Performance recording in South Africa was initially done by the National beef improvement scheme run by the Agricultural Research Council (ARC) consisting of Phase A1 (Reproduction phase), A2 (suckling phase) and post wean phases B-D (Agricultural Research Council, 2022). Animal recording systems and genetic evaluations services have been privatised and SA beef cattle breeders can utilise services provided by companies such as SA Stud Book and the Livestock Registering Federation (LRF) (Livestock Registering Federation, 2024.; SA Studbook, 2024). On-farm recording mainly involves measuring live weights and growth rates, with technologies like ultrasonic scanners advancing fat and muscle measurements (Scholtz, 2010; Kinghorn *et al*., 2014).

2.1.3. Brief overview of the SA Hereford, Angus and Charolais breeds

The Hereford and Aberdeen Angus beef cattle breeds were introduced into South Africa in 1892 and 1895 from England and Scotland respectively where they had been well established during the British agricultural revolution in the 1800s (Schreuder, 1931; Van Marle, 1974; Scholtz *et al.*, 2019; Angus Society of South Africa, 2023; The Hereford Cattle Breeders' Society of South Africa, 2023). The Charolais breed was imported after the second world war in 1955 from eastern France for its value as a terminal sire breed (Loubser *et al*., 2007; SA Charolais Breeders' Society, 2023). European taurine cattle offered a breeding advantage with regard to improved growth and carcass traits. Since they were genetically distinct from the local Sanga breeds, heterosis could be exploited using crossbreeding (Van Marle, 1974; Macneil & Matjuda, 2007; Van Marle-Köster *et al*., 2021). As these breeds have now been in South Africa for over or close to 100 years and have been subjected to selection under the local climatic conditions they are well adapted and are present in many climatic conditions across the country as seen in Figure 2.2 (Adesina *et al.*, 2016; Microsoft bing image creator; SA Stud Book, 2022). The size of the breed icons represents the number of breeders in the area.

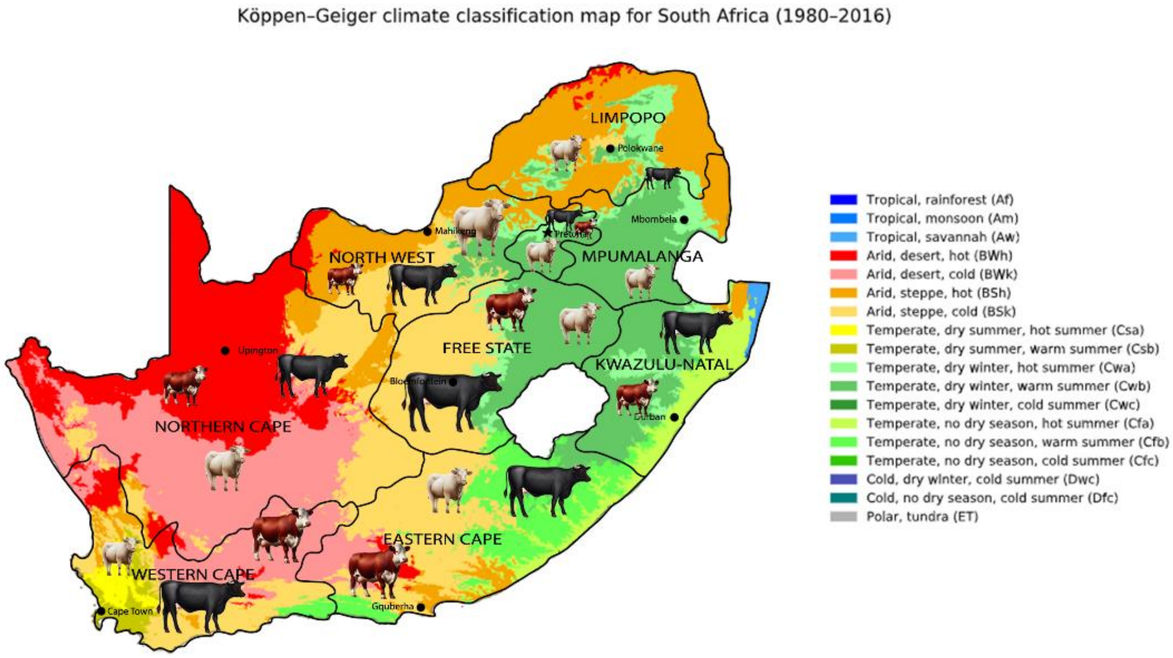


Figure 2.2 Illustrated representation of the distribution of the Angus, Charolais and Hereford breeds across South Africa

The breeder's society in South Africa for the Hereford and Angus breeds were both established in 1917, with the Charolais Breeder's Society established later in 1966 (Schreuder, 1931; Scholtz *et al.*, 2019; Angus Society of South Africa, 2023; SA Charolais Breeders' Society, 2023; The Hereford Cattle Breeders' Society of South Africa, 2023). In Table 2.3 the number of stud breeders and registered animals for each breed in South Africa are summarised. All three of the Breed Societies have compulsory participation in animal recording for the recording of fertility, maternal and growth traits up to weaning. The number of registered breeders for Angus, Charolais, and Hereford in South Africa is significantly smaller compared to the United States, which has 25 000, 74, and 4 317 registered breeders for these breeds, respectively (American Angus Association, 2024; American Charolais Association, 2024; American Hereford Association Annual Report, 2024).

Table 2.3 Number of Angus, Charolais and Hereford registered stud breeders and animals in South Africa in the year 2022

Breed	Number of registered breeders (SA)	Number of registered animals (SA)	Reference
Angus	106	18 480	(SA Stud Book, 2022)
Charolais	38	5 620	(SA Stud Book, 2022)
Hereford	33	5 109	(SA Stud Book, 2022)

A breeding objective is essential for breeders as it outlines the economically important traits that result in a desired outcome for their herd. It should be specific, measurable, cost effective and have biological relevance (Goddard, 1998; Kluyts *et al*., 2003; Sölkner *et al*., 2008; Miglior *et al*., 2017; Cole *et al*., 2021). The rate of genetic advancement in beef cattle faces challenges due to the innately low reproduction rate (high number of replacement animals need to be kept), abundance of economically important traits (limits selection differential) and long generation interval (Gregory *et al*., 1961; Sölkner *et al*., 2008; Seroba *et al*., 2011; Miglior *et al.,* 2017). Despite reproduction traits having a low heritability, their economic importance drives genetic improvement endeavours (Kinghorn *et al*., 2015).

The development and timeline of beef cattle improvement and selection are shown in Figure 2.3, compiled from literature (Hunlun, 1989; Van Marle, 1974; Garrick *et al*., 2008). While conformation and size were the primary observable type traits 100 years ago, animal recording programs and the development of computer and molecular technologies present the modern-day breeders with selection tools such as EBVs and Genomically Enhanced Breeding Values (GEBVs) to further advance selection capabilities.

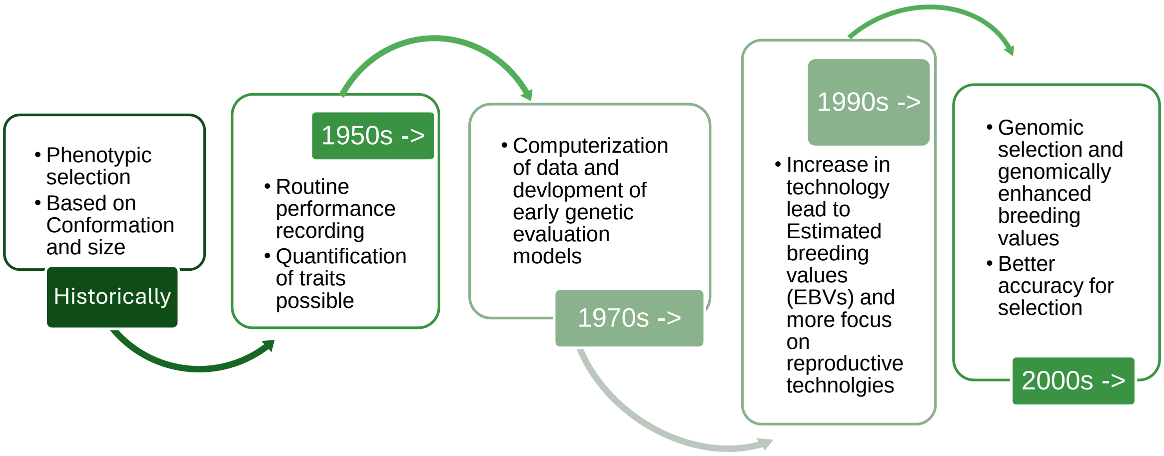


Figure 2.3 Timeline of breed improvement and selection

Over the past 100 years, breeding objectives for Angus, Charolais, and Hereford cattle have focused on distinct traits of economic importance. Angus cattle are noted for superior meat quality (marbling and tenderness) and low birth weights. Charolais cattle are valued for their growth ability, lean carcasses, and high adaptability. Hereford cattle are recognized for their fertility, easy calving, docile temperament, and meat quality (Bartoň *et al*., 2011; The Hereford Cattle Breeders' Society of South Africa, 2023; Angus Society of South Africa, 2023; SA Charolais Breeders' Society, 2023). Angus cattle are naturally polled, while the majority of SA Hereford are polled, and preference is given among breeders for selection of polled cattle. Despite compulsory participation in animal recording, the depth of participation varies among the traits as seen in Table 2.4 (SA Stud Book, 2023). Recording of traits up to weaning is high, while post weaning growth recording varies among the breeds. Growth tests are intensive feeding tests that can either take place on farm (Phase D) or at a test station (Phase C), these are costly, and participation is low among breeders (Hunlun *et al*., 2007; Bergh, 2010; Seroba *et al*., 2011).

Table 2.4 The depth of recording of growth traits between 2018 and 2022 (% of all animals recorded) for the SA Angus, Charolais and Hereford cattle breeds in South Africa (SA Stud Book, 2023).

Breed	Birth weight	Weaning weight	12-month weights	18-month weights	Growth tests
Angus	99%	73%	22%	16%	6%
Charolais	98%	82%	59%	24%	2%
Hereford	96%	62%	15%	12%	13%

Besides the growth traits shown in Table 2.4, fertility traits are recorded including Inter-calving Period (ICP), Age at First Calving (AFC) and conception rate (Kinghorn *et al.*, 2014). In the Angus Real-time Ultrasound (RTU) measurements are important due to the selection emphasis on carcass quality (Seroba, 2011). In Table 2.5 the average performance values for economically important traits can be seen for the period 1980 – 1992 as reported by Bosman (1994) compared with these values in 2023 for South African Angus, Charolais and Hereford cattle breeds obtained from SA Stud Book (2023) report. The Angus breed was not included in the report by Bosman (1994). The overall depth of performance recording affects genetic parameter estimations and genetic evaluations for all breeds interested in EBVs (Scholtz, 2010).

The majority of cattle breeds worldwide, including those discussed here, have historically employed a data-driven approach for genetic improvement, with economic value driving trait selection (Garrick & Golden, 2009). From the 1930s to the 1970s, the focus was primarily on increasing production, despite concerns that this singular focus could negatively impact overall fitness. The industry pursued maximum genetic gains in production due to its financial benefits. However, challenges such as climate change and changing consumer preferences now necessitate a goal-driven approach (Cassandro, 2020). Recognition of the correlated genetic decline in other important traits such as longevity and fertility has led many countries to adopt more balanced selection objectives, incorporating more emphasis on previously undervalued non-yield traits (Golden *et al.*, 2009; Miglior *et al.*, 2017; ARC Annual Beef Bulletin, 2022).

Table 2.5 Average performance for traits of economic importance in the Angus, Charolais and Hereford beef cattle breeds (Bosman, 1994; SA Stud Book, 2023)

Trait	Breed	Performance average 1980 -1992	Performance average 2023
Birth Weight (kg)	Angus	-	34.2
	Charolais	41	40.1
	Hereford	35	36.5
Weaning Weight (kg)	Angus	-	246
	Charolais	235	241
	Hereford	194	235
Yearling Weight (kg)	Angus	-	308
	Charolais	317	314
	Hereford	254	310
18- month Weights (kg)	Angus	-	395
	Charolais	404	400
	Hereford	321	407
Average Daily Gain (g)	Angus	-	1 783
	Charolais	1 798	1 931
	Hereford	1 541	1 698
Scrotal circumference (mm)	Angus	-	351
	Charolais	349	348
	Hereford	316	349

2.1.4. Genetic parameters for traits of economic importance in beef cattle

For over a century, beef cattle selection has been concentrated on fertility traits (e.g., calving ease, conception rates, and maternal ability), production traits (e.g., growth rate, feed efficiency, and carcass yield), and quality traits (e.g., tenderness, flavour, and marbling) (Gregory et al., 1961; Haskell et al., 2014). Most economically important traits are largely governed by additive inheritance, where multiple loci contribute to an animal's genotype. Ronald Fisher, as early as 1918, described these polygenic traits in terms of genotypic variance and covariances among relatives, partitioning effects into additive genetic variance (VA), dominance effects within loci (VD), and epistatic interactions between loci (VI or VAD) (Hill, 2010, 2014). Sewell Wright later expanded this model, examining the effects of inbreeding and genetic relationships on additive trait variation (Hill, 2014).

In 1922, Fisher proposed Maximum Likelihood (ML) methods for estimating variance components, and in 1930, he introduced Analysis of Variance (ANOVA) for balanced data as a method to estimate these components (Searle, 1994; Hofer, 1998; Lee, 2000). While ML can accommodate unbalanced data by specifying data distribution, ANOVA traditionally performs best with balanced data, although it is also applicable to unbalanced data. A limitation of early ML methods was computational constraints, which restricted dataset size and led to potential bias, as the method could not account for degrees of freedom lost to fixed effects in models (Harville, 1977; Meyer, 1991; Shaw, 1991; Hofer, 1998; Lee, 2000; Thompson, 2008; Hill, 2010).

A major factor to determine the additive variation or genetic component is the environment consisting of a variety of factors which may have a significant influence on polygenic traits (Bourdon, 2000; Rohmer *et al.*, 2022), The amount of genetic progress will be determined by the proportion of variation resulting from both genetic and non-genetic factors. It was therefore necessary to define these factors in a linear model to account for these effects (Gregory *et al.*, 1961; Scholtz, 2010; Rohmer *et al.*, 2022).

Jay Lush in the 1930s was the first to describe heritability in the narrow sense as the proportion of additive genetic to phenotypic variation (Hill, 2014) as represented by the following equation:

$$\boldsymbol{h^2 = \frac{\sigma^2 A}{\sigma^2 P}}$$

Where $\boldsymbol{\sigma^2 A}$ is the additive genetic variance (breeding value) and $\boldsymbol{\sigma^2 P}$ is the total phenotypic variance. Both of these components require phenotypic records and pedigree information to calculate, therefore they are prerequisites to determining heritability values (Visscher et al., 2008; Hill, 2014; Getabalew et al., 2019). Heritability is an important genetic parameter as it allows comparison of traits within populations, is required in developing breeding objectives for selection and predicting the response to selection (Meyer & Enfield, 1975; Visscher *et al.*, 2008; Getabalew *et al.*, 2019; Rameez *et al.*, 2022). Lush developed the “Breeders Equation” to be able to estimate this response in terms of the selection differential,

$$\mathrm{R = h^2S}$$

Where **R** is equal to the response in the first generation of selection, $\boldsymbol{h^2}$ is the narrow sense heritability and **S** is the selection differential (Hill, 2010). Heritability estimates are a population specific parameter and can change due to selection, inbreeding, migration, or mutation, therefore it is important for these parameters to be updated to give us the most accurate predictions of genetic progress (Visscher *et al.*, 2008; Preston & Willis, 2013; Getabalew *et al.*, 2019). In Table 2.6, a selected summary of heritability values for traits of importance in beef cattle are summarised for Angus, Hereford and Charolais cattle breeds. Selecting for a greater number of traits reduces the intensity of selection for each individual trait.

Table 2.6 Average direct heritability estimates for weight and growth traits in the Angus, Charolais and Hereford beef cattle breeds

Trait	Breed	Average heritability estimate	References
Birth Weight (kg)	Angus	0.36 – 0.42	(Trus & Wilton, 1988; Meyer, 1992)
	Charolais	0.36 – 0.50	(Orenge *et al*., 2009; Herrera-Ojeda *et al*., 2019)
	Hereford	0.21 – 0.58	(Koch, 1972; Trus & Wilton, 1988; Meyer, 1992; Orenge *et al*., 2009)
Weaning Weight (kg)	Angus	0.19 – 0.63	(Meyer, 1992; Dodenhoff *et al*., 1998; Kaps *et al*., 1999; Bradfield *et al*., 2000)
	Charolais	0.13 – 0.30	(Orenge *et al*., 2009; Kachman *et al*., 2013; Herrera-Ojeda *et al*., 2019)
	Hereford	0.13 – 0.66	(Koch, 1972; Meyer, 1992; Bullock *et al*., 1993; Orenge *et al*., 2009)
Yearling Weight (kg)	Angus	0.27 – 0.56	(Baker *et al*., 1991; Meyer, 1992; Kachman *et al*., 2013)
	Charolais	0.28 – 0.29	(Kachman *et al*., 2013; Herrera-Ojeda *et al*., 2019)
	Hereford	0.16 – 0.36	(Bullock *et al*., 1993; Torres-Vázquez & Spangler, 2016)
18- month Weights (kg)	Angus	0.30 – 0.47	(Morris et al., 1992)
	Charolais	0.46	(Arthur *et al*., 2001)
	Hereford	0.30 – 0.47	(Morris *et al*., 1992)
Average Daily Gain (g)	Angus	0.28	(Bradfield *et al*., 2000)
	Charolais	0.25	(Orenge *et al*., 2009)
	Hereford	0.10	(Orenge *et al*., 2009)

Traits with low heritability respond less to selection compared to those with high heritability. Focusing on traits of little economic value or low heritability diminishes the opportunity for selecting traits of higher importance and heritability. To maximize genetic progress, selection efforts should prioritize traits with the greatest economic value (Gregory *et al*., 1961; Scholtz, 2010). The reliability of a heritability estimate depends on its sampling error, which is determined by the sample size and pedigree structure of the data and bias through selection. Therefore, sample size and missing parentage information can be a limitation for the estimation of genetic parameters (Shaw, 1991; Cowley & Atchley, 1992; Visscher *et al*., 2008).

Linear Mixed Models (LMM) have been in use since the 1950s as they are used to account for the genetic and environmental effects in breeding data (Rohmer *et al*., 2022). The development of mixed model methodology arose from the need to compare animals across different farms, herds, years, seasons, and generations. This approach allows animals to be ranked by genetic merit, eliminating the "environmental variability" that previously hindered accurate ranking (Loubser *et al*., 2007). Analysis of LMM equations is required for the estimation of variance components and subsequently breeding values if the variance components are estimated correctly (Rameez *et al*., 2022; Rohmer *et al*., 2022).

There are several methods available to determine variance components, a modified ML method known as the Restricted Maximum Likelihood (REML) method is one of the most widely used methods as it provides unbiased estimations and accounts for the loss of degrees of freedom due to fixed effects (Patterson & Thompson, 1971; Meyer *et al*., 1991; Searle, 1994; Laporte *et al*., 2022; Rameez *et al*., 2022; Rohmer *et al*., 2022). Large sample theory forms the basis of this approach, assuming that the parameter estimates are asymptotically multivariate normally distributed, with the covariance matrix being the inverse of the information matrix (Rameez *et al*., 2022; Rohmer *et al*., 2022). In table 2.7 software packages are summarised which provide solutions in Mixed Model Equations (MME) and estimate variance components by using REML methodology (Misztal, 1994; Hofer, 1998; Groeneveld, 2010; Madsen & Jensen, 2014).

As early as 1943 Hazel and Lush developed the theory for the development of selection indexes (Hazel, 1943; Scholtz, 2010). Hazel estimated genetic correlations and used them in multi-trait selection indices while Lush in 1947 investigated the most appropriate way to assign weights for individual and sibling records for traits in an index (Hill, 2014; Weigel *et al*., 2017). Pleiotropy, where a single gene influences multiple traits, is a key factor behind genetic correlations. Understanding these correlations is of paramount importance for developing effective selection indexes. When traits have a positive genetic correlation, increasing one trait through selection is likely to lead to simultaneous increase in the correlated trait, which can be positive or negative. Conversely, negative genetic correlations necessitate careful consideration in selection programs to prevent unintended regressions in other important traits. Like heritability, genetic correlations are specific to the population, making their inclusion in selection indexes essential for accurate and balanced genetic progress (Wang *et al.*, 2010; Preston & Willis, 2013).

Table 2.7 Software packages for variance component estimation

Software package	Free to use?	Main functions	Limitations
Average information Sparse Restricted Maximum Likelihood (ASREML)	No	Fits linear mixed models using advanced REML techniques for complex data sets	Requires specific syntax for model specification which can be difficult to learn and use
Derivative- Free REML (DFREML)	Yes	Hypothesis testing and likelihood ratio testing for significance of variance component estimates	Less efficient than algorithms which used derivatives and potentially less accurate estimates, no longer supported, or updated since 2005
Multiple Trait DFREML (MTDFREML)	Yes	User friendly general analyses of experimental data	Less efficient than algorithms which used derivatives and potentially less accurate estimates. Also, can be limited if not complete/unknown pedigrees are present
Parameter Estimation (PEST)	No	Straightforward calculations resulting in unbiased estimators; PEST estimators are minimum variance quadratic unbiased. Works well in conjunction with VCE	It may require large data sets to produce reliable estimates; can become complex when dealing with multiple traits
Variance Component Estimation (VCE)	No	Efficient in solving large-scale problems	It can be a computational demanding program when dealing with very large data sets
DMU	Yes	General package, efficient for both small and large data sets	Accurate estimation requires high-quality data without missing values

2.1.5 Genetic evaluations

2.1.5.1 Estimated breeding values

Traditional parameter estimation methods, such as analysis of variance or regression, fail with unbalanced data or intricate pedigrees. The animal model allows the phenotype of each animal to be defined in terms of various effects as well as incorporating variance and covariances of those effects. The basic animal model is shown by,

$$\mathrm{y} = \mathrm{Xb} + \mathrm{Za} + \mathrm{e}$$

Where **y** is the vector number of observations and **X** is the design matrix related to fixed effects records, **b** is a fixed effects vector, **a** is a random effects vector, **Z** is a design matrix relating appropriate random effects to each individual and **e** is equal to the random error vector.

The model is adjustable and allows for multiple traits, and covariance factors such as the common environment for full siblings, recurring events as well as maternal effects. The next major development was by Henderson in 1950 with the development of Best Linear Unbiased Prediction (BLUP). BLUP has significantly advanced genetic evaluation in cattle breeding by integrating both fixed environmental and random genetic effects into a mixed model. Initially sire models were applied in 1972 at Cornell University, BLUP enabled accurate ranking of sires by genetic merit without environmental variability (Gilbert, 2008; Weigel *et al*., 2017). However, the sire model couldn't fully address biases from non-random mating, leading to the integration of the animal model in 1989 (Weigel *et al*., 2017). This model, based on the infinitesimal model, allowed the simultaneous prediction of breeding values for multiple traits by combining performance data, progeny testing, pedigrees, maternal effects, heritability, inbreeding, and index information. While Henderson's selection index techniques, Best Prediction (BP) or Best Linear Prediction (BLP), addressed some issues, these models remained influenced by genetic trends, assortative breeding, and culling practices. Performance testing, preferred by farmers for its simplicity and early selection benefits, had limitations, including inaccuracy for low heritability traits and non-genetic phenotypic differences (Hunlun, 1988). BLUP overcomes these limitations by using a numerator relationship matrix, which incorporates information from all relatives (males and females) and handles various data sources simultaneously. This results in accurate EBVs, genetic trend analysis, and accommodation of non-random mating and selection bias (Kinghorn *et al*., 2015).

Proper parentage recording and well-defined Contemporary Groups (CG), consisting of uniformly managed animals, are essential for accurate genetic evaluations and stud breeding (Hunlun *et al*., 2007; Bergh, 2010; Klápště *et al*., 2019). CGs are foundational to BLUP evaluations, defined as animals managed uniformly within the same sex, herd, year, and season (Larry *et al.,* 2007; Boligon *et al.,* 2009; Osorio-Avalos *et.al.,* 2015). The accuracy of CGs comparisons depends on the number of animals included. An animal's genetic merit is calculated as breeding values relative to the average of its group mates (Henderson, 1975b; Bourdon, 2000). Smaller group sizes lead to less precise estimates of breeding values (Legarra *et al*., 2005; Santana Jr *et al*., 2013). To ensure reliable genetic evaluations, CGs should ideally contain at least five animals, with a minimum of three (Tosh & Wilton, 1994). The concept of genetic linkages, crucial for benchmarking genetic merits across different herds, seasons, and management groups, emerged with BLUP technology. Genetic connectedness between CGs is very important to increase the accuracy of EBVs (Kennedy & Trus, 1993; Larry *et.al*., 2007). Progeny of at least two sires needs to be present in each CG to increase genetic linkage. The better the linkage between groups the higher the accuracy of their EBVs. Connectedness is especially important for traits that are lowly heritable as these also generally have lower accuracies (Osorio-Avalos *et al*., 2015). BLUP remains the most accurate method for predicting an animal's breeding value, enhancing genetic progress and selection response in breeding programs (Gowane *et al*., 2022). BLUP offers several advantages, such as simultaneous adjustment for environmental effects, it encompasses the entire breed or all performance-recorded animals for effective population size and providing accurate breeding value estimations for broader genetic comparisons and selection (Scholtz, 2010). Assigning correct parentage is crucial for genetic evaluations as it influences breeding value accuracy. The more performance-tested relatives included in the BLUP analysis, the more accurate the breeding value predictions (Bergh, 2010; Scholtz, 2010; Klápště *et al*., 2019). It can also be useful for sex-limited traits and those like carcass merit which cannot be directly measured in all breeding animals, often requiring selection decisions before knowing each animal's performance for every trait. Therefore, using information about the performance of relatives can enhance genetic progress in a breeding program (Hazel, 1943; Klápště *et al*., 2019).

Advances in computer technology and the drive to accurately identify genetically superior animals have led to the inclusion of more complex models in animal breeding, incorporating factors previously overlooked (Neser *et al*., 1998; Nayeri *et al.*, 2019). For example, weaning weight is affected by various random factors related to the dam, and interactions can be significant when analysed across herds. The importance is documented through literature by Koch (1972) who found that maternally related variance accounts for 29% to 38% of the gain from birth to weaning (Koch, 1972). Meyer (1992) and Meyer *et al.* (1993, 1994) highlighted the importance of including permanent maternal environment in weaning weight analysis for Australian beef cattle. The use of Artificial insemination (AI) across herds means some sires may have offspring in all these environments. If there is a herd-year-season by sire interaction (HYSxS), it affects the accuracy of genetic parameter estimates and breeding values (Neser *et al*., 1998). Correctly quantifying interactions is crucial. A sire x herd interaction assumes that all progeny of a sire in the herd share the same environmental covariance regardless of time. A year-season x sire interaction assumes the same environmental covariance for all progeny of a sire at a certain time, regardless of place or management. In contrast, a herd-year-season x sire interaction implies that progeny of a sire in a specific herd-year-season are environmentally correlated, but records from different herd-year-seasons in the same herd are not (Meyer, 1987; Neser *et al*., 1998). Accurate prediction of breeding values requires knowledge of the (co)variances of random effects in a model. Incorrect (co)variance components can bias breeding values, especially in multiple trait analyses of growth traits, where records may erode over time due to selection and culling, leading to incorrect assessments of genetic selection effectiveness (Neser *et al*., 2012).

2.1.5.2. Genomically enhanced breeding values

Over the past 25 years, numerous Quantitative Trait Loci (QTL) have been identified using genetic markers, facilitating Marker-Assisted Selection (MAS). Despite its effectiveness for simple traits, MAS often underperforms for complex traits due to the limited and overestimated genetic variance explained by few QTL and low marker-QTL linkage disequilibrium (Snehi *et al.*, 2024). Various genomic evaluation methods treat marker effects as random variables with prior statistical distributions. These models either explicitly incorporate marker effects or describe genomic breeding values using marker-based covariance structures (Boichard *et al*., 2016). High-density mapping through Single Nucleotide Polymorphism (SNP) arrays has transformed the estimation of genetic variances and breeding values (Hill, 2010; Chang *et al.*, 2018). The development of genetic markers mitigated some limitations for variance component estimation as genetic markers can infer relatedness between animals as individuals from the same family will share more marker alleles, this can then be correlated to their phenotypic information and genetic parameters can then be calculated for these animals (Visscher *et al*., 2008). The inclusion of genotypic data enables the calculation of GEBVs, surpassing the accuracy of traditional EBVs by precisely assessing shared genes among siblings, excluding environmental and maternal influences (Calus, 2010; Koivula *et al*., 2012; Meuwissen *et al*., 2016; Weigel *et al*., 2017). Initially, SNP data was integrated into BLUP models as a random effect (SNP BLUP, BayesB), but it can also be utilized in Genomic BLUP (GBLUP), where the Genomic Relationship Matrix (GRM) replaces the standard pedigree matrix, assuming uniform SNP contributions to additive genetic variance (Koivula *et al*., 2012; van Marle-Köster *et al*., 2013; Meuwissen *et al*., 2016; Boichard *et al*., 2016; Misztal & Legarra, 2017). Despite disregarding the true genetic determinism, GBLUP is highly efficient for polygenic traits (VanRaden, 2008). In populations with limited genotyped but phenotyped animals, Single-Step BLUP (ssBLUP) combines a Numerator Relationship Matrix (NRM) with the GRM (Legarra *et al*., 2014; Weigel *et al*., 2017).

Bayesian regression models, as seen in Table 2.8 (adapted from Hayes & Goddard, 2010), are also commonly used for genomic prediction (Bayes A, Bayes B, etc. These models tend to be better than GBLUP if a QTL with large effects is present whereas GBLUP is better when the inheritance pattern of the gene is similar to that of the infinitesimal model (Weigel *et al*., 2017).

Table 2.8 Summary of underlying principles for SNP-based approaches to genomic EBV estimations

Name	Distribution of SNP effects	The best scenario for use	Reference
GBLUP	Normal	Utilizes genomic relationships to predict breeding values	(Van Raden, 2008)
ssBLUP	Normal	Integrates pedigree and genomic information for more accurate predictions	(Legarra *et al*., 2009)
BayesA	*t* distribution	Many QTL with small effect and a small proportion with moderate to large effect	Meuwissen *et al*., 2001)
BayesB	Combined zero effects and *t*-distribution effects	Many genome regions with no effect and a small proportion of QTL with moderate effects	Meuwissen *et al*., 2001)

The accuracy of GEBVs relies on the parameters used within the model as well as the statistical model used when estimating (Calus, 2010; Berry *et al*., 2016). The accuracy also relies on consistent Linkage Disequilibrium (LD) between the marker and QTL loci between the individual's whose GEBV are being estimated and the reference population (relationship between the animal and those found in the reference population), as well as accurate estimation of marker effects (Goddard, 2009). As the LD between the marker and QTL is dependent on the marker density, accuracy can be increased by increasing the number of SNP markers used. Accuracy can also be increased by including a larger number of animals in the reference population (Meuwissen *et al*., 2001), increasing sampling within family structures (Legarra *et al*., 2009), and increasing the heritability of the trait (Calus *et al*., 2008; Solberg *et al*., 2008). In simulation studies, it was seen that the accuracy of GEBVs will decrease at a slower rate when random mating is observed (Meuwissen *et al*., 2001; Solberg *et al*., 2008), and at a faster rate when selection is applied (Calus, 2010). The disassociation of LD with markers due to recombination will lower the accuracy of GEBV prediction over generations and determines the duration between re-estimation of SNP effects (Calus, 2010).

Implications of genomic selection in beef cattle

Within-breed selection is the primary target for contemporary applications of genomic markers in genomic prediction. This approach aims to enhance the precision of EBVs for selection candidates before puberty. Additionally, genomic prediction allows the generation of novel EBVs for traits relevant to breeding objectives but not captured by traditional performance recording methods. Other applications of genomic analyses include parentage verification, genetic disease identification, selection signature detection, breed composition prediction in crossbred animals, and QTL mapping (Garrick, 2011).

In the past the limited recording of performance traits by beef cattle farmers posed a challenge in the implementation of genomic selection. Especially the recording of traits related to fertility, longevity, and carcass quality, which are traits that could benefit the most due to their low heritability (van Marle-Köster *et al*., 2013). In comparison with dairy cattle, there is less AI used in beef cattle herds which decreases the genetic linkage between herds as well as decreases the number of animals with accurate EBVs. There is also a challenge of the large number of beef breeds in South Africa compared to fewer dairy breeds which complicates the creation of a suitable training population (van Marle-Köster *et al.*, 2013). Training populations for genomic prediction rely on statistical methods that leverage individuals with both comprehensive genotypic data (high density genotypes) and their corresponding phenotypic records. The volume of data necessary for training is influenced by several factors, most notably the heritability of the target trait. One strategy for training involves employing sires whose genetic merit can be more accurately estimated through the performance of their progeny, compared to solely relying on the measurements of the sire itself (Garrick, 2011).

As the latest method of single-step BLUP (ssBLUP) became more popular many of these issues have been solved. ssBLUP improves upon GBLUP by addressing the limitations of the latter's exclusive reliance on genotyped individuals (Stolpovsky *et al.*, 2020). GBLUP only uses genomic data, which can limit its accuracy when the reference population is small or when not all animals are genotyped. ssBLUP, on the other hand, combines genomic data, traditional pedigree information, and phenotypic data, allowing it to account for both genotyped and non-genotyped animals simultaneously, which eliminates the need for separate analyses for genotyped and non-genotyped animals (Stolpovsky *et al.*, 2020; McGowan *et al.*, 2021). This hybrid approach increases the accuracy of breeding value estimates by making full use of all available data, which is especially important for small populations or rare breeds. ssBLUP also offers improved computational efficiency over methods that require multiple steps, as it integrates all information into a single analysis. Furthermore, ssBLUP can deal more effectively with traits that have low heritability, where the limited genetic information available from genotyped animals alone may not provide sufficient predictive power (Stolpovsky *et al.*, 2020).

2.1.6. Conclusion

This review emphasized the importance of accurate (co)variance component estimations for effective genetic evaluations in SA Angus, Hereford, and Charolais beef cattle breeds. By incorporating these components, EBVs become more reliable, enabling breeders to make informed selection decisions. Future research avenues could explore the impact of breed-specific selection practices on covariance components and investigate the potential for incorporating additional traits into genetic evaluations for these breeds, as well as breed type specific genotyping for more accurate GEBVs. Ultimately, continued refinement of methodology for genetic parameter estimations and evaluations will be instrumental in propelling genetic improvement programs for these commercially significant beef cattle breeds.

Chapter 3: Materials and Methods

3.1 Introduction

Direct and maternal heritability, correlation and error variances were estimated for birth weight, weaning weight, yearling weight and 18-month weights for the South African Angus, Charolais and Hereford cattle breeds. Only direct heritability, correlation and error variances were estimated for the post-wean growth test traits, average daily gain, hip height, body length and scrotal circumference. The (co)variance components were estimated for all three breeds followed by the heritability and correlation estimates. Estimated breeding values and genetic trends were estimated for the Angus breed only. Permission was received from the Angus, Charolais and Hereford South African stud breeder societies respectively for the access and use of their data on the SA Stud Book Logix database. This project received ethical clearance from the Natural and Agricultural Sciences (NAS) department of the University of Pretoria with ethics number: NAS125/2023.

3.2 Materials

The data was accessed on the SA Stud Book Logix system for all three breeds. Data received consisted of a pedigree file, files containing information for the birth weight, weaning weight, yearling weight and 18-month weights as well as a file containing growth test information such as Average Daily Gain (ADG), shoulder height, hip height, body length and scrotal circumference. Tables 3.1a, b and c show the unedited data structure of traits under study. All files were received in excel csv format. As seen in the unedited data tables the total number of records varied between the three breeds for all traits under investigation.

Table 3.1a Number of records for the SA Angus (unedited data files)

Trait	Number of records	Min	1st Quarter	Median	Mean	3rd Quarter	Max
Birth weight (kg)	179 001	4	32	34	34.63	38	95
Dam age (months)	244 694	9	39	60	67.36	87	1248
Weaning weight (kg)	128 960	60	200	230	229.9	260	478
Weaning age (days)	128 960	59	193	213	211.7	232	481
Yearling weight (kg)	52 715	70	250	300	308.7	356	768
Yearling age (days)	53 109	251	349	373	372.8	398	610
18-month weight (kg)	31 183	160	350	409	424.1	485	900
18-month age (days)	31 183	370	525	553	552.7	582	794
ADG (g/day)	16 929	170	955	1254	1311.0	1667	3119
Shoulder height (cm)	8 535	116	1170	1210	1205.0	1240	1550
Hip height (cm)	7 350	1000	1200	1240	1238.0	1270	1480
Body length (cm)	15 864	132	1350	1400	1401.0	1450	1970
Scrotal circumference (cm)	16 522	200	335	355	354.6	375	505

Table 3.1b Number of records for the SA Charolais (unedited data files)

Trait	Number of records	Min	1st Quarter	Median	Mean	3rd Quarter	Max
Birth weight (kg)	60 418	14	37	40	40.64	44	80
Dam age (months)	84 928	11	45	65	71.93	95	716
Weaning weight (kg)	42 074	55	207	237	237.4	267	508
Weaning age (days)	42 074	60	193	214	212.6	233	477
Yearling weight (kg)	26 830	70	250	300	308.7	356	768
Yearling age (days)	26 910	251	349	373	372.8	398	610
18-month weight (kg)	16 697	150	357	410	426.2	481	885
18-month age (days)	16 697	432	516	546	546.2	578	679
ADG (g/day)	3 555	330	1188	1503	1505	1821	3052
Shoulder height (cm)	2 659	123	1180	1220	1217	1250	1420
Hip height (cm)	774	1100	1265	1264	1300	1430	2798
Body length (cm)	3 425	145	1380	1430	1430	1480	1720
Scrotal circumference (cm)	3 533	200	315	335	335.3	355	480

Table 3.1c Number of records for the SA Hereford (unedited data files)

Trait	Number of records	Min	1st Quarter	Median	Mean	3rd Quarter	Max
Birth weight (kg)	83 420	1	34	36	36.19	39	68
Dam age (months)	155 453	12	39	59	63.78	83	396
Weaning weight (kg)	64 133	26	180	210	211.3	240	485
Weaning age (days)	64 133	63	193	213	212.5	233	366
Yearling weight (kg)	30 573	89	240	285	294.4	340	690
Yearling age (days)	30 696	255	346	373	371.5	400	470
18-month weight (kg)	21 222	110	319	378	395.6	461	898
18-month age (days)	21 222	431	523	550	549.8	579	689
ADG (g/day)	8 631	-135	1087	1345	1345	1607	2761
Shoulder height (cm)	4 692	112	1140	1190	1187	1240	1580
Hip height (cm)	3 277	1050	1200	1230	1231	1260	1400
Body length (cm)	8 096	140	1350	1400	1395	1450	1760
Scrotal circumference (cm)	6 796	200	325	340	341.4	360	441

3.3 Methodology

3.3.1. Data editing and file preparation

The same methods were applied for all three breeds. The datasets were imported into the statistical R Studio software program, using the readxl package (RStudio Team, 2020) for data editing, manipulation, and statistical analysis using the inherent R Stats Package. Before editing and cleaning of the imported files, simple statistics on both datasets were done including calculating the minimum, 1st quartile, median, mean, 3rd quartile, maximum and Standard Deviation (SD). Shoulder height measurements were removed because hip height is more widely measured and accepted. The data underwent extensive editing and cleaning to eliminate errors from multiple sources, ensuring accuracy and reliability while preventing erroneous analyses. Data editing consisted of removing duplicate animals, animals born before their dam and whose dam was younger than 15 months old, removing all animals that are not Studbook Proper (SP), removing all embryo calves and only keeping animals that were raised as a single calf who suckled on their own mother. Using the accepted production norms which are applied in the Logix National Genetic Evaluation, the biological limits were assessed for implementation in editing of the data for this study's genetic evaluation and the confidence intervals (at a 95% level) were determined. The standard deviation was then used to determine realistic biological limits on the data. Table 3.2 shows the biological intervals that were followed for weight traits and ages when editing, therefore all animals outside of those intervals were removed.

Table 3.2 Weight ranges and associated ages for the Angus, Charolais and Hereford data used in the study

Trait	Number of SD	Angus	Charolais	Hereford
Birth weight (kg)	4	15 - 54	17 - 64	16 - 57
Weaning weight (kg)	3	94 - 366	100 - 375	74 - 348
Weaning age (days)	3	151 – 270	151 - 270	151 - 270
Yearling weight (kg)	3	72 - 545	94 - 548	66 – 523
Yearling age (days)	3	271 - 450	271 - 450	271 – 450
18-month weight (kg)	3	116 - 733	127 - 725	187 – 604
18-month age (days)	3	451 - 634	451 - 634	451 – 634

Table 3.3 shows the accepted intervals for growth traits as calculated, and animals were removed outside these limits; growth traits biological limits ranges were all three SD wide.

Table 3.3 Ranges for growth traits for the Angus, Charolais and Hereford animals in the study

Trait	Angus	Charolais	Hereford
ADG (g/day)	398 – 2224	217 – 2792	186 – 2505
Hip Height (cm)	1078 – 1398	1120 – 1409	1080 – 1636
Body length (cm)	1152 – 1650	1188 – 1671	1154 - 1636
Scrotum circumference (cm)	263 - 446	242 - 2792	259 - 423

Animals were also removed which did not complete either a C12 (84 d central standardised test at ARC), C22 (84 d central standardised test private), D11 (270 d on farm single owner test) or a D21 (270 d on farm multiple owner test) growth test. Simple statistics on both clean datasets were then determined including calculating the minimum, 1st quartile, median, mean, 3rd quartile, maximum, standard deviation. This aided in comparing the unedited data with the edited, clean data statistics. The spread of the datasets was also assessed with the aid of distribution graphs, such as histogram plots and kurtosis values with standard error. Kurtosis, skewness and standard errors were calculated using the moments package in R. These representations can be found in the results for the Angus, and in Addendum A for the Charolais and Hereford respectively. Kurtosis values were calculated in order to assess the distribution of the data.

3.3.2. Analysis of Variance (ANOVA)

Environmental effects that significantly influence the traits of interest were determined in order to construct contemporary groups and to allow for adjustment for these factors in the model when estimating the variance components of the traits. This was done by ANOVA, using R (RStudio Team, 2020). ANOVA type 2 test was used to test which factors significantly influenced the traits of interest at a significance level of 0.05. The following model equation was used:

$$\mathrm{y} = \text{intercept} + \text{significant fixed effects} + \text{significant covariate functions} + \text{error}$$

Where: y = observation for trait under analysis; Fixed effects = categorical effects such as sex and herd; Covariate functions = continuous traits such as age at weighing treated as a regression factor

ANOVA tests were conducted on all traits to assess the effect of different seasonal groupings on environmental variance. Seasons were defined based on the distribution of births per month across all years (Figure 3.1a-c), with a clear breeding season evident for each breed. The months with the highest birth frequencies were grouped as season one, while consecutive lower-frequency months formed season two, optimizing the model's ability to capture environmental variance associated with seasonality.

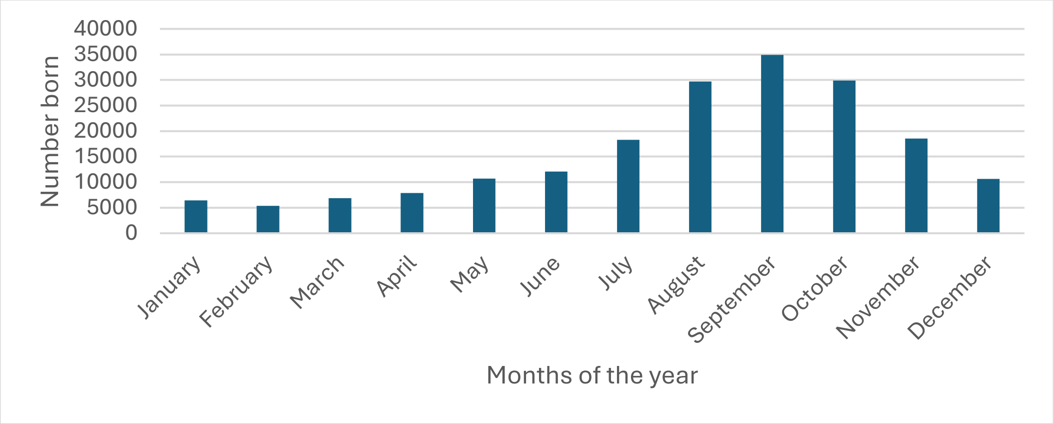


Figure 3.1a Distribution of births per month of the year for the Angus population

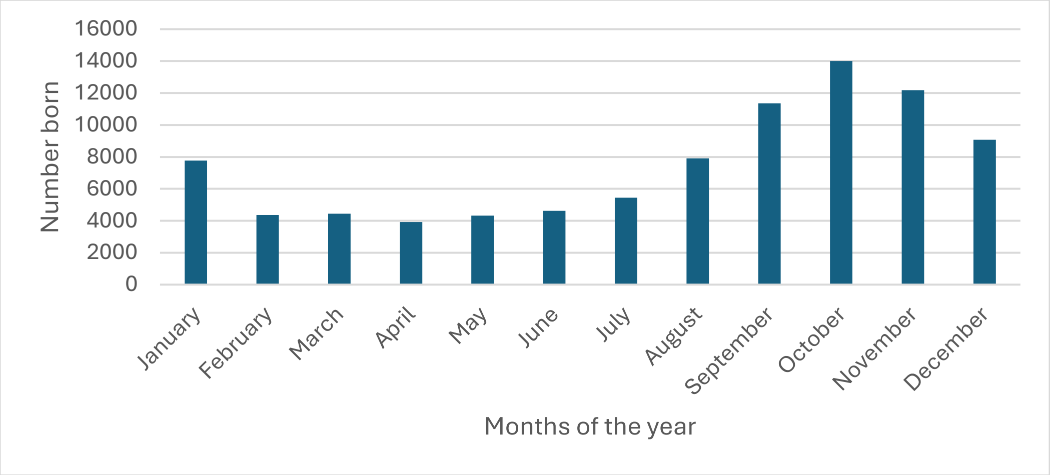


Figure 3.1b Distribution of births per month of the year for the Charolais population

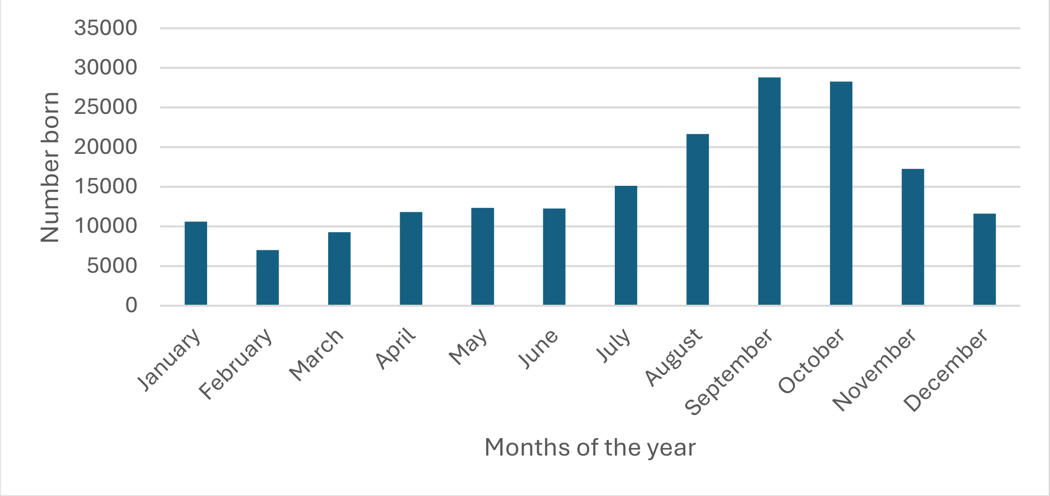


Figure 3.1c Distribution of births per month of the year for the Hereford population

The size of the pedigree files for all three breeds were too large for computational ease so two data sets were created. The first data set had the records from the year 2012 to 2022, the last 10 complete years as animals born in 2023 would not have sufficient records available yet. The second data set was created with the last 20 years data (2002-2022) to include more generations to determine if it would result in better estimates. In order to evaluate all traits in the ANOVA, quadratic ages treated as a regression factor was added for all traits as well as quadratic dam ages to be tested for significance in the ANOVAs. When creating the dataset, only weaning weight was set as a compulsory trait as making all the weight traits compulsory resulted in too few animals remaining to result in reliable estimates.

Formation for the contemporary groups was as follows: for birth weight a Herd x year x season (HYS) contemporary group was created. For the other weight traits weaning weight to 18-month weights, contemporary groups were formed according to their participant number x beef test code x feeding status for each weight trait group. Feeding status referred to whether they received creep feed or any further supplemental feed they received. For the post-wean growth traits one contemporary group was formed called PTC which consists of the participant number x test code for their growth test.

Final editing in R Studio, using the dyplr package, (RStudio Team, 2020) consisted of simultaneously removing contemporary groups if they contained less than five animals for all groups (HYS, Wean CG, Year CG, 18-m CG, PTC), contained less than two unique sires in each group and groups whose sire was not present in at least two other contemporary groups to establish genetic linkage across groups.

All model effects were tested as categorical and continuous in the ANOVA to determine which was the most significant. All linear and quadratic ages were kept as a continuous effect measured in days, fixed effects were included as categorical effects such as sex and contemporary groups. ANOVAs were run and adjusted until the highest adjusted R-squared value was obtained with biologically relevant effects.

3.3.3. Estimating variance components

Variance components were estimated using multi-trait animal models that included the environmental effects that significantly influenced the data traits as fixed or continuous effects, as well as random permanent environmental and sire x herd effects, depending on the trait. With regards to the genetic effects, a direct as well as maternal genetic effect were included. A pedigree depth of three generations was used. These variance components were estimated using the VCE6 package based on REML methodology (Groeneveld, 2010). Restricted Maximum Likelihood (REML) has become the main method of variance component estimation in animal breeding.

The final animal model applied was as follows:

$$Y_{ijklmnop} = \mu + cg_i + sex_j + Age_k + \text{Age\_of\_dam}_l + PE_m + Sire\ x\ herd_n + mat_o + animal_p + e_{ijklmnop}$$

Where:

$Y_{ijklmnop}$ is the observation of the trait under investigation of the pth animal,

μ is the mean of the observations of the trait under investigation,

cg_i is the contemporary group (i),

Sex_j is the sex j of animal p,

Age_k is the age of animal p,

Age of dam_l is the linear and quadratic regressions on age of dam of animal p,

PE_m is the random permanent environmental effect m associated with the dam of animal p,

Sire x $herd_n$ = sire x herd effect on animal p

mat_o is the random maternal additive genetic effect of dam o of animal p,

$animal_p$ is the random direct additive genetic effect of animal p, and $e_{ijklmnop}$ = random residual effect

The process of estimating variance components began with creating a parameter file in Notepad, compatible with PEST (Groeneveld & Kovac, 1990) on a Linux system, to recode pre- and post-weaning growth trait files for VCE6. A three-generation pedigree file was also created based on the edited data. Using the recoded files from PEST, a new VCE6 parameter file was prepared, incorporating birth-to-18-month weight models with significant ANOVA effects, as well as maternal and permanent environmental (PE) effects. Weaning weight was included as an anchor trait for post-weaning growth test traits such as ADG etc.. VCE6 (Groeneveld, 2010) was then used to estimate heritability and correlations for each trait, starting with single-trait evaluations. Several model adjustments were made, including the removal of Sire by Herd (SXH) and PE effects when they were not significant. The significance of these effects was evaluated using standard error parameters, and models were refined to achieve more reliable estimates. A log-likelihood ratio test was conducted using AG log-likelihoods from VCE6 (Groeneveld, 2010) to compare model fits. This test helped assess model significance and select the best model for genetic evaluation, an essential step for accurate estimation in livestock breeding programs. Once the optimal models were determined, multi-trait models were run to finalize heritability, and correlation estimates for all traits under investigation. The dataset containing 10 years of data proved insufficient, so the more robust 20-year dataset was used for further analysis and estimation of breeding values, resulting in improved data structure and more accurate estimates.

3.3.4. Estimated breeding values

Estimated breeding values were determined for birth weight, weaning weight, yearling weight and 18-month weight for the SA Angus breed using the 20-year data set estimates. They were estimated using BLUP methodology in the PEST2 version 0.2.5 program (Groeneveld & Kovac., 1990). The variance component file was recoded in VCE 6.0.2 package (Groeneveld, 2010). The recoded matrices were used to create a new PEST2 parameter file with the data file, which contains all animals with production records for breeding value estimation. The only edits done to the data file was the removal of extreme outliers as well as ensuring contemporary groups had at least 3 animals per group. A new pedigree file was also created on this larger dataset. This new input file with its parameter file results in breeding value estimates. A new output file was created containing breeding values as well as animal information and performance data. A genetic trend of the average estimated breeding values over the years was estimated and graphed using a base year of 2000.

Chapter 4: Results

4.1. Descriptive statistics

In Figures 4.1a to h show the frequency distribution plots for the traits under investigation in this study for the SA Angus.

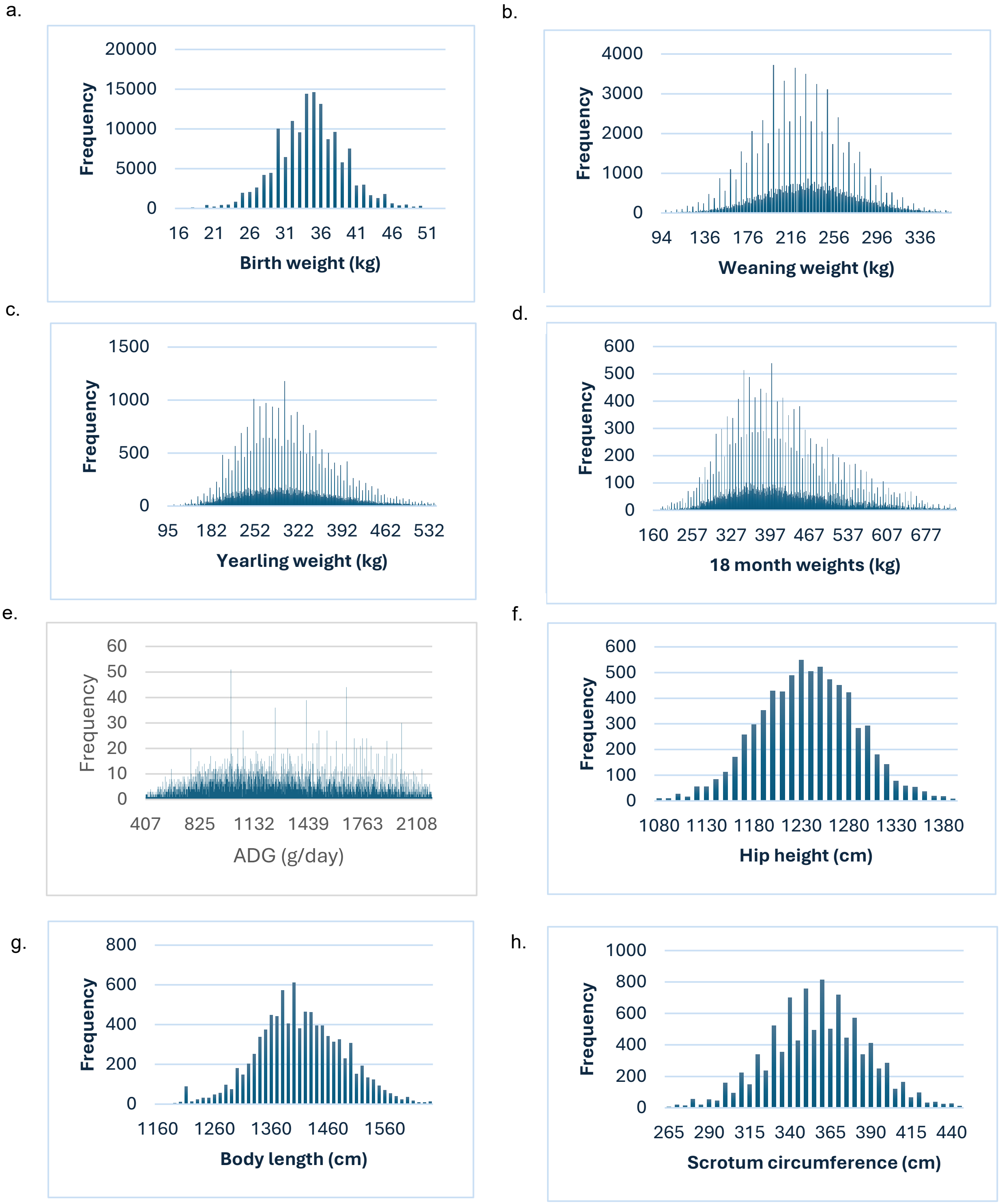


Figure 4.1 Histogram distribution plots of (a) birth weight, (b) weaning weight, (c) yearling weight, (d) 18- month weights, (e) average daily gain, (f) hip height, (g) body length, (h) scrotal circumference for the Angus cattle breed.

Distributions for the SA Charolais and SA Hereford can be found in addendum A. To further assess trait distributions, Table 4.1 presents the kurtosis and skewness values, along with their standard errors, for each trait across the three breeds. A kurtosis value near 3 indicates a normal distribution, while a skewness of zero suggests symmetry. For Angus, traits such as birth weight, ADG, and body length exhibit the least symmetry, as shown in Figure 4.1, where these traits display wider distributions and greater variability with more outliers.

Table 4.1 Kurtosis and skewness with their standard errors for distribution plots of all three breeds

	Breed					
	Angus		**Charolais**		**Hereford**	
Trait	**Kurtosis**	**Skewness**	**Kurtosis**	**Skewness**	**Kurtosis**	**Skewness**
Birth weight	3.84 ± 0.13	0.18 ± 0.07	4.82 ± 0.17	0.68 ± 0.09	3.45 ± 0.21	0.18 ± 0.11
Weaning weight	2.94 ± 0.13	0.03 ± 0.07	3.03 ± 0.17	0.18 ± 0.09	2.89 ± 0.21	0.32 ± 0.11
Yearling weight	2.68 ± 0.13	0.31 ± 0.07	3.28 ± 0.17	0.52 ± 0.09	2.52 ± 0.21	0.17 ± 0.11
18-month weight	3.52 ± 0.13	0.62 ± 0.07	3.21 ± 0.17	0.79 ± 0.09	2.59 ± 0.21	0.01 ± 0.11
Average daily gain	2.17 ± 0.11	0.18 ± 0.05	2.83 ± 0.42	0.42 ± 0.21	2.63 ± 0.15	0.24 ± 0.08
Hip height	2.75 ± 0.11	-0.14 ± 0.05	2.54 ± 0.42	0.002 ± 0.21	3.34 ± 0.15	0.09 ± 0.08
Body length	2.53 ± 0.11	0.15 ± 0.05	2.32 ± 0.42	0.06 ± 0.21	3.32 ± 0.15	0.09 ± 0.08
Scrotal circumference	2.75 ± 0.11	-0.06 ± 0.05	3.36 ± 0.42	-0.09 ± 0.21	2.85 ± 0.15	-0.09 ± 0.08

4.2. ANOVA analyses

Tables 4.2 and 4.3 represent the results of the ANOVA analyses completed for all three breeds for all traits under investigation. Most effects were significant across breeds and traits, except for Herd × Sire, Heifer effects, and the age of the animal and dam (and their quadratic terms), which were less commonly significant for weight traits. For the post-weaning growth traits the weaning contemporary group effects and heifer effects were the least significant across the traits with age and age quadratics for the animal and dam also in some cases not significant. The Adjusted R-squared metric represents how well the model explains the variance in the data, while the Residual Standard Error (RSE) quantifies the average deviation of observed values from the predicted values providing a measure of the model's accuracy (Wooditch *et al.*, 2021).

Table 4.2 Significant effects in ANOVA analysis for weight traits under investigation for all three breeds

Model Effects	Angus - Birth Weight	Charolais - Birth Weight	Hereford - Birth Weight	Angus - Weaning Weight	Charolais - Weaning Weight	Hereford - Weaning Weight	Angus - Yearling Weight	Charolais - Yearling Weight	Hereford - Yearling Weight	Angus - 18-Month Weight	Charolais - 18-Month Weight	Hereford - 18-Month Weight
CG*	X	X	X	X	X	X	X	X	X	X	X	X
Sire x Herd *				X	X		X			X		X
Sex	X	X	X	X	X	X	X	X	X	X	X	X
Age				X	X	X	X	X	X		X	X
Age^{2}*	X			X								
Dam Age	X	X	X	X	X	X	X		X	X		X
Dam Age^{2}*	X			X	X	X	X		X	X		X
Heifer effect*			X						X		X	X
Adjusted R^{2}	0.3543	0.4105	0.3027	0.6785	0.655	0.5932	0.8346	0.8153	0.8164	0.8309	0.8375	0.7793
Residual SE*	3.348	3.592	4.757	22.06	20.54	24.44	27.03	27.04	29.65	35.57	42.12	33.05

*CG is the Contemporary group, Sire x Herd is the effect of using a sire in different herds, Age^{2} is the quadratic effect of age on the trait, Dam age^{2} is the quadratic effect of dam age, Heifer effect is whether the dam is a first calver, Residual SE is the residual standard error of the model

Table 4.3 Significant effects in ANOVA analysis for growth traits in all three breeds

Model Effects	Angus - ADG	Charolais - ADG	Hereford - ADG	Angus - Hip Height	Charolais - Hip Height	Hereford - Hip Height	Angus - Body Length	Charolais - Body Length	Hereford - Body Length	Angus - Scrotal Circumference	Charolais - Scrotal Circumference	Hereford - Scrotal Circumference
CG*	X	X	X	X	X	X	X	X	X	X	X	X
Wean CG*				X			X					
Age	X	X	X	X	X	X	X	X	X	X	X	X
Age^2*	X						X			X		X
Dam Age		X	X	X	X	X	X	X	X	X		X
Dam Age^2*		X	X	X		X	X		X	X		X
Heifer effect*			X									
Adjusted R^2	0.7313	0.6832	0.7068	0.6176	0.5698	0.5718	0.6844	0.7369	0.5626	0.5396	0.4685	0.4239
Residual SE*	201.3	188.6	174	32.33	34.99	29.97	42.45	46.29	45.23	21.94	21.21	21.4

*CG is the Contemporary group, Wean CG is the weaning weight contemporary group, Age^2 is the quadratic effect of age on the trait, Dam age^2 is the quadratic effect of dam age, Heifer effect is whether the dam is a first calver, Residual SE is the residual standard error of the model

All model effects in the SA Angus analysis were highly significant ($p < 0.001$), with the exception of the herd x sire effect for weaning weight ($p < 0.01$) and the wean age effect ($p < 0.05$) for weaning weight, and the dam age effect ($p < 0.01$) for 18-month weight. In contrast, SA Charolais model effects demonstrated a slightly lower level of significance, with the dam age effect in the birth weight model ($p < 0.05$), the heifer effect in the weaning weight model ($p < 0.01$), and the heifer effect in the 18-month weight model ($p < 0.01$) being the only less significant effect compared with the other effects. SA Hereford models exhibited a similar pattern to SA Charolais, with the sex effect in the birth weight and weaning weight models ($p < 0.05$ and $p < 0.1$, respectively), the sex effect in the yearling weight model ($p < 0.01$), and the sire x herd effect, dam age linear, dam age quadratic, and animal age effects in the 18-month weight model (all $p < 0.01$) being the only less significant effect compared to the other effects in the model.

4.3 Final animal models for each trait

Pre-wean model equations for Angus

The final model equation for birth weight was:

$$\mathbf{Y_{ijklmn} = \mu + cg_i + sex_j + age\_of\_dam_k + PE_l + mat_m + animal_n + e_{ijklmn}}$$

Where:

Y_{ijklmn} = Birth weight of the nth animal

μ = mean weight

cg_i = contemporary group I (Herd x year x season)

sex_j = sex j of animal n

$age\_of\_dam_k$= linear and quadratic regressions on age of dam of animal n

PE_l= random permanent environmental effect m associated with the dam of animal n

mat_m = random maternal additive genetic effect of dam m of animal n

$animal_n$ = random direct additive genetic effect of animal n

and e_{ijklmn} = random residual effect

The final model for weaning weight was:

$$\mathbf{Y_{ijklmno} = \mu + cg_i + sex_j + age_k + age\_of\_dam_l + PE_m + mat_n + animal_o + e_{ijklmno}}$$

Where:

$Y_{ijklmno}$ = weaning weight of the oth animal

μ = mean weight

cg_i = contemporary group I (Participant x beef test code x feeding status)

sex_j = sex j of animal o

age_k = linear and quadratic regressions age k of animal o

$age\_of\_dam_l$ = linear and quadratic regressions on age of dam of animal o

PE_m = random permanent environmental effect m associated with the dam of animal o

mat_n = random maternal additive genetic effect of dam n of animal o

$animal_o$ = random direct additive genetic effect of animal o

and $e_{ijklmno}$ = random residual effect

Post-wean model equations for Angus

The final model for yearling weight was:

$$\mathbf{Y_{ijklmn} = \mu + cg_i + sex_j + age_k + PE_l + mat_m + animal_n + e_{ijklmn}}$$

Where:

Y_{ijklmn} = Yearling weight of the nth animal

μ = mean weight

cg_i = contemporary group I (Participant x beef test code x feeding status)

sex_j = sex j of animal n

age_k = linear and quadratic regressions age k of animal n

PE_l = random permanent environmental effect l associated with the dam of animal n

mat_m = random maternal additive genetic effect of dam m of animal n

$animal_n$ = random direct additive genetic effect of animal n

and e_{ijklmn} = random residual effect

The final model for 18-month weight was:

$$\mathbf{Y_{ijklmnop} = \mu + cg_i + sex_j + age_k + age\_of\_dam_l + sire\ x\ herd_m + PE_n + mat_o + animal_p + e_{ijklmnop}}$$

Where:

$Y_{ijklmnop}$ = 18-month weight of the pth animal

μ = mean weight

cg_i = contemporary group I (Participant x beef test code x feeding status)

sex_j = sex j of animal p

age_k = linear and quadratic regressions age k of animal p

$age\_of\_dam_l$ = linear and quadratic regressions on age of dam of animal p

sire x $herd_m$ = sire x herd effect on animal p

PE_n = random permanent environmental effect n associated with the dam of animal p

mat_o = random maternal additive genetic effect of dam o of animal p

$animal_p$ = random direct additive genetic effect of animal p

and $e_{ijklmnop}$ = random residual effect

The model equations for Charolais were identical to those of the Angus breed, except that the Permanent Environment (PE) effect was excluded for all traits. In contrast to the Angus, the Hereford models included PE across all traits. Additionally, neither Charolais nor Hereford models incorporated the sire-by-herd (SXH) interaction effect for any trait.

4.4 Log likelihood ratio test

Table 4.4 shows the log-likelihood ratio test results for the final models for all three breeds.

Table 4.4 Log likelihood ratio for multi-trait model for SA Angus, Charolais and Hereford breeds

Breed	Model	Log-likelihood (L)	Log-likelihood ratio (LLR)	Critical Value (0.05)	Conclusion
Angus	Null Model: Without PE Alternative Model: With PE	L_0=15299.9893 L_1=15311.3989	LLR = -2 * (15299.9893 - 15311.3989) = -2 * (-11.4096) = 22.8192	3.84	The LLR (22.8192) is greater than the critical value, so we reject the null hypothesis. The model including PE significantly improves the fit.
Charolais	Null Model: With all PE, no SXH Alternative model: Model with no sxh, no PE in weaning weight	L_0=90528.9077 L_1 = 48886.0157	LLR = -2* (90528.9077 - 48886.0157) = -2 * 41642.892 = 83285.784	3.84	The LLR (83285.784) is much greater than the critical value, so we reject the null hypothesis. The model including PE and excluding SXH improves fit.
Hereford	Null Model: With all PE Alternative Model: No SXH	L0=−∞ L_1=117834.7627	LLR=−∞	3.84	The null model log likelihood is -∞, leading to an LLR of -∞. This rejects the null hypothesis, indicating that the model without SXH is a better fit.

4.5 (Co)variance component estimations

Tables 4.5a to 4.5c present the data structures of the two different data sets (10 years vs 20 years of data). The main difference between the two data sets is increased number of animals and contemporary groups in the 20-year data set.

Table 4.5a Comparison of the number of measurements and contemporary groups (CGs) for each trait for the 10-year versus 20-year data set for the Angus breed

Trait	Number of animals 10 years	Number of animals 20 years	Number of CGs 10 years	Number of CGs 20 years
Birth weight	7 194	12 295	331	474
Weaning weight	7 224	12 295	440	605
Yearling weight	2 702	12 295	201	614
18-month weight	1565	9 433	146	357
Growth test traits*	1708	1926	94	112

*Growth test traits = ADG, hip height, body length and scrotal circumference

Table 4.5b Comparison of the number of measurements and CGs for each trait for the 10-year versus 20-year data set for the Charolais breed

Trait	Number of animals 10 years	Number of animals 20 years	Number of CGs 10 years	Number of CGs 20 years
Birth weight	5221	8 631	259	632
Weaning weight	5286	8 776	400	800
Yearling weight	3781	6 129	329	632
18-month weight	1397	3 400	138	344
Growth test traits*	71	71	11	11

Table 4.5c Comparison of the number of measurements and CGs for each trait for a 10-year versus 20-year data set for the Hereford breed

Trait	Number of animals 10 years	Number of animals 20 years	Number of CGs 10 years	Number of CGs 20 years
Birth weight	6465	12 720	262	677
Weaning weight	6583	13 376	397	854
Yearling weight	1360	4 134	113	357
18-month weight	1035	2 917	89	278
Growth test traits*	719	719	68	68

Pre-weaning single-trait models

Table 4.6 summarizes single-trait heritability, and correlation estimates between the direct and maternal heritability estimates for Angus birth weight across two data periods. In the 2012-2022 period, direct heritability was high at 0.49. For the 2002-2022 period, direct heritability decreased to 0.41. The Permanent Environmental (PE) effect, included in Model 1, provides additional variance explanation for birth weight.

Table 4.6 Single-trait heritability and correlation estimates with their associated standard errors for the Angus birth weight models

Data period	**Trait**	**Direct heritability**	**Maternal heritability**	**Correlation**	**Permanent environment (PE)**	**Residual**
2012-2022	Model 1	0.49 ± 0.04	0.11 ± 0.02	-0.54 ± 0.07	0.06 ± 0.01	0.58 ± 0.04
	Model 2	0.49 ± 0.04	0.16 ± 0.02	-0.45 ± 0.07		0.32 ± 0.04
2002 - 2022	Model 1	0.41 ± 0.04	0.07 ± 0.02	-0.51 ± 0.08	0.07 ± 0.02	0.62 ± 0.043
	Model 2	0.39 ± 0.04	0.11 ± 0.02	-0.39 ± 0.08		0.66 ± 0.04

Table 4.7 presents the single-trait heritability, and correlation estimates for Angus weaning weight models based on each of the two data periods. For 2012-2022, Model 2 showed a higher direct heritability of 0.26 (2012 – 2022) compared with the other dataset, Model 3 produced a moderate direct heritability of 0.19.

Table 4.7 Single-trait heritability and correlation estimates with their associated standard error for various Angus weaning weight models

Data period	**Trait**	**Direct heritability**	**Maternal heritability**	**Correlation**	**Permanent environmental (PE)**	**Sire by herd (SXH)**	**Residual**
2012 - 2022	Model 1	0.04 ± 0.03	0.05 ± 0.02	0.51 ± 0.58	0.15 ± 0.01	0.07 ± 0.98E-02	0.65 ± 0.02
	Model 2	0.26 ± 0.03	0.12 ± 0.02	-0.52 ± 0.09	0.17 ± 0.02		0.63 ± 0.03
	Model 3	0.25 ± 0.03	0.28 ± 0.02	-0.39 ± 0.09			0.68 ± 0.03
2002 - 2022	Model 1	0.02 ± 0.02	0.06 ± 0.02	0.30 ± 0.64	0.18 ± 0.01	0.04 ± 0.90E-02	0.69 ± 0.02
	Model 2	0.19 ± 0.03	0.09 ± 0.02	-0.51 ± 0.10	0.19 ± 0.017		0.66 ± 0.03
	Model 3	0.19 ± 0.03	0.25 ± 0.02	-0.44 ± 0.09			0.75 ± 0.03

Post-wean single-trait models

Table 4.8 reports the single-trait direct and maternal heritability as well as correlation estimates between the direct and maternal heritability estimates for Angus 12-month weights. Model 1 based on data for the 2012 – 2022 period had a lower direct heritability (0.05 ± 0.03) than for the 2002 – 2022 period (0.09 ± 0.038). The opposite was seen for the rest of the models, where data for the 2002 – 2022 period had lower heritability estimates.

Table 4.8 Single-trait heritability and correlation estimates with their associated standard error for various Angus yearling weight models

Data period	Trait	Direct heritability	Maternal heritability	Correlation	Permanent environmental (PE)	Sire by herd (SXH)	Residual
2012 - 2022	Model 1	0.05 ± 0.03	0.08 ± 0.02	1.00 ± 0.002	0.06 ± 0.029	0.10 ± 0.02	0.70 ± 0.05
	Model 2	0.43 ± 0.07	0.08 ± 0.04	-0.77 ± 0.12	0.22 ± 0.03		0.56 ± 0.07
	Model 3	0.40 ± 0.07	0.14 ± 0.05	-0.56 ± 0.14			0.73 ± 0.07
2002 - 2022	Model 1	0.09 ± 0.038	0.04 ± 0.02	-0.12 ± 0.34	0.07 ± 0.01	0.06 ± 0.01	0.76 ± 0.03
	Model 2	0.31 ± 0.03	0.09 ± 0.02	-0.66 ± 0.08	0.08 ± 0.02		0.75 ± 0.04
	Model 3	0.30 ± 0.04	0.13 ± 0.02	-0.56 ± 0.08			0.79 ± 0.04

Table 4.9 reports the single-trait heritability and correlation estimates for Angus 18-month weights. The 2002 – 2022 period had higher direct heritability estimates across all the models tested.

Table 4.9 Single-trait heritability and correlation estimates with their associated standard error for various Angus 18-month weight

Data period	Trait	Direct heritability	Maternal heritability	Correlation	Permanent environmental effect (PE)	Sire by herd (SXH) effect	Residual
2012-2022	Model 1	0.25 ± 0.14	0.02 ± 0.03	-1.00 ± 0.001	0.31 ± 0.03	0.05 ± 0.04	0.51 ± 0.10
	Model 2	0.43 ± 0.09	0.05 ± 0.03	-0.99 ± 0.001	0.34 ± 0.04		0.47 ± 0.09
	Model 3	0.37 ± 0.08	0.003 ± 0.007	-0.99 ± 0.01			0.69 ± 0.08
2002-2022	Model 1	0.28 ± 0.07	0.02 ± 0.03	-0.80 ± 0.34	0.08 ± 0.03	0.04 ± 0.02	0.70 ± 0.07
	Model 2	0.44 ± 0.06	0.05 ± 0.03	-0.86 ± 0.16	0.08 ± 0.03		0.69 ± 0.07
	Model 3	0.42 ± 0.06	0.08 ± 0.04	-0.64 ± 0.12			0.73 ± 0.06

Multi-trait models

Table 4.10 presents the multi-trait heritability and correlation estimates between direct and maternal heritability for Angus weight traits. For the 2012–2022 data, the heritability for birth weight direct was (0.50 ± 0.02), with a strong correlation being observed between yearling and weaning weights (0.92 ± 0.03). Single trait analyses of the SA Charolais and SA Hereford breeds are reported in addendum B.

Table 4.10 Multi-trait model heritability and correlation estimates with their associated standard error for Angus weight traits for the period 2012 – 2022

Trait	BWD	WWD	YWD	18m WD	BWM	WWM	YWM	18m WM
BWD	0.50 ± 0.02	0.39 ± 0.04	0.35 ± 0.05	0.48 ± 0.08	-0.45 ± 0.03	-0.33 ± 0.04	-0.36 ± 0.07	-0.50 ± 0.12
WWD		0.31 ± 0.24	0.92 ± 0.03	0.40 ± 0.08	-0.17 ± 0.09	-0.54 ± 0.05	-0.59 ± 0.05	-0.41 ± 0.13
YWD			0.50 ± 0.04	0.49 ± 0.07	0.048 ± 0.09	-0.43 ± 0.07	-0.56 ± 0.06	-0.37 ± 0.13
18m WD				0.35 ± 0.06	-0.00 ± 0.11	0.17 ± 0.15	0.04 ± 0.18	-0.24 ± 0.21
BWM					0.15 ± 0.01	0.56 ± 0.06	0.38 ± 0.08	0.62 ± 0.11
WWM						0.22 ± 0.02	0.96 ± 0.02	0.85 ± 0.07
YWM							0.22 ± 0.03	0.86 ± 0.07
18m WM								0.09 ± 0.03

BWD = Birth weight direct, WWD = Weaning weight direct, YWD = 12-month direct, 18m WD = 18-month weight direct, BWM = Birth weight maternal, WWM = weaning weight maternal, YWM = 12-month maternal, 18m WM = 18-month weight maternal

In Table 4.11, heritability for birth weight was lower at to 0.43 ± 0.02, and correlations among traits are more conservative, particularly for weaning weight direct (0.43 ± 0.04) and yearling weight direct (0.28 ± 0.04).

Table 4.11 Multi-trait analysis heritability and correlation estimates with their associated standard errors for Angus weight traits for the years 2002 – 2022

Trait	BW direct	WW direct	YW direct	18-month W direct	BW maternal	WW maternal	YW maternal	18-month W maternal
BW direct	0.43 ± 0.02	0.43 ± 0.04	0.28 ± 0.04	0.38 ± 0.06	-0.54 ± 0.05	-0.34 ± 0.07	-0.29 ± 0.07	-0.30 ± 0.09
WW direct		0.27 ± 0.02	0.91 ± 0.02	0.80 ± 0.06	-0.02 ± 0.06	-0.65 ± 0.045	-0.71 ± 0.05	-0.68 ± 0.09
YW direct			0.36 ± 0.03	0.86 ± 0.05	0.02 ± 0.06	-0.49 ± 0.06	-0.68 ± 0.05	-0.58 ± 0.08
18-month W direct				0.39 ± 0.03	-0.21 ± 0.09	-0.53 ± 0.09	-0.67 ± 0.08	-0.71 ± 0.07
BW maternal					0.08 ± 0.01	0.13 ± 0.09	0.13 ± 0.09	0.25 ± 0.11
WW maternal						0.13 ± 0.01	0.90 ± 0.03	0.90 ± 0.06
YW maternal							0.11 ± 0.01	0.94 ± 0.04
18-month W maternal								0.09 ± 0.02

Table 4.12 shows the multi-trait analysis heritability and correlation estimates for the Charolais. Birth weight maternal heritability estimates (0.15 ± 0.03) was lower than for direct birth weight estimate (0.36 ± 0.04). The rest of the traits also had a higher direct than maternal heritability estimate.

Table 4.12 Multi-trait analysis heritability and correlation estimates with their associated standard error for Charolais weight traits for the years 2012 – 2022

Trait	BWD	WWD	YWD	18m WD	BWM	WWM	YWM	18m WM
BWD	0.36 ± 0.04	0.30 ± 0.11	0.52 ± 0.14	0.36 ± 0.13	-0.59 ± 0.07	-0.23 ± 0.12	-0.35 ± 0.17	-0.25 ± 0.87
WWD		0.18 ± 0.03	0.94 ± 0.05	0.51 ± 0.18	0.30 ± 0.10	-0.49 ± 0.11	-0.56 ± 0.16	-0.18 ± 0.85
YWD			0.07 ± 0.02	0.70 ± 0.15	0.10 ± 0.16	-0.28 ± 0.19	-0.40 ± 0.20	-0.25 ± 0.80
18m WD				0.10 ± 0.04	0.07 ± 0.27	0.43 ± 0.19	0.34 ± 0.22	-0.64 ± 0.61
BWM					0.15 ± 0.03	-0.02 ± 0.13	-0.01 ± 0.19	-0.20 ± 1.17
WWM						0.10 ± 0.02	0.98 ± 0.08	-0.25 ± 0.89
YWM							0.05 ± 0.02	-0.26 ± 0.77
18m WM								0.003 ± 0.01

Table 4.13 shows the multi-trait analysis heritability and correlation estimates for the Charolais weight traits for the period 2002 – 2022. The birth weight direct (0.42 ± 0.03) was higher than for the period 2012 – 2022. All other estimates for the 2002 – 2022 period were lower than those for 2012 – 2022 for the Charolais breed.

Table 4.13 Multi-trait analysis heritability and correlation estimates with their associated standard error for Charolais weight traits for the years 2002 – 2022

Trait	BWD	WWD	YWD	18m WD	BWM	WWM	YWM	18m WM
BWD	0.42 ± 0.03	0.30 ± 0.08	0.30 ± 0.09	0.20 ± 0.11	-0.53 ± 0.05	-0.20 ± 0.09	-0.23 ± 0.12	-0.50± 0.30
WWD		0.19 ± 0.03	0.96 ± 0.03	0.62 ± 0.12	-0.06 ± 0.11	-0.44 ± 0.11	-0.05 ± 0.14	-0.54 ± 0.36
YWD			0.13 ± 0.03	0.81 ± 0.08	-0.01 ± 0.12	-0.30 ± 0.13	-0.40 ± 0.14	-0.52 ± 0.30
18m WD				0.17 ± 0.04	0.11 ± 0.14	0.08 ± 0.20	-0.03 ± 0.21	-0.32 ± 0.27
BWM					0.15 ± 0.02	0.33 ± 0.11	0.40 ± 0.14	0.53 ± 0.27
WWM						0.21 ± 0.03	0.99 ± 0.02	0.85 ± 0.17
YWM							0.07 ± 0.02	0.91 ± 0.13
18m WM								0.02 ± 0.01

Table 4.14 presents heritability and correlation estimates from the multi-trait analysis of Hereford weight traits. For the 2012–2022 dataset, heritability for birth weight direct was 0.32 ± 0.03, with strong correlations noted for weaning weight direct (0.63 ± 0.07) and yearling weight direct (0.73 ± 0.07) with birth weight direct.

Table 4.14 Multi-trait analysis heritability and correlation estimates with their associated standard errors for Hereford weight traits for the years 2012 – 2022

Trait	**BW direct**	**WW direct**	**YW direct**	**18-month W direct**	**BW maternal**	**WW maternal**	**YW maternal**	**18-month W maternal**
BW direct	0.32 ± 0.03	0.63 ± 0.07	0.73 ± 0.07	0.57 ± 0.08	-0.54 ± 0.09	-0.52 ± 0.08	-0.47 ± 0.10	-0.45 ± 0.09
WW direct		0.20 ± 0.03	0.69 ± 0.07	0.70 ± 0.05	-0.42 ± 0.09	-0.69 ± 0.06	-0.60 ± 0.08	-0.60 ± 0.10
YW direct			0.32 ± 0.06	0.94 ± 0.05	-0.46 ± 0.13	-0.50 ± 0.11	-0.75 ± 0.07	-0.67 ± 0.09
18-month W direct				0.46 ± 0.08	-0.50 ± 0.13	-0.39 ± 0.12	-0.67 ± 0.10	-0.62 ± 0.11
BW maternal					0.06 ± 0.01	0.42 ± 0.11	0.51 ± 0.12	0.46 ± 0.12
WW maternal						0.13 ± 0.02	0.84 ± 0.10	0.90 ± 0.06
YW maternal							0.17 ± 0.04	0.96 ± 0.17
18-month W maternal								0.18 ± 0.05

Table 4.15 reports the multi-trait analysis heritability estimates for the Hereford for the years 2002–2022. The maternal component was removed due to data structure limitations that did not support its inclusion. Consequently, heritability estimates for direct weights were significantly lower than the 2012-2022 period, with birth weight direct at 0.21 ± 0.004. The weaning weight direct (0.24 ± 0.01) and yearling weight direct (0.23 ± 0.01) also reflect lower heritability values. Overall, these findings between datasets highlight the importance of both direct and maternal genetic factors in the expression of Hereford weight traits.

Table 4.15 Multi-trait analysis heritability and correlation estimates with their associated standard error for Hereford weight traits for the years 2002 – 2022 with no maternal component

Trait	**BWD**	**WWD**	**YWD**	**18m WD**
BWD	0.21 ± 0.004	0.03 ± 0.01	0.03 ± 0.01	0.03 ± 0.01
WWD		0.24 ± 0.01	0.03 ± 0.01	0.03 ± 0.01
YWD			0.23 ± 0.01	0.03 ± 0.01
18m WD				0.24 ± 0.01

Table 4.16 shows the heritability and correlation estimates for Angus growth traits. Significant correlations were found between traits: average daily gain with hip height (0.63 ± 0.14), body length (0.81 ± 0.10), and scrotal circumference (0.52 ± 0.13); hip height with body length (0.81 ± 0.08) and scrotal circumference (0.41 ± 0.12); and body length with scrotal circumference (0.52 ± 0.13).

Table 4.16 Multi-trait analysis heritability and correlation estimates with their associated standard errors for Angus growth test traits

Trait	Average daily gain	Hip height	Body length	Scrotal circumference
Average daily gain	0.19 ± 0.05	0.63 ± 0.14	0.81 ± 0.10	0.52 ± 0.13
Hip height		0.31 ± 0.06	0.81 ± 0.08	0.41 ± 0.12
Body length			0.18 ± 0.05	0.52 ± 0.13
Scrotal circumference				0.38 ± 0.07

Table 4.17 presents the heritability, and correlation estimates for Charolais growth traits. Significant correlations were observed between traits: average daily gain with hip height (0.88 ± 0.72), body length (0.62 ± 0.70), and scrotal circumference (-0.42 ± 0.58); hip height with body length (0.82 ± 0.66) and scrotal circumference (-0.31 ± 1.20); and body length with scrotal circumference (0.29 ± 0.67).

Table 4.17 Multi-trait analysis heritability and correlation estimates with their associated standard error for Charolais growth test traits

Trait	Average daily gain	Hip height	Body length	Scrotal circumference
Average daily gain	0.39 ± 0.30	0.88 ± 0.72	0.62 ± 0.70	-0.42 ± 0.58
Hip height		0.06 ± 0.15	0.82 ± 0.66	-0.31 ± 1.20
Body length			0.28 ± 0.51	0.29 ± 0.67
Scrotal circumference				0.57 ± 0.28

Table 4.18 presents the heritability, and correlation estimates for Hereford growth traits. Significant correlations were found between traits: average daily gain with hip height (0.16 ± 0.25), body length (0.59 ± 0.24), and scrotal circumference (-0.05 ± 0.29); hip height with body length (0.65 ± 0.23) and scrotal circumference (-0.42 ± 0.28); and body length with scrotal circumference (-0.50 ± 0.37).

Table 4.18 Multi-trait analysis heritability and correlation estimates with their associated standard errors for Hereford growth test traits

Trait	Average daily gain	Hip height	Body length	Scrotal circumference
Average daily gain	0.31 ± 0.10	0.16 ± 0.25	0.59 ± 0.24	-0.05 ± 0.29
Hip height		0.30 ± 0.10	0.65 ± 0.23	-0.42 ± 0.28
Body length			0.12 ± 0.06	-0.50 ± 0.37
Scrotal circumference				0.21 ± 0.10

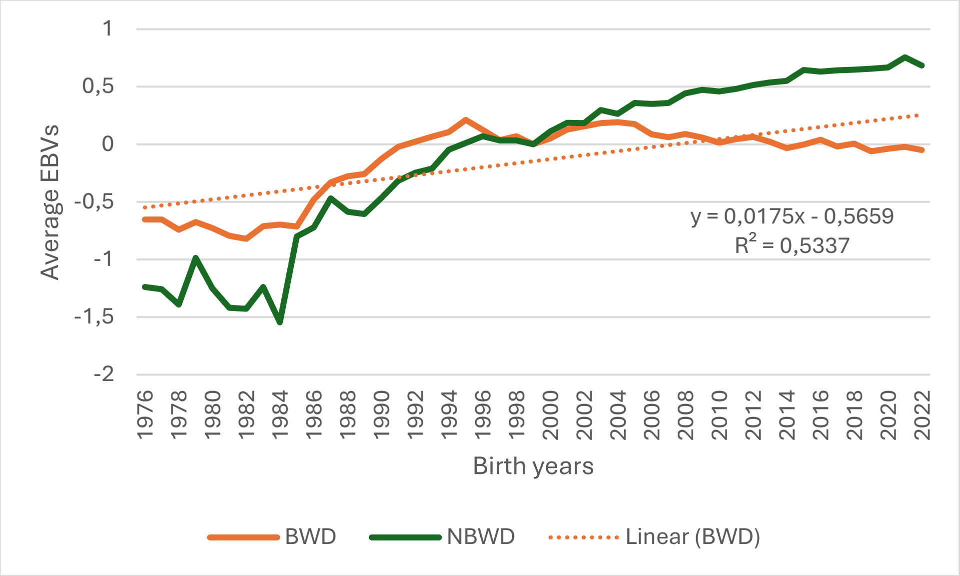
4.6 Genetic trends for SA Angus

Genetic trends are highly dependent upon the heritability estimates used. In table 4.19 the heritability estimates for this study are compared to the heritability estimates of the SA Stud Book national evauluation. Heritability estimates obtained in this study were all higher than the previously estimated values from SA Stud Book except for the birth weight maternal heritability estimate which was lower. The difference in values is possibly due to data structure differences and different models used.

Table 4.19 Heritability estimates used for genetic trends for Angus

Traits	Heritability estimates from this study for the period 2002 - 2022	SA Stud Book heritability estimates
Birth weight direct	0.43	0.28
Birth weight maternal	0.08	0.11
Wean weight direct	0.27	0.23
Wean weight maternal	0.13	-
12-month weight direct	0.36	0.24
18-month weight direct	0.39	0.32

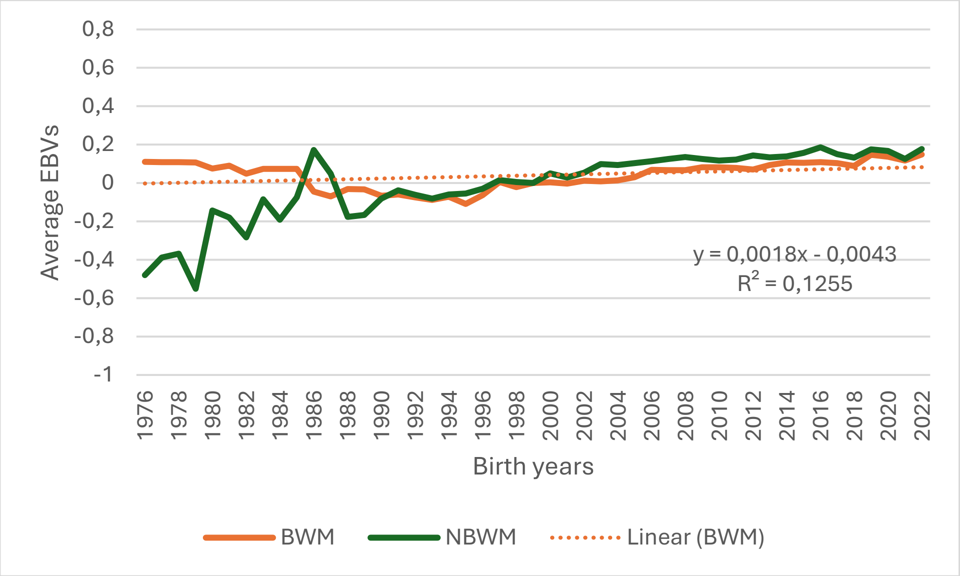
Figure 4.2 illustrates the genetic trends for birth weight direct Estimated Breeding Values (EBVs) in SA Angus cattle from 1976 to 2022. This figure compares the EBVs derived from the current study with those obtained from a national study conducted by SA Stud Book. The graph demonstrates a consistent upward trend in EBVs over the examined period, indicating a decrease in average birth weight. Notably, the genetic trend for this study (orange line) is more conservative compared to the earlier national study (green line), reflecting the differences in the models used.



BWD = Birth weight direct, NBWD = National birth weight direct

Figure 4.2 Genetic trends of estimated breeding values for birth weight direct for the SA Angus cattle breed

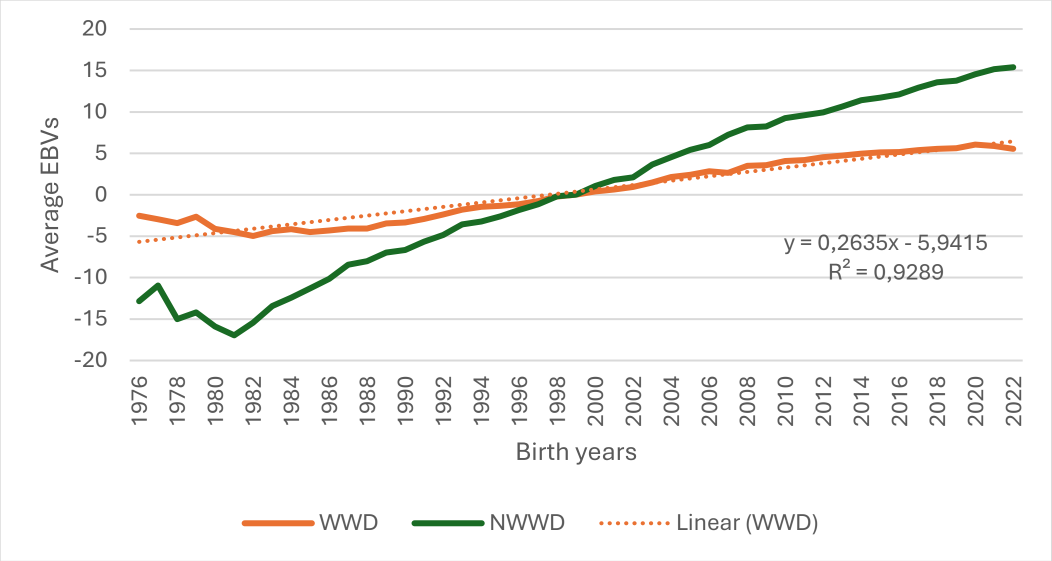
Figure 4.3 illustrates the genetic trends for birth weight maternal EBVs in SA Angus cattle from 1976 to 2022. The graph demonstrates a mostly upward trend in EBVs over the examined period, indicating a decrease in birth weight maternal resulting in lower birth weights.



BWM = Birth weight maternal, NBWM = National birth weight maternal

Figure 4.3 Genetic trends of estimated breeding values for birth weight maternal for the SA Angus cattle breed

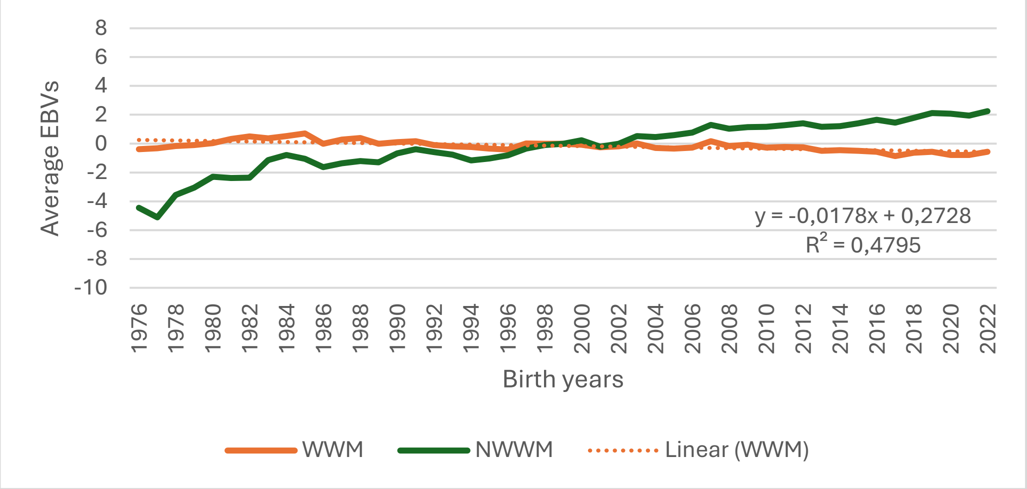
Figure 4.4 illustrates the genetic trends for weaning weight direct EBVs in SA Angus cattle from 1976 to 2022. The graph demonstrates a steady upward trend in EBVs over the examined period, indicating genetic improvement in wean weight direct. Notably, the EBVs from the recent estimations are more conservative ending at a lower estimate compared to the earlier national study, reflecting different models, different heritability estimates and data selection.



WWD = Weaning weight direct, NWWD = National weaning weight direct

Figure 4.4 Genetic trends of estimated breeding values for weaning weight direct for the SA Angus cattle breed

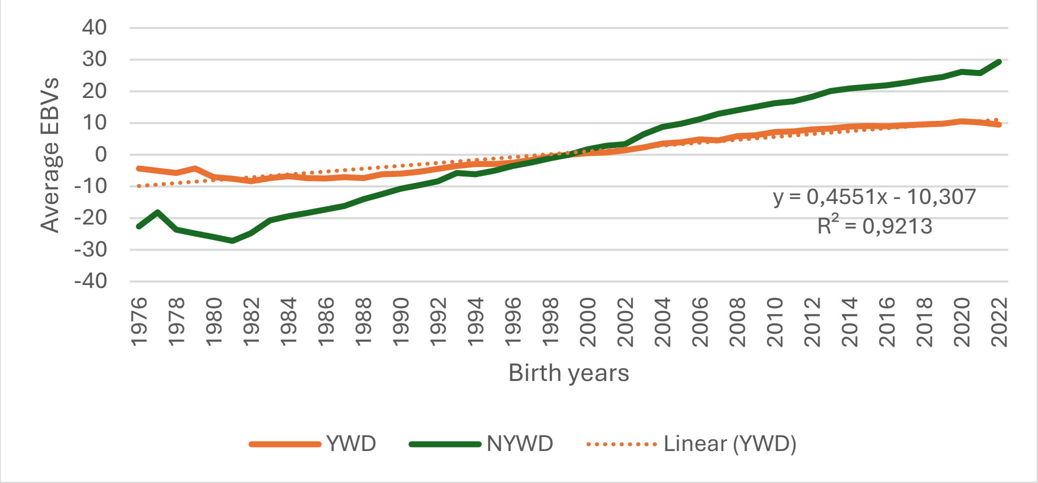
Figure 4.5 illustrates the genetic trends for weaning weight maternal EBVs in SA Angus cattle from 1976 to 2022. The EBVs from the national study exhibit a consistent upward trend, culminating in a significantly higher estimate by 2022. In contrast, the EBVs obtained in the current study demonstrate a more stable trend, with the 2022 values closely resembling those from 1976. This discrepancy in trends may be attributed to differences in the models and data structures used in the respective studies.



WWM = Weaning weight maternal, NWWM = National weaning weight maternal

Figure 4.5 Genetic trends of estimated breeding values for weaning weight maternal for the SA Angus cattle breed

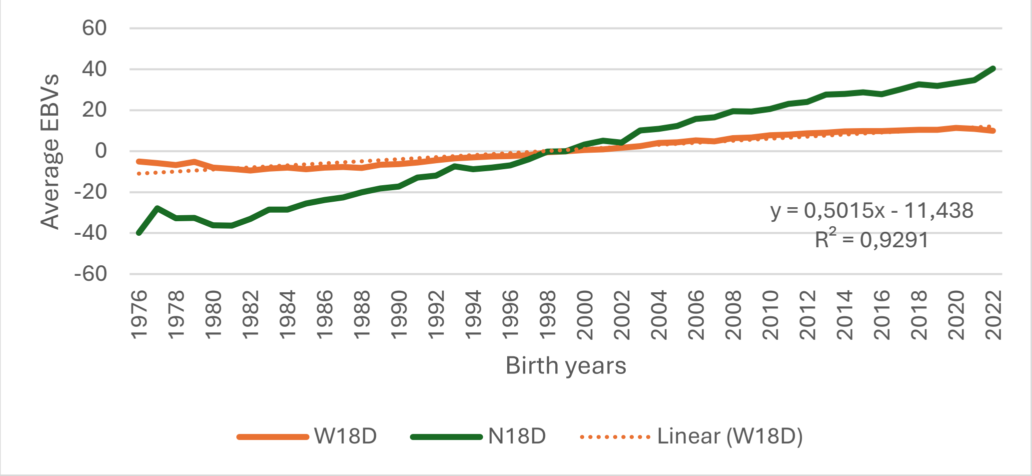
Figure 4.6 illustrates the genetic trends for yearling weight direct EBVs in SA Angus cattle from 1976 to 2022. This figure presents a comparison between the EBVs generated in this study and those reported in past national analyses by the SA Stud Book. Both estimates show an upward trend across the years with the estimates from this study yielding more conservative results than the previously estimated.



YWD = 12-month weight direct, NYWD = National 12-month weight direct

Figure 4.6 Genetic trends of estimated breeding values for yearling weight direct for the SA Angus cattle breed

Figure 4.7 illustrates the genetic trends for 18-month weight direct EBVs in SA Angus cattle from 1976 to 2022. This figure compares the EBVs derived from the current study with those obtained from a national study conducted by SA Stud Book in previous years. Both estimates show an upward trend across the years with the estimates from this study yielding more conservative stable results than the previously estimated.



W18D = 18-month weight direct, N18D = National 18-month weight direct

Figure 4.7 Genetic trends of estimated breeding values for 18-month weight direct for the SA Angus cattle breed

Chapter 5: Discussion

5.1. Introduction

Variance component estimation is a fundamental statistical tool for understanding the genetic structure of complex traits (Gianola & Sorensen, 2004). In the context of beef cattle breeding, this technique is invaluable for quantifying the relative contributions of genetic and environmental factors to phenotypic variation. By partitioning the total phenotypic variance, researchers can gain insights into the heritability of traits, which is essential for making informed breeding decisions and developing accurate Estimated Breeding Values (EBVs) (Hill, 2010).

This study aimed to estimate variance components for a suite of economically important traits in Angus, Charolais, and Hereford beef cattle breeds participating in animal recording. The available data sets varied with regard to available records and with the most recordings over all traits available for the Angus, followed by the Hereford and Charolais. Traits included were pre-weaning and post-weaning growth, birth weight, weaning weight, yearling weight, 18-month weight, and growth test traits such as average daily gain, hip height, body length, and scrotal circumference. The primary objectives were to: explore the data structure, determine significant effects for model development and estimate variance components for all three breeds. A BLUP analysis was also included for the SA Angus breed. To accomplish these objectives, a combination of data editing techniques, Analysis of Variance (ANOVA), and specialized software (VCE 6.0.2 and PEST) were employed. In this discussion chapter, the results and implications are discussed with reference to the potential applications of variance component estimation in beef cattle breeding.

5.2. Descriptive statistics

The Angus, Charolais, and Hereford beef cattle breeds were introduced into South Africa during the 1800-1900s and since then have been selected and farmed under diverse climatic conditions (Van Marle, 1974; Scholtz *et al*., 2019; Angus Society of South Africa, 2023; The Hereford Cattle Breeders' Society of South Africa, 2023; SA Charolais Breeders' Society, 2023). The Angus and Hereford are classified as early maturing breeds with small to moderate frames and the Charolais is considered a large frame late maturing breed. There were 13 507, 3 817 and 3 526 registered female animals active on the Logix system as of October 2023 (SA Studbook, 2023) for the SA Angus, Charolais and Hereford respectively. These breeds are smaller in population size in South Africa compared with breeds such as the Bonsmara with a much larger population of over 150 000 animals (Van der Westhuizen *et al*., 2014).

Pre-wean growth traits

The Angus and Hereford, which are both regarded as British beef breeds had mean birth weights of 34.56 kg and 36.24 kg, respectively, while the Charolais had a mean birth weight of 40.70 kg as can be expected from a large-framed breed. Inspection of the maximum birth weights showed potential of the Charolais to have a heavier birth weight with maximum of 63 kg, the Hereford had a maximum of 56 kg and the Angus had a maximum birth weight of 53 kg due to selection for calving ease in the Angus and Hereford (Bartoň *et al*., 2011; The Hereford Cattle Breeders' Society of South Africa, 2023; Angus Society of South

Africa, 2023), which fits the ranges of values obtained in our SA population obtained from this study. For Angus cattle, literature reports an average birth weight of 38.04 kg (Szabó *et al.*, 2006; Torres-Vázquez et al., 2018), for Charolais cattle exhibited a range for birth weight of 37.09 kg to 46.9 kg (Szabó *et al.*, 2006; Stádník *et al.*, 2008; Toušová *et al.*, 2014) and for Hereford an average of 37.14 kg (Bullock *et al.*, 1993). Selection for calving ease in the Angus and Hereford (Bartoň *et al.*, 2011) is evident from the average birth weights found in this study and which aligns with estimates reported in literature. Moderate birth weights and calving ease remain important traits in all beef breeds to avoid dystocia and unnecessary economic loss (Bartoň *et al.*, 2011; Cammack *et al.*, 2009).

The average dam ages for the three breeds varied between 66.59 months (5.5 years) for the Angus with a maximum of 418 months. The average dam age for the Hereford was 63.47 months (5.29 years) with a maximum of 286 months. The Charolais had an average dam age of 72 months (6 years) and a maximum of 549 months. High maximum dam ages could be due to limitations in the recording of these animals or failure to cancel the animal by the breeders but were still fit within in the biological limits. Age of dam is a very important parameter taken into consideration when estimating genetic parameters, whether the dam is a cow or a heifer will impact the growth and weight of her calf and therefore, age of dam is generally considered in terms of the parity number across evaluations (Crews & Porteous., 2003; Pritchard *et al.*,2021).

Weaning weight reflects the milk provision and mothering ability of the cow (Meyer *et al.*, 1994). In this study the mean weaning weights at 212 days differed from 229.8 for the Angus, 237.2 kg for the Charolais and 211.5 kg for the Hereford breed. Weaning weights of 206 kg – 229.37 kg (Angus), and 204 kg – 310.7 kg (Charolais) and an average of 221.62 kg (Hereford) have been reported which aligns with the findings of the current study (Bullock *et al.*, 1993; Szabó *et al.*, 2006; Stádník *et al.*, 2008; Toušová *et al.*, 2014; Torres-Vázquez et al., 2018).

Post-wean growth traits

Post weaning growth traits analysed in this study included 12-month weight, 18-month weight, Average Daily Gain (ADG), hip height, body length and scrotal circumference. These traits are measured in phase C (central test station) and phase D (on farm) and are recorded by qualified professionals (Bradfield *et al.*, 2000). In this study 12-month weight averages at 370 days ranged from 293 kg for the Hereford to 307 kg and 319 kg respectively for Angus and Charolais. 18-month weight averages at 550 days were 421.6 kg, 424.3 kg and 385.9 kg for the Angus, Charolais and Hereford respectively. This is expected as the Charolais is a larger framed breed followed by the Angus and the Hereford. In literature, 12-month weight reported for Charolais was 436.55 and 371.27 kg for the Angus and 353.88 kg for the Hereford as well as 600-day weights of 511.81 kg for the Angus and a mature weight of 552.38 - 545 kg for the Hereford (Bullock *et al.*, 1993; Bene *et al.*, 2007; Stádník *et al.*, 2008; Torres-Vázquez *et al.*, 2018).

The results for intensive growth tests on the three breeds revealed a mean ADG of 1370 g/day with a body length of 139.5 cm for Angus cattle, which is lower than literature reports of 1590 g/day for ADG and a hip height of 166 cm at 2 years of age with a height at the rump of 133.8 cm (Bene *et al.*, 2007; Torres-Vázquez *et al.*, 2018). Average scrotal circumference for Angus bulls reported in the literature was 33.5 ± 3.0 cm at the age of 12-18 months recorded during growth tests (Arango *et al*., 2002; Menegassi *et al*., 2019) which is slightly lower than the mean scrotal circumference of 36 cm found in this study. Charolais cattle had a high mean ADG, 1563 g/day, and showed a wide range of ADG (384 to 2756 g/day) in this study, reflecting the difference between intensive and extensive growth tests. They had a hip height of 137.4 cm and body length of 142.0 cm, in line with a larger frame size. In the literature the average hip height at 2 years was 122 cm and at maturity Charolais had a height at the rump of 141.5 cm (Bene *et al*., 2007). Hereford cattle had an average ADG of 1417 g/day with a body length of 132.6 cm and a hip height of 117 cm. Average height at the rump of 132.0 cm at 2 years of age in Hereford cattle was indicated by Bene et al., (2007), but not directly comparable due to different ages and rations reported.

The means for the different traits are subjected to the number of recordings submitted by the breeders and represent breeders farming in quite diverse climates of South Africa. Quality control of the data was performed and the average kurtosis for the Angus breed trait distributions was 2,89 indicating that the traits are generally platykurtic with fewer extreme outliers. The average kurtosis for the Hereford breed was 2.95 and is similar to that of the Angus being slightly more platykurtic with few extreme outliers, while the Charolais breed (3.18) can be regarded as leptokurtic with more extreme outliers and fairly positively skewed (0.32). The Charolais was leptokurtic possibly due to having fewer records. Angus (0.16) and Hereford (0.13) were also slightly positively skewed. The Kurtosis of a normal distribution is 3: if greater than 3, it is leptokurtic which means it has more outliers, less than 3 means its platykurtic and has fewer extreme outliers (Groeneveld & Meeden, 1984). If the skewness value is close to zero it means it is more symmetrical, a positive value means it is skewed to the right (positively skewed) and if it results in a negative value then the distribution is left skewed (negatively skewed).

5.3. Estimation of environmental effects for model development

In this study, an ANOVA was performed to identify which factors significantly influence weight and growth traits across Angus, Charolais, and Hereford breeds. The ANOVA Type II tests assessed the significance of all the effects. The average adjusted R-squared values for Angus, Charolais, and Hereford models were 0.66, 0.65, and 0.59, respectively, while the Residual Standard Error (RSE) values were 48.25, 48.05, and 45.31, respectively. The main differences between breeds were observed in the inclusion of effects such as Sire x Herd (SXH) interaction, heifer effects, and quadratic age effects. Other significant effects like dam age, contemporary group, sex, and age were consistent across breeds. Overall, the models provide a reasonable fit, with Angus and Charolais performing slightly better than Hereford based on R-squared and RSE values (Wooditch *et al*., 2021).

Environmental factors like breed, management, and statistical methodology can influence the estimation of genetic parameters. Koots *et al.* (1994) found that heritability estimates for growth traits from field data were similar to those from experimental data. However, biological studies often face unbalanced data due to missing observations, unequal sample sizes, or incomplete responses, which can bias parameter estimates and hypothesis testing (Shaw & Mitchell-Olds, 1993). In this study, missing values and unequal trait recording affected breeds differently. Angus estimates remained relatively stable due to sufficient data, but Charolais 12-

and 18-month estimates were more variable due to fewer records. Hereford data were more affected by missing or incorrect parentage information rather than missing records.

When determining which effects to include in an ANOVA, it's essential to account for the data structure and interactions between factors. Main effects should always be included, but interaction effects require more careful consideration with unbalanced data (Shaw & Mitchell-Olds, 1993). Koots *et al*. (1994) emphasized the importance of including maternal effects and age adjustments in heritability estimates. For traits influenced by maternal effects, animal models typically showed only minor differences in heritability when compared to models without maternal effects. For example, birth weight direct heritability was 0.34 (with maternal effect) compared to 0.36 (without maternal effect). Although the differences are small, including maternal effects improves the accuracy of genetic evaluations, as was observed in this study where better model fit and more variances were captured with the inclusion of maternal effects.

5.4. (Co)variance component estimation

Two data sets were applied in this study for the three breeds in order to determine which data structure would be more accurate for genetic evaluation. The 20-year dataset for both breeds proved to be more complete for the (co)variance estimation, 20 years of data provided opportunity for better contemporary group (CG) construction with more animals and had improved pedigree depth compared to the 10-year dataset. A larger CG can result in higher accuracy of estimates as there are many data points across which the environmental effects can be distributed (Cuyabano *et al.*, 2024). The CG construction in this study was consistent across the three breeds, birth weight had a CG that consisted of herd x year x season. Weaning to 18-month weights CG were comprised of the participant number x beef test code x feeding status. CG for ADG, hip height, body length and scrotal circumference comprised of the participant number x test code for their growth test.

Single trait models

Single-trait variance component analysis was conducted to evaluate model fit and identify potential areas for refinement. Standard errors provide an indication of precision associated with the estimated variance components where a smaller standard error is preferred as it indicates a more precise estimate (Wooditch et al., 2021). Effects with larger standard errors may be less significant or have more uncertainty associated with their estimates. Therefore, the standard errors were evaluated with their heritability estimates for all random additive effects to determine which effects to remove from the models.

The sample size also plays a crucial role in heritability estimates. Smaller datasets increase sampling error, inflating residual variance and reducing the genetic component, leading to underestimation of heritability. A smaller sample size decreases statistical power, making it difficult to detect genetic effects (Barry *et al.*, 2023). Low heritability traits, in particular, require large datasets of adequate phenotypic records for accurate selection. Berry *et al.* (2019) highlighted that traits with heritability as low as 0.03 may need records from 127 progeny per parent to achieve a 0.70 accuracy in selection, underscoring the importance of large, well-recorded datasets for genetic evaluations.

Analysis of these single-trait results across both data sets (2002-2022 and 2012 to 2022) for all three breeds revealed that genetic factors play a significant role in determining birth through to 18-month weight, although their relative importance varied. Different models were assessed where environmental effects such as SXH and Permanent Environment (PE) were included or excluded. The Angus single-trait birth weight exhibited higher direct heritability estimates across the models (0.41 - 0.49) compared to weaning weight (0.02 - 0.26), yearling weight (0.05 - 0.43), and 18-month weight (0.25 - 0.44). The Charolais estimate of direct heritability for birth weight (0.34 – 0.42) was also higher compared to weaning weight (0.01 – 0.17), yearling weight (0.04 – 0.09) and 18-month weight trait (0.12 – 0.18). The Hereford single-trait direct heritability estimates varied across the traits and models with large variability, birth weight (0.001 – 0.29), weaning weight (0.03 – 0.19), yearling weight (0.07 – 0.25) and 18-month weights (0.01 – 0.56). This variability in direct heritability estimates across the models indicates the large effect of the inclusion of various environmental effects on the models. Literature on single-trait models for these breeds is not widely available. Available literature indicated Angus had a direct birth weight heritability of between 0.46 – 0.56 across various lines investigated in an article by Baker *et al.*, (1993) which is in the range observed in this study. Dodenhoff *et al.*, (1998) reported Hereford direct heritability estimates of 0.14 for birth weight and a range of 0.13 – 0.20 for weaning weight which aligns with results reported in this study.

A consistent negative correlation between direct and maternal genetic effects was observed across all traits under investigation. Several explanations for this type of bias have been suggested in the literature, including sire misidentification (Lee and Pollack, 1997a), a lack of genetic connectedness between herds (Clément *et al*., 2001), exclusion of the random sire × herd × year effect (Lee & Pollack, 1997b; Hagger, 1998), and environmental covariances between dam and offspring records (Koch, 1972; Bijma, 2006). However, in practice, obtaining perfectly designed data that fits complex models is not always feasible when estimating genetic parameters for evaluation (Dodenhoff *et al*., 1999), which leads to some uncertainty regarding the true value of the direct-maternal genetic correlation. It is therefore, indicated in literature that the direct-maternal genetic correlation be set to zero to avoid unwanted bias (David *et al.*, 2015).

The inclusion of SXH effect for all three breeds models consistently increased residual variance, emphasizing the importance of considering environmental factors at the herd level. The main causes of variation due to the SXH interaction have not been fully identified, though several potential sources have been suggested across the literature which include preferential treatment, non-random mating, the use of selected sires, which all may result in unequal residual and additive genetic variance across herds (Tong *et al.*,1977), and the extensive use of specific sires within certain herds. The breeds included in this study have been subjected to intense selection for growth over many decades and being small populations could experience extensive use of selected sires (Meyer, 1987). As a result, failing to account for the SXH interaction in evaluation models could inflate genetic variance and lead to overestimation of the heritability estimates (Tong *et al*.,1977; Banos & Shook, 1990).

Additionally, the PE effect was found to influence birth to 18-month weight, highlighting the role of stable environmental conditions. Permanent environmental effects, which contribute consistently to an individual's phenotype across repeated measures and accumulate over time (Kruuk & Hadfield, 2007; Schaeffer, 2011), play a critical role in shaping an animal's performance. In a study by Kelleher *et al.*, (2016), permanent environmental effects had a similar or even greater influence on the variation in reproductive performance compared to additive genetic effects, with the former ranging from 0.01 to 0.09 and the latter from 0.004 to 0.04 (Kelleher et al 2016). These findings emphasize the significant impact of permanent environmental factors on the expression of traits with low heritability, underscoring the importance of incorporating them into genetic evaluation models to ensure more accurate predictions of phenotypic outcomes.

The log-likelihood ratio test was used to evaluate the significance of including some environmental effects in multi-trait analyses for Angus, Charolais, and Hereford cattle. In Angus, the inclusion of PE significantly improved the model fit compared to the null model without PE (LLR = 22.82, $p < 0.05$). For Charolais, the model including PE, but excluding SXH interactions, provided a significantly better fit than the model excluding PE in weaning weight and SXH (LLR = 83285.78, $p < 0.05$). In Hereford, however, the null model with all PE resulted in a log-likelihood of negative infinity, suggesting potential data structure issues. Excluding SXH in Hereford led to a significantly improved fit but the log-likelihood remains poor (LLR = $-\infty$, $p < 0.05$). Overall, these findings underscore the importance of considering various environmental effects such as PE and SXH in multi-trait analyses for these cattle breeds and highlight the need for further research to understand the genetic mechanisms underlying environmental components and address potential data structure problems.

Multi-trait models: Pre-weaning growth traits

Using a multi-trait model provides the advantage of improved accuracy in genetic evaluations by incorporating correlated information across traits, especially valuable when certain records are missing or when traits are genetically related (VanRaden *et al*., 2014).

The multi-trait heritability estimates for direct birth weight for Angus (0.50 ± 0.02, 0.43 ± 0.02), Charolais (0.36 ± 0.04, 0.42 ± 0.03) and Hereford (0.32 ± 0.03, 0.21 ± 0.004) obtained in this study for the periods 2012 – 2022 and 2002 – 2022 respectively, are consistent with previous research where multi-trait heritability estimates of 0.36-0.42 were reported for direct birth weight for Angus (Trus & Wilton, 1988; Meyer, 1992), 0.36-0.50 for Charolais (Orenge *et al*., 2009; Herrera-Ojeda *et al*., 2019) and Hereford 0.36 – 0.42 (Trus & Wilton, 1988). The direct heritability estimates for weaning weight were as follows: (0.31 ± 0.24, 0.27 ± 0.02) for Angus, (0.18 ± 0.03, 0.19 ± 0.03) for Charolais and (0.20 ± 0.03, 0.24 ± 0.005) for Hereford for the two time periods respectively. These values are consistent with literature reports of (0.19-0.63) for Angus (Meyer, 1992; Bradfield *et al*., 2000), (0.13-0.30) Charolais (Orenge *et al*., 2009; Kachman *et al*., 2013; Herrera-Ojeda *et al.*, 2019) and (0.16 – 0.66) and Hereford (Koch, 1972; Meyer, 1992; Orenge *et al.*, 2009).

Multi-trait model: Post weaning growth traits

The multi-trait heritability estimates found in this study for the periods 2012 to 2022 and 2002 to 2022, respectively were: direct 12-month weight for Angus (0.50 ± 0.04, 0.36 ± 0.03), Charolais (0.07 ± 0.02, 0.13 ± 0.03) and for Hereford the direct 12-month weight heritability was (0.32 ± 0.06, 0.23 ± 0.006). In the literature the following values are observed for 12-month weight direct multi-trait heritability estimates, (0.27-0.46) for

Angus (Meyer, 1992; Kachman *et al*., 2013), Charolais are slightly lower than the literature range of (0.28-0.29) (Kachman *et al*., 2013; Herrera-Ojeda *et al*., 2019), and Hereford reported values between (0.16 – 0.36) (Torres-Vázquez & Spangler, 2016). 18-month direct heritability estimates for the periods 2012 – 2022 and 2002 – 2022 were as follows: (0.35 ± 0.06, 0.39 ± 0.03) for Angus, (0.10 ± 0.04, 0.17 ± 0.04) for Charolais and (0.46 ± 0.08, 0.24 ± 0.01) for Hereford 18-month direct heritability. Ranges from the literature are (0.30 - 0.47) for Angus 18-month weight direct heritability (Morris *et al*., 1992), Charolais values were lower than literature value of 0.46 (Arthur et al., 2001) and Hereford values obtained in this study were in line with reported literature of (0.30 - 0.47) (Morris *et al*., 1992). Differences in estimates in this study compared with those in the literature could be due to a change in population structure to a larger population, differences in data quality, decreased environmental variation, different models and data analysis techniques or possible intense directional selection between the studies resulting in reduced genetic variation (Meyer & Enfield, 1975, Getabalew *et al*., 2019).

In the Charolais, the heritability estimates for 12-month and 18-month weight in this study were lower than those for birth weight and weaning weight, which can be partially attributed to the smaller data sizes and fewer contemporary groups available for these traits. With a larger dataset, the statistical power to detect genetic effects increases, leading to more precise estimates. Additionally, a larger dataset can capture a wider range of genetic variation, improving the reliability of heritability estimates (Barry *et al*., 2023).

In the larger dataset (2002-2022) for the Hereford, heritability estimates for direct weight traits were significantly lower than the other data set (2012-2022) due to the absence of maternal component information. The maternal component could not be included due to the data structure and possible missing/incorrect pedigree information leading to inaccurate estimations. Incomplete or incorrect parentage information, particularly missing sire data, can significantly impact the accuracy of heritability estimates in genetic evaluations (Harder *et al*., 2005; Nilforooshan *et al*., 2008). Missing or misidentified sire information introduces bias in estimating genetic parameters, leading to inflated or deflated estimates of breeding values and genetic progress (Harder *et al*., 2005; Nilforooshan *et al*., 2008). Studies have shown that increasing levels of missing sire information (MSI) result in reduced rank correlations between true and estimated breeding values, particularly for low heritability traits. For example, when MSI reaches 40%, the variance of estimated breeding values can decrease by as much as 14% for test bulls and 8% for proven bulls (Harder *et al*., 2005). This reduction in variance causes inaccuracies in ranking top-performing sires and diminishes the overall genetic gain, with losses in selection response reaching up to 12.6% for traits with lower heritability estimates. Consistent with these findings, Nilforooshan *et al.* (2008) observed that missing sire data led to underestimation of genetic variances and heritability estimates, with models missing sire information showing significantly lower correlations with complete animal models, particularly in low heritability traits. Nilforooshan's study further found that missing sire data disrupts genetic relationships within and between herds, weakening the ability of models to account for the merit of herd mates, and reducing the precision of genetic evaluations. Additionally, the study highlighted that models missing dam information tend to overestimate heritability estimates, adding further biases that can mislead breeding decisions. These biases from incomplete or incorrect parentage information underscore the importance of accurate pedigree recording to ensure more reliable heritability estimates and genetic evaluations, which ultimately supports selection decisions and genetic gains (Harder et al., 2005; Nilforooshan et al., 2008).

Post-wean growth test traits heritability estimates were estimated on the larger data set of 2002-2022 and these estimates varied among breeds. Angus demonstrated moderate to high heritability for average daily gain (0.19 ± 0.05), hip height (0.31 ± 0.06), body length (0.18 ± 0.05), and scrotal circumference (0.37 ± 0.07). Charolais exhibited moderate heritability for average daily gain (0.39 ± 0.30) and scrotal circumference (0.57 ± 0.28), but lower estimates for hip height (0.06 ± 0.15) and body length (0.28 ± 0.50). Hereford cattle showed moderate heritability for average daily gain (0.31 ± 0.10) and hip height (0.29 ± 0.09), but lower estimates for body length (0.12 ± 0.06) and scrotal circumference (0.21 ± 0.10).

In literature, the average daily gain (ADG) for Angus was (0.28 kg) and Charolais (0.25 kg) were found to be consistent with values reported in this study (Bradfield *et al*., 2000; Orenge *et al*., 2009). However, the ADG for Hereford (0.31 ± 0.10 kg) was significantly higher than previous studies (0.10 kg) (Orenge *et al.*, 2009), which is possibly due to overestimation because of low records and data structure issues. Genetic correlations also varied among breeds. Angus and Charolais both exhibited strong positive correlations between ADG, hip height, and body length, indicating potential for simultaneous improvement in these traits. In contrast, Hereford showed weaker correlations between ADG and hip height due to fewer phase C and D records. For Angus, literature heritability estimates for hip height at 400 days is 0.6, with body length at 0.24, and genetic correlations between weight and body dimensions range from 0.66 (height) to 0.89 (length) (Afolayan *et al*., 2007). In the literature the Hereford breed has lower heritability estimates for hip height (0.42) and body length (0.25) but still shows strong genetic correlations between weight and body dimensions (0.61 to 0.90) (Afolayan *et al.,* 2007). Literature is sparse but the Charolais estimates are expected to display similar growth trends as the other two breeds due to its strong growth potential and large frame size. Overall, high genetic correlations between weight and body dimensions suggest that selection for one trait will lead to improvements in others.

The data structure significantly impacted the accuracy of genetic evaluations for all three breeds. Angus, with the largest dataset spanning 20 years, yielded the most reliable results with log-likelihood confirming the most appropriate models, demonstrating the importance of sufficient data for accurate variance component estimation. Charolais, despite having a smaller dataset, achieved satisfactory results due to its well-structured data, highlighting the potential for robust genetic evaluations even with limited data. Hereford, with a larger dataset than Charolais but a less optimal data structure, struggled to estimate maternal components, leading to less accurate results as seen with the maternal component that could not be determined. These findings highlight the critical role of data quality and quantity in genetic evaluation. A larger or well-structured dataset can enhance the accuracy and reliability of genetic components. Breeders should prioritize data collection and management to ensure the availability of high-quality data for genetic evaluations.

5.5. Estimated breeding values

Estimated Breeding Values (EBVs) are the primary product of genetic evaluation and the selection tool available for stud breeders. In this study EBVs were calculated for the SA Angus breed using a 20-year dataset spanning 2002 to 2022, which was deemed more comprehensive than a 10-year dataset (2012-2022) for assessing long-term genetic trends. The resulting EBVs were standardized to a base year of 2000 and compared to historical estimates from SA Stud Book.

Pre-wean traits

The genetic trend for birth weight direct started at an average EBV of -0.65 in 1976 ending at an average of -0.05 in 2022 showing an upward trend at the start and then tapering off around the average towards 2022 with a genetic decrease in birth weight of 0.60 kg. Comparatively the national trend previously estimated for birth weight direct started at an average of -1.24 in 1976 and increased with a constant upward trajectory to a value of 0.68 in 2022, showing a 1.92 kg genetic decrease in birth weight. This difference is possibly due to the current data set having more data values, different heritability estimates and different models used between the studies. The trend also showed a stabilisation of birth weight EBVs In the Angus population. The genetic trend for birth weight maternal began at an average EBV of 0.11 and ended at an average EBV of 0.16 showing a genetic decrease of 0.05 kg in birth weight from 1976 to 2022. Maternal EBVs can provide more information for the prediction of calf size, this trend indicates that cows with a greater ability to restrict calf growth in utero were possibly selected for between 1976 and 1995 and then as cow size increased, they could select for larger calves at birth to an above average EBV (Lykins *et al.*, 2000; Herd & Oddy, 2023). The national trend for birth weight maternal in 1987, where more records could be investigated, had an upward trend ending at an average EBV of 0.17. The end points for both trend lines are very close together indicating more similar heritability estimates in later years.

The genetic trend for wean weight direct showed a genetic increase of 8.08 kg for weaning weight over the period (1976 to 2022). The national trend in comparison showed a much larger variation and genetic increase of 28.22 kg to 2022. This reflects an intensified selection for increased weaning weights within the population, as calf weaning weight serves as a key indicator of cow-calf productivity and is thus favoured by the industry to enhance overall efficiency and profitability (Melucci *et al.*, 2009; Lalman *et al.*, 2019) with the trend calculated with data from this study being more conservative than the national study, possibly reflecting different genetic evaluation methods and heritability estimates. The genetic trend for wean weight maternal started at an average EBV of -0.38 and ended at an average of -0.57 (0.19 kg genetic decrease) which shows a downward trend in maternal ability in the population which is most likely due to the very high negative correlation between direct and maternal wean weight heritability estimates of -0.65 previously discussed (David *et al.*, 2015). In contrast the national trend for weaning weight maternal started at -4.45 and ended at an average EBV of 2.25 (6.70 kg genetic increase) showing an upward trend with some deviations along the trend line. This difference could be due to increased data in this study and refined genetic evaluation methods resulting in more conservative results.

Post-wean traits

The 12-month weight genetic trend and national trend both had upward trends with this study’s trend starting at -4.31 and ending at 9.53 and the national trend starting at -22.66 and ending at an average EBV of 29.32 in 2022. This shows a genetic increase of 13.84 kg and 51.98 kg for the current studies genetic trend and the national trend respectively. This indicates that there has been selection for increased post-natal growth resulting in heavier animals at 12-months of age (Carter *et al.*, 2012; Bennett *et al.*, 2021) with the trend in this study resulting again in more conservative results and a straighter trend line. Similar results are seen for the trend of average 18-month EBVs. The genetic trend from this study started at -5.12 and ended at 10.02 and the national trend started at a value of -39.87 and ended at an average EBV of 40.35. This indicates a genetic increase of 15.14 kg and 80.22 kg for the current study's genetic trend and the national trend respectively. Showing an increase in the average 18-month weights in the Angus breed which is expected as 18-month weight is highly positively correlated with 12-month weight (Carter *et al.*, 2012). The trend from this study was more consistent showing improved data recording where the national trend had a stepper upward trend due to fewer records.

Overall, the results highlight the effectiveness of genetic selection programs in SA Angus cattle. However, the current study estimated a high negative correlation between for weaning weight direct and weaning weight maternal (-0.65), which might have caused the negative genetic trend for weaning weight maternal, which needs further investigation. The consistent genetic improvement observed for most traits demonstrates the positive impact of breeding efforts on the breed's productivity and performance. However, further research is needed to elucidate the underlying factors influencing genetic trends and optimize breeding strategies for sustainable genetic progress.

5.6. Conclusions and recommendations

5.6.1 Conclusions

This study underscores the foundational role of robust data quality and advanced model selection in driving genetic improvement in beef cattle. The analysis focused on economically important traits in Angus, Charolais, and Hereford cattle breeds, utilizing extensive datasets and advanced statistical methods. The traits examined included pre-weaning and post-weaning growth, birth weight, weaning weight, yearling weight, 18-month weight, and growth test traits such as average daily gain, hip height, body length, and scrotal circumference. The primary objectives were to explore the data structure, determine significant effects for model development, and estimate variance components for all three breeds. Additionally, a BLUP analysis was conducted for the South African Angus breed.

Single-trait models proved invaluable for identifying significant environmental effects, such as the Sire × Herd (SXH) interaction, which highlighted breed-specific responses to management factors. For instance, the inclusion of SXH and Permanent Environment (PE) effects in models for traits like birth, weaning, and 18-month weights increased the accuracy of genetic evaluations by accounting for stable influences and reducing residual variance.

Multi-trait models, in turn, leverage genetic correlations among traits to improve heritability estimates and accuracy in predicting breeding values, especially for complex and interrelated traits. By allowing for shared information across correlated traits, multi-trait models capture a broader range of genetic variance and effectively compensate for missing records or incomplete data in individual traits. These models have driven genomic selection efforts forward, as they offer a more comprehensive evaluation of growth and productivity traits, accelerating genetic gains. This advancement supports long-term breeding goals by selecting animals with superior genomic potential, optimizing both production traits and adaptability to diverse environments in the beef industry.

However, data limitations, such as small datasets, small contemporary groups, and incomplete pedigree information, particularly affect the reliability of heritability estimates and genetic parameter accuracy. Small datasets, or those lacking crucial pedigree data like sire identification, introduce biases, reduce rank correlations, and lead to under- or overestimation of heritability estimates, especially for low-heritability traits. Incomplete pedigree data weakens genetic connectedness within and across herds, impairs model accuracy, and can lead to inaccuracies in ranking animals.

The study also highlights how the presence of complete, long-term data enhances genetic evaluations. For example, the 20-year dataset for the Angus breed provided deeper pedigree depth and broader contemporary group structure, improving the accuracy of genetic parameter estimation and facilitating more reliable EBVs. Conversely, the Charolais with smaller data sets but more complete recording resulted in more reliable estimates than the Hereford which has a larger dataset but less optimal data structure and therefore, faced greater challenges in estimating maternal and other genetic components accurately. Such observations underscore the importance of complete and high-quality data in achieving accurate genetic evaluations and maximizing the benefits of selection programs.

In conclusion, a robust and comprehensive data structure, along with the application of both single-trait and multi-trait models, is essential for accurate genetic evaluations and informed breeding decisions. By enhancing data collection practices and refining model approaches, breeders can achieve greater genetic gain, ensure sustainable improvements in productivity, and support future genomic selection programs tailored to the beef cattle industry's evolving demands.

5.6.2 Recommendations

Future studies could explore various data structures and recording depths to further explore the impact of small data sets on heritability and breeding value estimates. For instance, comparing results from a study including only breeders with complete data for all traits to a dataset with incomplete records would demonstrate the importance of comprehensive data collection and its impact on genetic estimates and their reliability. Additionally, an in-depth investigation into how pedigree depth and accuracy influence these estimates could provide valuable insights. Using parentage verification to assess pedigree accuracy and analyse the impact of resolving pedigree conflicts on model effects, such as maternal effects, could further enhance our understanding of the genetic architecture of traits and improve genetic evaluation models. These studies would contribute to the development of more accurate and reliable genetic evaluations, ultimately leading to increased genetic improvement in beef cattle breeding programs.

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Addendum A

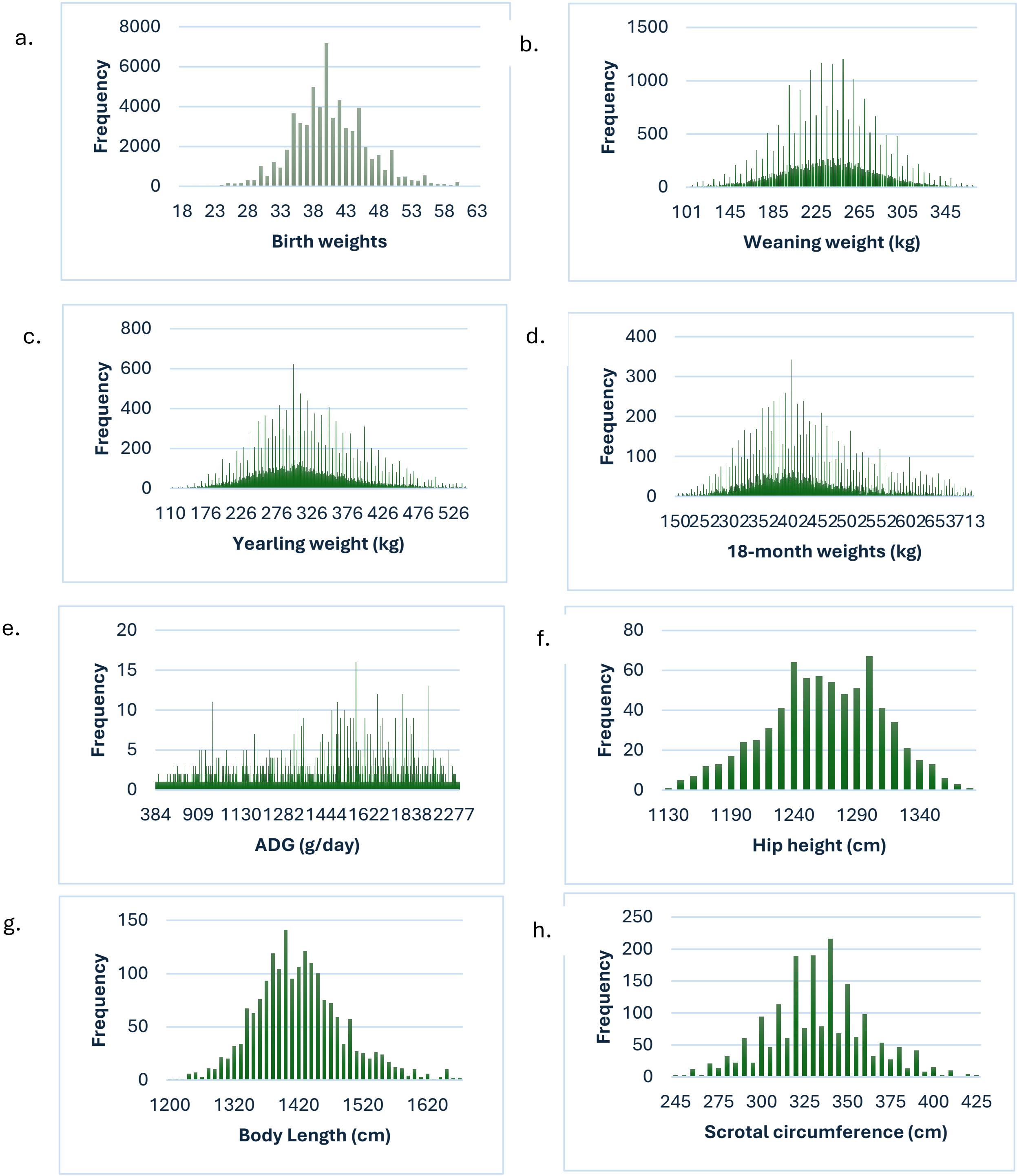

Figure 1A Histogram distribution plots of (a) birth weight, (b) weaning weight, (c) yearling weight, (d) 18- month weights, (e) average daily gain, (f) hip height, (g) body length, (h) scrotal circumference for the Charolais cattle breed

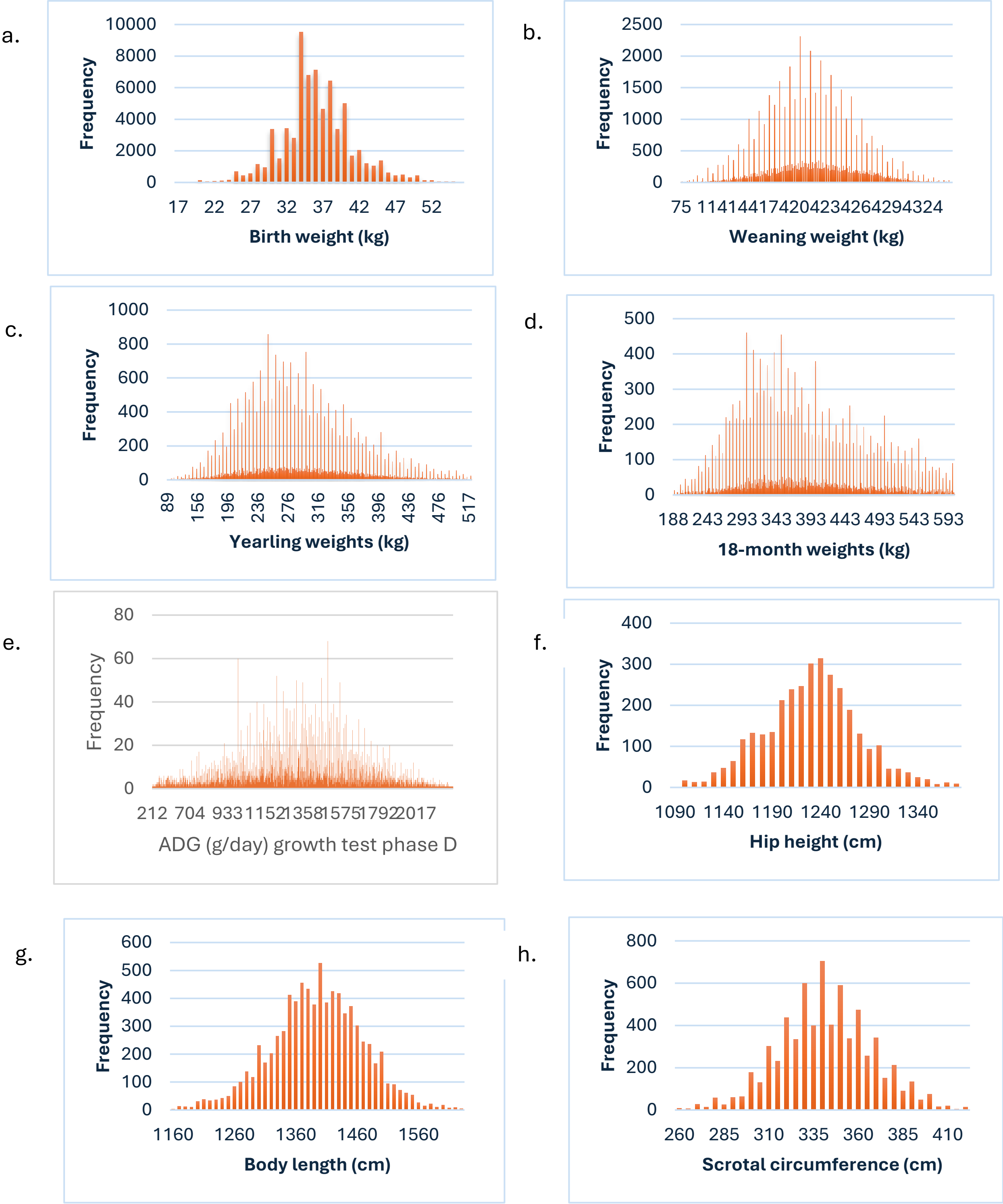

Figure 2A Histogram distribution plots of (a) birth weight, (b) weaning weight, (c) yearling weight, (d) 18- month weights, (e) average daily gain, (f) hip height, (g) body length, (h) scrotal circumference for the Hereford cattle breed.

Addendum B

Table 1B Single-trait heritability and correlation estimates with their associated standard error for various Charolais birth weight models

Data selection	Trait	Direct heritability	Maternal heritability	Correlation	Permanent environmental effect (PE)	Residual
2012 -2022	Model 1	0.35 ± 0.06	0.16 ± 0.04	-0.63 ± 0.11	0.08 ± 0.03	0.70 ± 0.07
	Model 2	0.35 ± 0.06	0.23 ± 0.04	-0.55 ± 0.04		0.73 ± 0.06
2002 - 2022	Model 1	0.43 ± 0.05	0.11 ± 0.02	-0.65 ± 0.08	0.08 ± 0.02	0.67 ± 0.06
	Model 2	0.42 ± 0.05	0.15 ± 0.02	-0.53 ± 0.08		0.70 ± 0.05

Table 2B Single-trait heritability and correlation estimates with their associated standard error for various Charolais weaning weight models

Data selection	Trait	Direct heritability	Maternal heritability	Correlation	Permanent environmental effect (PE)	Sire by herd effect (SXH)	Residual
2012 - 2022	Model 1	0.01 ± 0.02	0.05 ± 0.03	1.00 ± 0.004	0.11 ± 0.02	0.04 ± 0.01	0.74 ± 0.03
	Model 2	0.16 ± 0.05	0.09 ± 0.04	-0.37 ± 0.27	0.12 ± 0.03		0.73 ± 0.05
	Model 3	0.16 ± 0.05	0.20 ± 0.04	-0.35 ± 0.22			0.77 ± 0.05
2002 - 2022	Model 1	0.01 ± 0.01	0.04 ± 0.02	0.98 ± 0.94	0.13 ± 0.02	0.08 ± 0.01	0.72 ± 0.02
	Model 2	0.17 ± 0.04	0.96 ± 0.03	-0.57 ± 0.14	0.15 ± 0.02		0.73 ± 0.04
	Model 3	0.17 ± 0.04	0.21 ± 0.03	-0.39 ± 0.16			0.77 ± 0.04

Table 3B Single-trait heritability and correlation estimates with their associated standard error for various Charolais yearling weight models

Data selection	**Trait**	**Direct heritability**	**Maternal heritability**	**Correlation**	**Permanent environmental effect (PE)**	**Residual**
2012 – 2022	Model 1	0.05 ± 0.03	0.02 ± 0.02	-0.76 ± 0.46	0.05 ± 0.03	0.93 ± 0.04
	Model 2	0.05 ± 0.03	0.05 ± 0.04	-0.51 ± 0.55		0.95 ± 0.03
2002 -2012	Model 1	0.09 ± 0.03	0.005 ± 0.01	-0.99 ± 0.02	0.05 ± 0.02	0.90 ± 0.04
	Model 2	0.10 ± 0.03	0.02 ± 0.02	-0.53 ± 0.31		0.93 ± 0.04
	Model 3	0.08 ± 0.03				0.92 ± 0.03

Table 4B Single-trait heritability and correlation estimates with their associated standard error for various Charolais 18-month weight models

Data selection	**Trait**	**Direct heritability**	**Maternal heritability**	**Correlation**	**Permanent environmental effect (PE)**	**Residual**
2012 - 2022	Model 1	0.15 ± 0.09	0.03 ± 0.03	-1.00 ± 0.00	0.22 ± 0.03	0.73 ± 0.08
	Model 2	0.12 ± 0.08	0.02 ± 0.03	-1.00 ± 0.00		0.96 ± 0.08
2002 - 2022	Model 1	0.18 ± 0.07	0.02 ± 0.03	-0.42 ± 0.38	0.31E-05 ± 0.41E-02	0.85 ± 0.07
	Model 2	0.18 ± 0.06	0.02 ± 0.03	-0.42 ± 0.41		0.85 ± 0.06
	Model 3	0.16 ± 0.05				0.84 ± 0.05

Table 5B Single-trait heritability and correlation estimates with their associated standard error for various Hereford birth weight models

Data selection	Trait	Direct heritability	Maternal heritability	Correlation	Permanent environmental effect (PE)	Residual
2012 - 2022	**Model 1**	0.30 ± 0.05	0.06 ± 0.02	-0.52 ± 0.14	0.09 ± 0.02	0.70 ± 0.05
	Model 2	0.28 ± 0.05	0.11 ± 0.03	-0.33 ± 0.12		0.73 ± 0.05
2002 - 2022	**Model 1**	0.001 ± 0.001	0.49 ± 0.01	-0.99 ± 0.01	0.11E-02 ± 0.53E-02	0.55 ± 0.28
	Model 2	0.002 ± 0.002	0.51 ± 0.01	-1.00 ± 0.001		0.55 ± 0.67E-02
	Model 3	0.10E-13 ± 0.62E-08				1.00 ± 0.62E-08

Table 6B Single-trait heritability and correlation estimates with their associated standard error for various Hereford weaning weight models

Data selection	Trait	Direct heritability	Maternal heritability	Correlation	Permanent environmental effect (PE)	Residual
2012 – 2022	**Model 1**	0.17 ± 0.04	0.11 ± 0.03	-0.71 ± 0.11	0.30 ± 0.02	0.61 ± 0.04
	Model 2	0.19 ± 0.05	0.52 ± 0.03	-0.66 ± 0.10		0.71 ± 0.05
2002 - 2022	**Model 1**	0.03 ± 0.02	0.62 ± 0.01	-0.25 ± 0.95	0.09 ± 0.01	0.33 ± 0.01
	Model 2	0.04 ± 0.02	0.64 ± 0.01	-0.24 ± 0.61		0.39 ± 0.01
	Model 3	0.07 ± 0.04				0.93 ± 0.04

Table 7B Single-trait heritability and correlation estimates with their associated standard error for various Hereford yearling weight models

Data selection	Trait	Direct heritability	Maternal heritability	Correlation	Permanent environmental effect (PE)	Residual
2012 – 2022	**Model 1**	0.07 ± 0.08	0.05 ± 0.06	-0.43 ± 0.67	0.18 ± 0.03	0.75 ± 0.09
	Model 2	0.08 ± 0.08	0.10 ± 0.07	-0.20 ± 0.60		0.86 ± 0.07
2002 - 2022	**Model 1**	0.25 ± 0.02	0.63 ± 0.01	0.05 ± 0.02	0.12E-16 ± 0.19E-18	0.09 ± 0.69E-02
	Model 2	0.21 ± 0.13	1.53 ± 0.04	-0.99 ± 0.05		0.40 ± 0.07
	Model 3	0.11 ± 0.09				0.89 ± 0.09

Table 8B Single-trait heritability and correlation estimates with their associated standard error for various Hereford 18-month weight models

	Trait	Direct heritability	Maternal heritability	Correlation	Permanent environmental effect (PE)	Sire by herd effect (SXH)	Residual
2012 - 2022	**Model 1**	0.01 ± 0.03	0.03 ± 0.04	1.000 ± 0.001024	0.12E-11 ± 0.20E-06	0.12 ± 0.02	0.80 ± 0.04
	Model 2	0.18 ± 0.11	0.03 ± 0.04	-1.000 ± 0.0031	0.31 ± 0.05		0.62 ± 0.05
	Model 3	0.21 ± 0.09	0.04 ± 0.08	-0.29237 ± 0.62318			0.81 ± 0.10
2002 - 2022	**Model 1**	0.22 ± 0.01	0.64 ± 0.01	0.04341 ± 0.024145	0.81E-16 ± 0.18E-17	0.76E-15 ± 0.12E-13	0.11 ± 0.01
	Model 2	0.34 ± 0.16	1.60 ± 0.06	-1.00 ± 0.001	0.83E-02 ± 0.25E-02		0.53 ± 0.13
	Model 3	0.56 ± 0.20	1.73 ± 0.09	-0.95 ± 0.22			0.59 ± 0.26
	Model 4	0.24 ± 0.16					0.76 ± 0.16