

**GENETIC IMPROVEMENT OF GROWTH TRAITS IN *JEBEL AKHDAR*
GOATS, *BATINAH GOATS*, AND *OMANI SHEEP* IN OMAN**

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Abstract

The objective of the present thesis was to estimate the genetic parameters associated with growth traits, specifically birth weight (BW), weaning weight (WW), six-month weight (W6), and yearling weight (W12), among Jebel Akhdar (JA) goats, Batinah (BA) goats, and Omani sheep (OS) in Oman. In addition, the level of inbreeding and its trend over 13 years were investigated for the three breeds. Finally, a simulation study was carried out to examine the feasibility of implementing genomic selection (GS) in OS sheep with the aim of enhancing the genetic improvement of these traits. The analysis utilised data obtained from the Wadi Qurayyat Livestock Research Station (WQLRS) in Oman over the years 2008 to 2020. The dataset comprises 2,826 records of JA goats, 2,609 records of BA goats, and 3,530 records of OS sheep.

The heritability estimates for BW, WW, W6, and W12 in JA goats were 0.13 ± 0.04 , 0.11 ± 0.04 , 0.19 ± 0.05 , and 0.21 ± 0.06 , respectively. In comparison, the values for BW, WW, W6, and W2 were found to be 0.17 ± 0.04 , 0.16 ± 0.04 , 0.16 ± 0.04 , and 0.24 ± 0.04 , respectively, in BA goats. In Omani sheep, the observed values for BW, WW, W6, and W12 were 0.16 ± 0.03 , 0.15 ± 0.03 , 0.28 ± 0.05 , and 0.48 ± 0.05 , respectively. The three breeds showed a positive genetic trend for all growth traits, although the phenotypic trend was only significant for the W12 phenotype. The annual genetic gain for BW, WW, W6, and W12 in JA goats was measured as 0.01 kg, 0.09 kg, 0.13 kg, and 0.20 kg, respectively. The BA goats exhibited an annual increase in genetic gain of 0.01 kg, 0.08 kg, 0.10 kg, and 0.18 kg for BW, WW, W6, and W12, respectively. The genetic gain for BW, WW, W6, and W12 in OS sheep exhibited annual increments of 0.01 kg, 0.13 kg, 0.22 kg, and 0.39 kg, respectively. The genetic

correlations between the different traits in the three breeds were found to be positive and strong, except for the correlations with the BW trait, which had low correlations. The results of this study highlight the potential for significant genetic improvement in the growth traits associated with the investigated Omani breeds, considering their sufficient genetic variability and the favourable genetic correlations seen between them, particularly with respect to post-weaning traits.

The inbreeding levels within the three breeds were found to be very low, with estimations of 0.67% in JA goats, 0.65% in BA goats, and 1.52% in OS sheep on average. The observed levels of inbreeding among the inbred animals were 3.88%, 3.39%, and 6.49% for the respective breeds. However, there has been a notable increase in inbreeding rates, especially in recent years, necessitating the need for continuous monitoring and the implementation of measures to control it.

The simulation study has indicated that the ssGBLUP method demonstrated superior performance on prediction accuracy of breeding values averaging (0.64) across the traits of BW, W6, and W12 in OS sheep compared to the methods of BLUP (0.56) and GBLUP (0.47). The precision of the three methods was enhanced with an increase in heritability. The genomic prediction accuracy of GBLUP and ssGBLUP was enhanced by increasing the reference size. The average improvements were 0.43, 0.48, and 0.50 for GBLUP, and 0.61, 0.64, and 0.67 for ssGBLUP. These improvements were observed at reference sizes of 500, 1000, and 2000 animals, respectively. For traits with low heritability in particular, ssGBLUP may be a useful method for increasing prediction accuracy when compared to BLUP and GBLUP. The outcomes provide a theoretical framework for implementing GS in OS sheep.

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Dedication

This thesis is dedicated to the pillars of my life, who have provided unwavering support, boundless love, and endless inspiration throughout this journey. To my beloved wife, whose strength, patience, and love have been my sanctuary. Your belief in me has been the light guiding me through the challenges. Your sacrifices have not gone unnoticed, and this achievement is as much yours as it is mine. To our cherished children, who remind me every day of the wonders and joys of life. Your laughter and curiosity fuel my determination to contribute to a world that holds a brighter future for you. This journey has been for you as much as it has been for me, hoping to inspire you to chase your dreams, no matter the hurdles. And to my dear parents, who instilled in me the values of hard work and perseverance. Your endless support and unconditional love have shaped me into the person I am today. This accomplishment is a tribute to your unwavering faith in me and a reflection of the lessons you have taught me. Each of you holds a place in this journey and in every page of this thesis. This is for you.

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List of Abbreviations

AIC	Akaike information criterion
AI-REML	Average Information REML
ANOVA	Analysis of variance
BA	Batinah
BLUP	Best Linear Unbiased Prediction
BT	birth type
BV	breeding value
BW	birth weight
CNV	copy number variations
DNA	Deoxy Ribonucleic Acid
EBV	estimated breeding value
EGBV	estimated genomic breeding value
EqG	Equivalent complete generations
F	inbreeding coefficient
FAO	Food and Agriculture Organization
GBLUP	Genomic Best Linear Unbiased Prediction
GBV	genomic breeding values
GEBV	genomic estimated breeding value
GS	genomic selection
IBD	identical by descent
IBS	identical by state
JA	Jebel Akhdar
LD	linkage disequilibrium
LogL	loglikelihoods
LRT	Loglikelihood ratio test
LS	litter size
MAF	Ministry of Agriculture and Fisheries, Oman
MAS	marker-assisted selection
MLE	Maximum likelihood estimation
MME	mixed model equations
MSA	mean squared between groups
MSE	mean square for the error
NCSI	National Centre for statistics information
OS	Omani sheep

QTL	Quantitative trail loci
REML	Restricted maximum likelihood estimation
SNP	Single nucleotide polymorphism
SR	small ruminants
ss-GBLUP	single step-Genomic Best Linear Unbiased Prediction
SSLPs	simple sequence length polymorphisms
SSR	single sequence repeats
TBV	true breeding value
W12	yearling weight
W6	six-month weight
WQLRS	Wadi Qurayyat livestock research station
WW	weaning weight

CHAPTER ONE

INTRODUCTION

1.1 Introduction

Goats and sheep play an important part in Oman's domestic livestock sector, contributing to both social and economic aspects. The importance of small ruminants (SR), namely sheep and goats, in Oman is clearly demonstrated by their population, which accounts for 81.38% of the overall livestock population. According to the National Centre for Statistics and Information (NCSI (2021), the livestock population in Oman totalled 3,791,000 animals. Out of these, goats comprised 64.44% of the total, while sheep accounted for 16.94% (**Figure 1**). Small ruminants (SR) are known to require minimum labour, and are easy to manage, so supporting sustainable business-related livestock (Bosso et al., 2007).

Due to the fact that SR are in abundant numbers in Oman compared to other livestock and have the ability to thrive in the challenging, mountainous environments that define many regions of Oman, goats and sheep may present significant contributions to the production of red meat (Mahgoub et al., 2010). Based on the data from the Ministry of Agriculture and Fisheries in Oman (MAF (2019), Oman accounts for producing 50% of the nation's domestic consumption of red meat. Therefore, the Omani government prioritises efforts to narrow the gap between the consumption and production of red meat. A potential strategy to achieve this objective involves improving the growth traits of the domesticated farm animals by subjecting them to breeding programmes, i.e., genetic improvement via within-population selection.

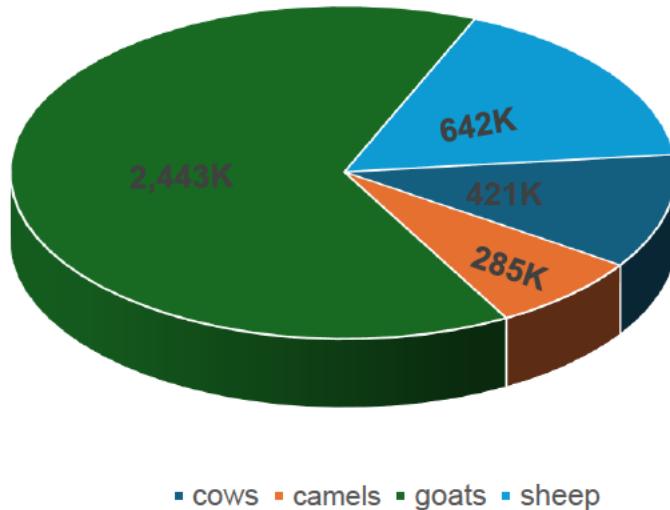


Figure 1. Total numbers of farm animals in Oman in 2021. K: thousand. Data from NCSI (2021).

Growth traits serve as an important component in livestock breeding, with a specific emphasis on increasing meat production. They essentially reflect an animal's potential to produce meat, and hence, enhancing these characteristics typically leads to increased productivity and profitability in meat production enterprises (Eisen, 1976). They are influenced by a combination of genetic and environmental factors, which means that their improvement would lead to enhancing the traits themselves (Bahreini Behzadi et al., 2007; Tesema et al., 2022).

To this end, the Ministry of Agriculture and Fisheries in Oman has set up a number of livestock research stations in an effort to implement breeding programmes. The Wadi Qurayyat livestock research station (WQLRS) is one of these stations located in Bahla city. It serves a key role in conserving and enhancing the genetic merit of nucleus herds/flocks of SR. The station houses two common breeds

of goats, which are Jebel Akhdar and Batinah, as well as a local breed of sheep known as Omani sheep.

To successfully carry out genetic improvement schemes, it is essential to accurately estimate a number of significant genetic parameters that define the population, including the heritability of the desired traits and the genetic correlations among those traits. The heritability of a trait provides information about how it will respond to selection, whereas genetic correlations reveal the direction and magnitude of the impact that the selected trait has on other traits being investigated (Singh et al., 2022). Also, it is imperative to evaluate these programmes by looking at the genetic trend, which involves monitoring changes in the genetic merit of the animals over a specific period of time. It serves as an indicator of the success and effectiveness of existing breeding strategies (Wilson et al., 2010) .

Genetic improvement projects, especially those that apply selection within a population, tend to give rise to increased rates of inbreeding. This is because the population is closed by nature, and individuals are under selection pressure. Progressive inbreeding can result in a reduction in genetic variation within a population, which is an essential aspect of animal breeding programmes. Consequently, this hinders the ability of individuals to respond appropriately to future selection and adapt to environmental changes (Ceyhan et al., 2011; Mandal et al., 2020). Furthermore, research studies have demonstrated that excessive inbreeding commonly results in negative effects, known as inbreeding depression, on the productivity, health, and reproductive capacities of animals (Falconer, 1996). Thus, it is critical to prioritise the estimation and control of inbreeding levels in the population undergoing genetic improvement while ensuring that genetic improvement is both efficient and sustainable.

The present chapter focuses on the following:

- 1. Factors of the environment and genetics that impact growth traits.**
- 2. Partitioned components of the phenotypic variance, which are then used to estimate genetic parameters, viz., heritability and genetic correlation, the importance of the genetic parameters in selection programmes, and various methods used to estimate them:**
 - Analysis of variance (ANOVA).
 - Maximum likelihood estimation (MLE).
 - Restricted maximum likelihood estimation (REML).
- 3. The genetic merit, also known as breeding value (BV) of animals and the common traditional methods used to estimate it:**
 - Selection index and BLUP.
- 4. Utilising molecular markers to precisely estimate breeding values:**
 - Quantitative trait loci (QTL).
 - Molecular markers :
 - Microsatellites.
 - Single nucleotide polymorphism (SNP).
 - Genomic approaches to predicting breeding values:
 - SNP-BLUP.
 - GBLUP.

- ssGBLUP.
- *Challenges to implementing genomic selection in sheep and goats.*

5. Inbreeding: the concept, the effects, control measures, and its quantifying methods.

1.2 Environmental and genetic factors influencing growth traits

Growth traits are a subset of quantitative traits that are influenced by a combination of genetic and environmental influences, as well as their interactions. The environmental factors influencing growth traits might be random or fixed. Several environmental fixed factors can impact the growth of animals (Bahreini Behzadi et al., 2007). Significant factors can include the animal's sex, type of birth, age of dam, herd, and year of birth (Baneh et al., 2012). The influence of these variables may differ depending on the particular trait and the population being studied. Accurately adjusting observations for fixed effects must be done in order to obtain unbiased estimates of the genetic parameters (Chauhan et al., 2021; Singh et al., 2022).

Baneh et al. (2012) found that traits of birth weight (BW), and weaning weight (WW) have been significantly influenced by herd, birth year, type of birth, sex, and dam age in Naeini goats. Likewise, the fixed effects of birth year, sex, birth type, and age of doe were significant in all the studied traits of growth in Markhoz goats (Shirzeyli et al., 2023). In their research on Dorper A indigenous sheep, Tesema et al. (2022) observed that the live body weights at different ages were influenced by factors such as the type of birth, sex, year, and season. Another study found that the growth traits were influenced only by year, sex, and birth type (Areb et al., 2021). Year, dam age, and sex factors have been found to influence the growth traits in Kermani sheep, while birth type was only significant with the WW trait (Bahreini Behzadi et al., 2007).

The variability observed among the levels of environmental fixed components, which contributes to the phenotypic expression, is typically attributed to variations in biological systems, climatic fluctuations, and the availability of feed resources. For instance, the impact of dam age may be attributed to the maturation of the uterus and

mammary glands, resulting in an increment in milk production as age progresses. The impact of birth type can be explained by the intrauterine competition between twins for limited uterine space and resources, such as milk, which is comparable to that of single offspring (Baneh et al., 2012). While the impact of sex on growth traits can be attributed to the influence of certain sex hormones on muscle and skeleton development (Tesema et al., 2022).

The expression of an individual's phenotype is determined not only by the direct effects of its direct additive genetic and environmental factors but also by the presence of maternal effects, particularly in early life traits (Tesema et al., 2022). The maternal influences may include factors such as mothering ability, milk production, and the uterine environment. They can be partially ascribed to the genetic influence of the dam or can be influenced by the environment given by the dam, in which they all influence maternal ability (Baneh et al., 2012; Mrode, 2014). Thus, by investigating these factors and incorporating them into the models used to estimate genetic parameters, more accurate estimations can be obtained, leading to the optimisation of genetic improvement. However, it is not always feasible to analytically separate the maternal components into additive genetics and a permanent environment due to the structure of the data (Meyer, 1992). For instance, Bangar et al. (2020) observed in their study on Jakhrana goats that the analytical model used was unable to separate between the various components of maternal effects because of the small sample size.

1.3 Partitioning the phenotypic variance (V_P)

According to Falconer (1996), the phenotypic value of an individual (P) is determined by its genetic effects (G), and environmental deviation (E). The E value here includes all non-genetic influences. Mathematically, it can be expressed as:

$$P = G + E \quad (1)$$

Yet, animal breeders have to deal with a value that can be transmitted from parents to offspring, a mean that cannot be accomplished solely through the G value, because the G value is not transmitted as it is but is formed in the progeny afresh from the parents. So, the animal breeder is interested in a value, which can be assigned to the individual genes rather than the genotype as a whole, that can be partitioned from the genetic value, and transferred to the offspring. This value is referred to as the average effect value (A). The mean deviation of offspring from the population average when one parent passes on a certain allele to their offspring and the other allele is inherited randomly from the population is known as the additive effect (A) of a gene.

Accordingly, the mean genetic value of offspring is determined by the overall effects of parental genes. The total summation of these average effects of genes exhibited by an individual is commonly referred to as the estimated breeding value (EBV), also known as the additive effect (A). In addition to the A values of the genes, the genotypic value of an individual is influenced by the interactions within a locus, namely the dominance effects (D), and the interactions between loci (I). Hence, equation (1) can be extended to become as (Bourdon & Bourbon, 2000; Falconer, 1996) :

$$P = A + D + I + E \quad (2)$$

The basis for understanding the genetic structure of a quantitative trait is in its variability, which involves splitting the variance in phenotypic expression into different components associated with a range of factors. The genetic properties of a population are determined by the relative contribution of these components to the phenotypic variance (Falconer, 1996). The progress of a genetic improvement programme principally relies on the existence of the genetic variation among the individuals, so that they can respond effectively to selection (Singh et al., 2022). From equation (2), the variance in the phenotypic values (V_P) can be attributed to variances in genotypic effects or its components, as well as environmental effects, which can be expressed mathematically as follows:

$$V_P = V_A + V_D + V_I + V_E \quad (3)$$

However, as previously stated, animal breeders are primarily concerned with the portion of variance that may be attributed to the additive effects of the genes, which refers to the variances between the breeding values of the animals, assuming that the dominance and epistasis effects are negligible. Consequently, equation (3) can be shortened to:

$$V_P = V_A + V_E \quad (4)$$

The additive genetic variance (V_A) is of the utmost importance in genetic improvement programmes as it primarily is responsible for the resemblance between relatives, thereby it influences the observable genetic properties within a population and serves a key role in determining the population's response to selection. Additionally, it is the only genetic component among other sources of genetic variation that can practically be calculated from observations that differ from the population average(Oldenbroek and van der Waaij, 2014). The relative contribution of the V_A to the V_P is one of the fundamental genetic parameters that needs to be estimated in genetic breeding programmes, which is known as the heritability (h^2). It quantifies the proportion of the phenotypic variance of a trait that can be attributed to the variance caused by the additive effects of genes, which can be modelled as:

$$h^2 = V_A/V_P \quad (5)$$

Another genetic parameter that can be estimated from partitioning the phenotypic variance is the genetic correlation (r_g), which quantifies the association among various traits caused by the additive genetic effects. It is calculated as:

$$r_g = \frac{Cov(trait_1, trait_2)}{\sqrt{V_{A_1}V_{A_2}}} \quad (6)$$

1.4 Genetic parameters (heritability and genetic correlation)

Animal breeding programmes rely on the estimation of heritability for the targeted trait, which evaluates the proportionate influence of the additive genetic effects on the overall variability of measurable traits within a population. It explains the extent to which the trait can be improved by genetic selection. So, its estimation is involved in predicting the response to selection and estimating the EBVs of individuals (Getabalew et al., 2019).

There are two distinct themes of heritability, namely broad sense-heritability (H^2) and narrow sense-heritability (h^2), which are differentiated based on the specific portion of the genetic variance (V_G) used in the estimation process. The calculation of H^2 involves determining the ratio between the total genetic variation V_G and the phenotypic variance V_P . This ratio quantifies the extent to which the overall genotypic variance contributes to the entire phenotypic variance of a given trait. While the estimation of h^2 is determined by the ratio of the additive genetic variance V_A to the total phenotypic variance V_P , which provides an estimate of the phenotypic variance that can be attributed only to the additive genetic variance (Falconer & Mackay, 1996). The transmission of the genetic material from parents to offspring, as explained in the part of variance partitioning above, occurs through the passing on of genes rather than genotypes. Consequently, the narrow sense heritability (h^2) emerges as a crucial parameter for animal breeders seeking to enhance the traits of successive generations of animals.

The heritability (h^2) of a trait can range from 0 to 1. A characteristic with a h^2 value of one indicates that all of the phenotypic variances can be attributed solely to additive genetic influences. Conversely, a h^2 value of zero suggests that the phenotypic differences of a trait are not driven by additive genetic factors. Accordingly, traits can be categorised as having low heritability ($h^2 < 0.20$), moderate heritability ($h^2 = 0.20 - 0.39$), or high heritability ($h^2 \geq 0.40$). It has been suggested that when the value of h^2 is smaller than 0.15, the efficacy of selecting animals based on their performance may be ineffective. In such cases, it may be more advantageous to rely on their EBVs instead (Faid-Allah et al., 2017).

For a given trait, different populations may have varying h^2 estimates, because the h^2 value is specific to the trait, population, and time period in which it was evaluated. This occurs due to the possible changes in the V_A over a time, which is influenced by the changes in allelic frequency resulting from various factors such as selection, genetic drift, and other mechanisms (John-Jaja et al., 2018). Also, the model used to estimate the V_A may give different results according to the fitted factors. Different breeds, and different environmental effects can result in varied h^2 estimates too (Singh et al., 2022).

As it was stated ahead that the trait expression may be influenced collectively by the animal's own genetic merit and its dam's genetic effects. This means that the h^2 might be expressed as direct heritability h_a^2 which is due directly to the influence of animal's additive genetic effects, and as h_m^2 which is attributed to the influence of dam's additive genetic effects (Sharif et al., 2022; Singh et al., 2016; Singh et al., 2022). Ignoring the influence of maternal effects in the estimation of genetic parameters,

particularly in the early traits can result in biased estimations (*i.e.*, overestimated h_a^2). Consequently, this may impact on the selection accuracy, and ultimately the effectiveness of the genetic improvement scheme (Chauhan et al., 2021; Singh et al., 2010). Several studies have shown that, models excluding maternal effects (*i.e.*, environmental, or genetic) may overestimate direct heritabilities (Bahreini Behzadi et al., 2007; Baneh et al., 2012; Tesema et al., 2022).

Another important parameter whose computation contributes to selective breeding programmes is the genetic correlations (r_g) between traits. It quantifies the association between traits in terms of its direction and strength. Thus, it indicates how an improved trait would impact other correlated traits, either in a positive or negative direction. Also, a correlated trait can serve as an indicator for improving a trait that is costly or challenging to measure (Rae, 1952). If two traits display a positive correlation, selecting for one trait will result in a comparable enhancement in the other trait. When two traits display a negative correlation, it indicates that the selection for one trait will result in the shift of the other trait in the opposite direction. Genetic correlations (r_g) span from -1 to +1, with a positive sign indicating positive correlation and a negative sign indicating negative correlation (Oldenbroek & van der Waaij, 2014). Robertson (1959) suggested that a minimum genetic correlation threshold of 0.80 between traits is recommended to minimise the influence of genotypes x environmental interactions, which may compromise the success of breeding programme. As an illustration, when $r_g \geq 0.80$ between two traits, selecting animals based on a certain trait would not lead to reranking of the same animals for the second trait.

1.4.1 Review of some studies on estimating genetic parameters of growth traits in sheep and goats

Numerous studies have been conducted regarding the estimation of genetic parameters of growth traits in various populations of sheep and goats (**Table 1**). The estimates of the heritability (h_a^2) for the various growth traits including BW, WW, W6, and W12 varied between 0.07 and 0.56, whereas the estimations of the maternal heritability (h_m^2) ranged from 0.03 to 0.34. Growth traits often exhibit moderate to high heritability, particularly those expressed throughout later stages of development.

Most of these studies found that the general pattern of the direct heritability (h_a^2) tends to increase with age, while the maternal heritability (h_m^2) tends to diminish gradually. This can be explained by recognising that as an animal grows up, its relying on its genetic merit for growing independently increases, while its dependence on the dam diminishes (Tesema et al., 2022). However, this might not always be the case according to studies such as Baneh et al. (2012) who found that the h_a^2 for the WW was lower than for the BW, Areb et al. (2021) who observed a decreasing trend of h_a^2 , as the animal matures, and Dhakad et al. (2022) who found inconsistent trend for the h_a^2 . Though the maternal effects have commonly an influence only on early growth traits, they may influence also during later stages at W6 and W12, as noticed by Bahreini Behzadi et al. (2007) in Kermani sheep who justified that to the carry over influence of dam genetics from before the weaning (Bangar et al., 2020).

Table 1. Review of estimates of direct and maternal heritabilities of some growth traits in various breeds of sheep and goats.

BW (birth weight), **WW** (weaning weight), **W6** (six-months weight), **W12** (yearling weight).

Breed	Growth trait	Direct heritability	Maternal heritability	Reference
Naeini goat	BW	0.25	-	(Baneh et al., 2012)
	WW	0.07	-	
Dorper X indigenous sheep	BW	0.003	0.20	(Tesema et al., 2022)
	WW	0.14	-	
West African Dwarf goat	BW	0.50	-	(Bossso et al., 2007)
	W6	0.43	-	
	W12	0.30	-	
Djallonke sheep	BW	0.39	-	(Bossso et al., 2007)
	W6	0.54	-	
	W12	0.21	-	
Nellore sheep	BW	0.08	0.07	(I et al., 2017)
	WW	0.03	-	
	W6	0.12	-	
	W12	0.10	0.11	
Bonga sheep	BW	0.56	0.34	(Areb et al., 2021)
	WW	0.36	0.20	
	W6	0.22	0.15	
	W12	0.13	0.39	
Malpura sheep	BW	0.15	0.11	(Dhakad et al., 2022)
	WW	0.13	0.03	
	W6	0.18	0.05	
	W12	0.16	0.06	
Harnali sheep	BW	0.23	0.08	(Chauhan et al., 2021)
	WW	0.10	0.08	
	W6	0.18	-	
	W12	0.11	-	
Jakhrana goat	BW	0.09	-	(Bangar et al., 2020)
	WW	0.21	-	
	W6	0.53	-	
	W12	0.16	-	
Barbari goat	BW	0.31	0.15	(Singh et al., 2022)
	WW	0.23	0.10	
	W6	0.18	0.10	
	W12	0.21	0.09	

The genetic correlations (r_g) between growth traits at various stages in sheep and goats, on the other hand, have been found to be positive, based on the aforementioned studies (**Table 2**). The correlations between the different traits ranged from moderate to high, with the observation that the traits that are close to one another have usually a higher correlation than the traits that are not. The correlations ranged from 0.04 (BW-W12 in Harnali sheep) to 0.99 (W6-W12 in Jakhrana goat).

Table 2. Review of estimates of genetic and phenotypic correlations among growth traits in some breeds of sheep and goats.

BW (birth weight), **WW** (weaning weight), **W6** (six-months weight), **W12** (yearling weight).

Breed	Correlated traits	Direct genetic correlation	Phenotypic correlation	Reference
West African Dwarf goat	BW-W6	0.74	0.30	(Bossu et al., 2007)
	BW-W12	0.73	0.19	
	W6-W12	-	0.74	
Djallonke sheep	BW-W6	0.47	0.40	(Bossu et al., 2007)
	BW-W12	-	0.23	
	W6-W12	-	0.65	
Nellore sheep	BW-WW	0.44	0.36	(I et al., 2017)
	BW-W6	0.62	0.27	
	BW-W12	0.68	0.24	
	WW-W6	0.94	0.76	
	WW-W12	0.79	0.59	
	W6-W12	0.85	0.64	
Bonga sheep	BW-WW	0.20	0.002	(Areb et al., 2021)
	BW-W6	0.23	0.01	
	BW-W12	0.11	0.02	
	WW-W6	0.61	0.52	
	WW-W12	0.19	0.31	
	W6-W12	0.46	0.49	
Malpura sheep	BW-WW	0.27	0.39	(Dhakad et al., 2022)
	BW-W6	0.18	0.28	
	BW-W12	0.21	0.24	
	WW-W6	0.80	0.76	
	WW-W12	0.54	0.53	
	W6-W12	0.68	0.70	
	BW-WW	0.46	0.23	
Harnali sheep	BW-W6	0.16	0.10	(Chauhan et al., 2021)
	BW-W12	0.04	0.07	
	WW-W6	0.47	0.41	
	WW-W12	0.20	0.22	
	W6-W12	0.33	0.55	
	BW-WW	0.91	0.34	
Jakhra goat	BW-W6	0.90	0.34	(Bangar et al., 2020)
	BW-W12	0.78	0.12	
	WW-W6	0.78	0.66	
	WW-W12	0.14	0.41	
	W6-W12	0.99	0.77	
	BW-WW	0.33	0.40	
Barbari goat	BW-W6	0.26	0.25	(Singh et al., 2022)
	BW-W12	0.26	0.21	
	WW-W6	0.76	0.68	
	WW-W12	0.39	0.46	
	W6-W12	0.85	0.67	

1.5 Methods to estimate variance components

1.5.1 Analysis of variance (ANOVA) estimator

The historical progress in variance estimation has mainly relied on the application of the analysis of variance (ANOVA) technique. This technique involves estimating the error variance (σ_e^2) in its most basic fixed model, as shown in equation (7), by equating the mean square for the error (MSE) to its expected value $E(MSE)$. This indicates that the expected value of the mean squared error ($E(MSE)$) is equal to the variance of the error term (σ_e^2), which leads to an estimated variance of the error term ($\hat{\sigma}_e^2$) being equal to the mean squared error (MSE). Subsequently, the extension was wider to include models that incorporate random variables. Initially, focus was on balanced data, and later on, the issue of unbalanced data was addressed (Searle, 1995).

$$y_i = \mu + e_i , \quad (7)$$

where:

The variable y_i represents the phenotypic record of the i th individual, μ is the population mean, and e_i represents the error term of the i th individual.

The extension of the simple fixed model (7) means fitting more random variables that contribute to the overall phenotypic variance rather than solely the error variance. It is known as linear mixed model when it includes fixed and random factors. For illustration, let us consider in a dairy farm that the random variable of i th sire effect (a_i) for the observation of j th daughter in milk production. The model now compared to equation (7) includes two variance components (equation 8), which are the sire effect

variance, and error variance. Both of which contribute to the overall phenotypic variance.

$$y_{ij} = \mu + a_i + e_{ij} \quad (8)$$

In order to calculate the estimated variance of the random components in *equation (8)*, it needs to extend the same principles used in the fixed model (7), which involves equating the mean squared error (*MSE*) and mean squared between groups of *a* (*MSA*) (Sires' groups) to their respective expected values as follows:

$E(MSE) = \sigma_e^2$, which means that $\hat{\sigma}_e^2 = MSE$, for the estimation of error variance.

While $E(MSA) = \sigma_e^2 + n \sigma_a^2$, which means that $MSA = \hat{\sigma}_e^2 + n \hat{\sigma}_a^2$, so the estimated value of the sire variance $\hat{\sigma}_a^2 = MSA - \hat{\sigma}_e^2/n$.

Though the *ANOVA* method is simple and straightforward, it may give a negative estimate for the variance, which is not the case in the parameter space of variance estimations. In addition, data collected from animal breeding programmes is usually not balanced, which was the interest of Henderson (1953) who developed three different methods of estimating variance components from an unbalanced design. These methods are based on selecting a subset of the sum squares and then applying the same logarithms used for the balanced *ANOVA* (Searle, 1995). Yet, indicated that these methods are not free from disadvantages, such as the fact that method 1 cannot be used for a mixed model and method 2 is not suitable when there is an interaction among fixed and random effects.

1.5.2 Maximum likelihood estimation method (MLE)

The maximum likelihood estimation (*MLE*) method is considered to be more efficient and flexible than the analysis of variance (*ANOVA*) in estimating variance components. For instance, it can utilize all available information, such as the covariances between parents and offspring and among full siblings. The *ANOVA* approach relies on the assumption of randomization in sample data, which may not hold true in animal genetics programmes that involve selection. The process of selection may introduce a potential bias in the estimated variance by *ANOVA*, whereas *MLE* takes into account selection (Meyer, 1989).

The *MLE* approach assumes a multivariate normal distribution for the observations. It calculates the likelihood of certain assumed parameters values that underline the distribution of observed data. So, it is the other direction of probability which is the probability of observing certain values in a given parameters (Meyer, 1989; Searle, 1995). The *MLE* maximizes the likelihood of the values of variance components in the positive space of the population parameters, given the data (Corbeil & Searle, 1976). If we consider that the observed variable (y) follows a normal distribution (N) with mean (μ) and a variance (σ^2), which is presented by $y = N(\mu, \sigma^2)$. Then, the probability density function $f(y)$ is calculated as:

$$f(y) = \frac{1}{\sigma\sqrt{2\pi}} e^{\frac{-1}{2}\frac{(y-\mu)^2}{\sigma^2}} \quad (9)$$

In a more general manner, such as in the linear mixed model, $y = N(Xb, V)$, where Xb and V are the parameters denoting the means of the fixed effects and the

variances of the random variables, respectively. The density function can be then represented as:

$$f(y) = \frac{1}{2\pi^{\frac{1}{2}N} |V|^{\frac{1}{2}}} e^{-0.5(y-Xb)'V^{-1}(y-Xb)} \quad (10)$$

Where:

N is the length of y records, $|V|$ is the determinant of V (the variance).

When the variable y is given, the function $f(y)$ becomes the likelihood, which can be maximized with respect to the parameters. The objective is to identify the parameters that yield the maximum value for $f(y)$. Practically, the log likelihood is used to be maximized instead of the likelihood function for its convenience mathematically (Shaw, 1987). The equation of calculating the log of likelihood for parameters (b) (i.e., the fixed means) and (V) (i.e., the variance) given that X (i.e., design matrix of fixed means) and (y) (i.e., observations) becomes as:

$$L(b, V | X, y) = \frac{-1}{2}N \log(2\pi) - \frac{1}{2} \log(V) - \frac{1}{2} (y - Xb)'V^{-1}(y - Xb) , \quad (11)$$

A major drawback associated with the use of the maximum likelihood estimation (MLE) technique for estimating variance components in linear mixed models is its failure to account for the loss in degrees of freedom that arises from fitting the fixed effects. This might potentially result in biased estimates for the variances, in particular the residual variance. This rise in biasedness can be considerable when more fixed effects are fitted in the statistical model, which is the case in analyses of animal genetics (Meyer, 1989), or when the sample size is insufficient (Hofer, 1998).

1.5.3 Restricted Maximum likelihood method (REML)

A modified version of the *MLE* method, which is the so-called restricted maximum likelihood (*REML*) suggested by Patterson and Thompson (1971) came to overcome the issues associated with the *MLE* method and became widely used by animal breeders to estimate genetic parameters. It is an iterative process to find the maximum of the likelihood function component that is not influenced by fixed factors. It involves replacing the original data with error contrasts, which refer to observations that have been adjusted for the fixed effects (Meyer, 1989). So, the maximization in the density function happens after correcting the observations for the fixed effects. Despite the assumption of a multivariate normal distribution for the variable of observations (y) in *REML*, it remains a favourable choice even if normality is not met (Meyer, 1990).

A number of algorithms have been proposed for the implementation of the *REML* technique. These algorithms could use derivatives of the likelihood function to find the maximum value, such as the expectation-maximization algorithm (*EM* algorithm) and the average information algorithm (*AI* algorithm) or they can be classified as derivative-free algorithms. The *EM* algorithm is not difficult to program because it just needs the solutions that can be obtained by solving mixed model equations (*MME*), and the trace of the inverse of the random effect of the coefficient matrix in an iteration process. It implies starting with an initial guess for the variance estimate and then calculating the solutions of the additive genetic effects that can be obtained by the method of best linear unbiased prediction (*BLUP*) using *MME equations*. In each iteration, new values of estimated variances and solutions are

obtained, and convergence is achieved when the difference is very small between the old and new values.

However, the *EM* algorithm necessitates the computation of the inverse of a matrix with dimensions equivalent to the number of levels of the random effects at each iteration, which might be restricted in multivariate (more than one trait) analysis. The *AI-REML* is now considered more robust and efficient for estimating variance components in animal breeding programmes. Various methods have been introduced to solve *AI-REML* estimates, including the Netwon-Rhapson method and Fisher's scoring method .

1.6 Breeding value

The breeding value (*BV*) of an animal measures the cumulative average additive effects (*a*) associated with the individual's genes, which can be inherited by their offspring. Thus, it is the genetic value that an individual carries through to their progeny, whereas the genotypic value (*G*) refers to the genetic merit of the animal itself. The animal breeder is interested, and able to estimate the *BV* rather than the *G*, since the *BV* represents the value attributed to genes that are passed on to the next generation. For a good response to selection, the main goal of selection programmes is to select animals and rank them according to their *BVs* (Falconer, 1996).

To understand how the animal's *BV* is estimated, the observation of an individual can be modelled in its simplest form as a result of the fixed mean effect, the genetic merit that it has, and the random environment, as explained by Mrode (2014) following the equation (12):

$$y_{ij} = \mu + g_i + e_{ij} , \quad (12)$$

where:

y_{ij} is the observation *j* of *i*th animal, μ is the overall population's mean which may include the means of the fixed effects, g_i is the genetic effect of *i*th animal, e_{ij} is the residual terms.

However, as it has been explained previously, that of the genetic component, the additive genetic effects (*a*) of individuals that passed on to offspring (summation of them is the *BV*), the model (12) can be fitted as:

$$y_{ij} = \mu + a_i + e_{ij} , \quad (13)$$

where:

a_i is the influence of the additive genetic effects only.

Given that the additive genetic values of genes are transmitted to offspring, it is essential to prioritise this component during the selection process. Breeding value (bv) is the average additive genetic effects that an animal inherits from both of its parents (Falconer, 1996). Other genetic influences, including dominance and epistasis, are assumed to have negligible significance on the phenotype, and they are included in the residual terms. Accurate prediction of animals' *BVs* plays an essential role in the effectiveness of genetic improvement schemes, as the level of precision serves as a primary factor in determining the expected response to selection according to the following equation (Falconer, 1996; Kennedy, 1981):

$$R = ir^2\sigma_y,$$

where:

R is the response to selection, **i** is the selection intensity, **r** is the accuracy of prediction, and σ_y is the standard deviation of variable **y** (phenotypic values).

The assessment of prediction accuracy is determined by the degree of correlation between the estimated breeding value (*EBV*) and the true breeding value (*TBV*). The values span a range from 0 to 1 (Oldenbroek & van der Waaij, 2014) . The selection of an appropriate approach and statistical model for estimating *EBVs* is a pivotal factor in enhancing the precision and reliability of the estimation process (Duchemin et al., 2012; Ferreira et al., 1999; Lodhi et al., 2016). Numerous methodologies and frameworks have been developed for the purpose of estimating *EBVs*, which vary depending on the amount and type of information available.

1.6.1 Selection index

The selection index incorporates all available information about the animal and its relatives to calculate an index (I) that reflects the EBV of the individual, as thoroughly illustrated by Mrode (2014). For example: if we have three records available for the animal i , and its parents' sire (s) and dam (d) as (y_i, y_s, y_d) , then the selection index (I_i) can be calculated as follows:

$$I_i = b_i(y_i - u_i) + b_s(y_s - u_s) + b_d(y_d - u_d) , \quad (14)$$

where:

b_i , b_s and b_d represent the regression coefficients of TBV on phenotype and mean for each record of i th animal, sire (s), and dam (d), respectively.

The coefficient of regression (b) can be then computed in the form of matrix as follows:

$$b = P^{-1}G , \quad (15)$$

where:

P is the phenotypic (Co)Variance matrix, and G is the (Co)Variance matrix between phenotypes and breeding value.

So, the equations for solving b and then the index (I) would be as follows:

$$\begin{pmatrix} b_i \\ b_s \\ b_d \end{pmatrix} = \begin{pmatrix} p_{ii} & p_{is} & p_{id} \\ p_{si} & p_{ss} & p_{sd} \\ p_{di} & p_{ds} & p_{dd} \end{pmatrix}^{-1} \begin{pmatrix} g_{ii} \\ g_{si} \\ g_{di} \end{pmatrix}$$

Selection index has the following properties: It reduces the average of all $(a_i - \hat{a}_i)^2$ by minimising the average square prediction error. The correlation between the *EBV* and the *TBV* is maximised. However, the necessity to a prior adjustments for the environmental fixed factors, and the inversion requirement of the phenotypic coefficient matrix for obtaining the solutions of (b) may not be feasible computationally particularly with large data.

1.6.2 Best linear unbiased prediction (BLUP)

The best linear unbiased prediction (*BLUP*) approach which presented by Henderson (1949) is widely used in estimating *EBVs* due to its statistical properties and application with many models, including sire, repeatability, and animal models (Mrode, 2014). According to Ambhore et al. (2018), the *BLUP* approach has been extensively employed for the estimation of animal's *EBV*. The efficacy of this procedure stems from its capacity to adjust phenotypic records by accounting for fixed effects, while also utilising the additive genetic relationship (*A*) between individuals to estimate *EBVs*. Therefore, fixed effects and *EBVs* can be estimated simultaneously by this method. Regard to its name, best because it minimizes the error variance and maximizes the correlation between estimated and true breeding value. Unbiased, because the estimation of random and fixed effects is unbiased (Mrode, 2014). This approach accounts for changes in genetic variance that may result from selection or inbreeding by incorporating the additive genetic relationships (*A*) between individuals into the *BLUP* calculation (Henderson, 1976).

If we consider the following animal linear mixed model:

$$y = Xb + Za + e , \quad (16)$$

where:

y , b , a , and e are vectors of observations (i.e., records), environmental fixed effects, random animal additive genetic effect (i.e., breeding value), and residual terms, respectively. X and Z are design matrices which associate the records to the fixed effects, and, to random animal genetic effects, respectively.

The assumed (Co)variance structure of the variables a and e of the *model (16)* is defined as:

$$\text{Var} \begin{pmatrix} a \\ e \end{pmatrix} = \begin{pmatrix} A\sigma_a^2 & 0 \\ 0 & I\sigma_e^2 \end{pmatrix},$$

Where:

A is the additive numerator (genetic) relationship matrix among individuals, and I is an identity matrix (i.e., diagonal elements are one and off-diagonals are zeroes).

Also, it is assumed that:

The expectations (E) of y , a , and e equals Xb , 0, 0, respectively.

The $\text{Cov}(a, e) = 0$, so the $\text{var}(y) V = ZA\sigma_a^2$.

The genetic (co)Variance $G = A\sigma_a^2$, so $V = ZG$.

$\text{Cov}(y, e) = Z \text{Cov}(a, e) + \text{Cov}(e, e)$, and because it is assumed that $\text{Cov}(a, e) = 0$, So

$\text{Cov}(y, e) = R = I\sigma_e^2$.

The mixed model equations (MME) set to give the solutions for the fixed effects (b) and additive genetic effect (a) is as follow:

$$\begin{pmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}X & Z'R^{-1}Z + A^{-1}\alpha \end{pmatrix} \begin{pmatrix} \hat{b} \\ \hat{a} \end{pmatrix} = \begin{pmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{pmatrix}, \quad (17)$$

where:

\mathbf{A} is the numerator additive genetic relationship between the animals, and α is the ratio of residual variance to the additive genetic variance ($\frac{\sigma_e^2}{\sigma_a^2}$), $\mathbf{R} = \mathbf{I}\sigma_e^2$.

The σ_a^2 and σ_e^2 of the population that used in (17) can be estimated by various methods as mentioned before including REML estimates.

Due to the assumption that \mathbf{R} is an identity matrix, \mathbf{R}^{-1} can be factored from both sides, and the MME in (17) is shorten to:

$$\begin{pmatrix} X'X & X'Z \\ Z'X & Z'Z + A^{-1}\alpha \end{pmatrix} \begin{pmatrix} \hat{b} \\ \hat{a} \end{pmatrix} = \begin{pmatrix} X'y \\ Z'y \end{pmatrix} \quad (18)$$

1.7 Genomic selection

1.7.1 Quantitative trait locus (QTL)

Most traits of economic importance in farm animals, including growth traits, are quantitative traits, which means they exhibit continuous variation and show a normal distribution. Partially, this variation is attributed to the genetic component of individuals (*i.e.*, genetic variation), and is driven by several major genes with significant effects plus the majority of polygenes with minor effects (Falconer, 1996; Gootwine, 2020). The polymorphic chromosomal site that harbours a gene or a group of genes that might contribute to this variation is called the quantitative trait locus (QTL) (Akond et al., 2019; Dhingani et al., 2015). Therefore, identification and detection of these molecular loci are important for animal breeders, who rely mainly on exploiting genetic variation to implement genetic improvement programmes.

With the advent of breakthrough advances in molecular technology, it has been possible to employ molecular markers to map significant QTLs (Zeng, 1994). Most traditional QTL mapping experiments in farm animals, including sheep and goat populations, have used microsatellite markers across the resource mapping population (Weber & May, 1989). The optimal spacing between markers involved in QTL detection and genome scans has been estimated to be between 10 and 30 cM (Maddox et al., 2001). The justification for QTL mapping in domestic animals comes from the biological essentials for understanding the complex genetic structure of the trait as well as the utilisation of genomic data in practical breeding strategies to improve selection (Andersson, 2001; Dekkers & Hospital, 2002).

According to Gholizadeh et al. (2008), identifying an animal's genetic makeup and predicting its trait phenotype with the help of molecular markers is an effective approach in animal breeding. The ultimate purpose of utilizing molecular markers is to detect the quantitative trait loci (QTLs), that influence the phenotype and accordingly enhance genetic improvement via marker-assisted selection (MAS) or genomic selection (GS).

1.7.2 Molecular markers

Molecular markers are the most useful genetic markers for analysing genetic variability, which might include microsatellite markers or single sequence repeats (SSR), mitochondrial markers, Y-chromosomal markers, copy number variations (CNV), and single-nucleotide polymorphisms (SNPs) (Saravanan et al., 2022). A molecular marker can be defined as a genetic locus that shows a polymorphism in the DNA sequence among individuals, which can be detected by molecular tools. Point mutations, duplication, translocation, insertion, and deletion are the sources of these polymorphisms (Nadeem et al., 2018).

The efficiency of utilizing molecular markers in animal and plant breeding programs has been demonstrated to be preferable to other genetic markers such as morphological, chromosomal, and biochemical markers. In general, morphological and chromosomal markers reveal a limited degree of variability and are therefore not helpful as genetic markers. The use of biochemical markers has led to suboptimal results as a result of their inherent dependency on factors such as sex, age, and vulnerability to environmental effects. Fortunately, the majority of these limitations have

been effectively solved by molecular markers. They are abundant and widely spread across the genome, unaffected by the environment. Most importantly, they are neutral to any phenotypic effect, as they are usually located in the non-coding regions (Collard et al., 2005; Ebegbulem & Ozung, 2013).

1.7.2.1 Microsatellites

Microsatellite markers are tandemly repeated sequences (usually 1 to 10 nucleotides) distributed abundantly across the genome. They are sometimes called simple sequence repeat (SSR) loci or simple sequence length polymorphisms (SSLPs). They are co-dominant markers (*i.e.*, the heterozygous can be distinguished of either homozygous), and very short, which makes their amplification easier. The tandem usually repeats 5-20 times in the genome (Al-Samarai & Al-Kazaz, 2015; Kalia et al., 2011; Vajed Ebrahimi et al., 2017), or the repeats can sometimes reach 40 times (Selkoe & Toonen, 2006). The common dinucleotide motif found in microsatellites in mammals is **(CA)*n***, where *n* represents the number of repetitions (Beuzen et al., 2000).

Microsatellite DNA markers have been extensively used to investigate genetic diversity among livestock breeds (Behl et al., 2007; Pandey et al., 2006; Penedo et al., 1999; Sollero et al., 2009). They have initially emerged as the preferred molecular markers for various applications in livestock species, such as genome mapping and marker-assisted selection (MAS) (Alberts, 2017; Bishop et al., 1995; Smith, 1993). Their preference over other DNA-based markers comes from their inheritance pattern as co-dominant, highly polymorphic (multiple alleles within a population), and abundantly distributed across the genome (Sheriff & Alemayehu, 2018). The

polymorphism helps researchers analyse and compare genetic variations in a population effectively. The downsides to adopting microsatellite-based approaches are relatively expensive development costs and technical challenges in manufacturing the species-specific primers (Miah et al., 2013).

1.7.2.2 Single nucleotide polymorphism (SNP)

SNP markers, as their name suggests, refer to single nucleotide polymorphisms in a DNA sequence, typically involving the substitution of two nucleotides at a specific locus within a population. They are co-dominant markers; however, unlike microsatellites, they are mostly bi-allelic (Vignal et al., 2002). In theory, four alleles can exist at each nucleotide site due to the four existing nucleotide types. However, in practice, only two variants occur. In other words, SNP markers are bi-allelic, as evidenced by the bias occurrence towards transitions, i.e., purine-purine (A G, T C) more than transversions (A C, A T, G C, G T) (Khlestkina & Salina, 2006). They are the most abundant in the genome among the other molecular markers. According to Koopaee and Koshkoiyeh (2014), SNPs account for approximately 90% of all genetic variations in any population, making them the best choice for population studies and genome mapping. They were detected for the first time on a genome-wide scale in the human genome (Mammadov et al., 2012).

As stated by Koopaee and Koshkoiyeh (2014), SNPs have the following advantages:

1. Most SNP markers are in DNA's non-coding region; therefore, they have no effect on the phenotype.
2. SNPs are considered to be a more suitable choice for high-throughput genetic study in comparison to microsatellites.
3. Compared to other DNA markers, they are more stably inherited and provide a greater number of potential markers in the vicinity of the locus of interest.
4. are devoid of phenotype effects.

The only limitation with SNP markers is that they are bi-allelic, meaning within a population there are only two alleles of each SNP. Consequently, they provide less information than multiallelic markers.

SNPs are the most commonly utilised DNA markers in animal genetics studies due to their suitability for high-throughput platforms and abundance throughout the genome (Vignal et al., 2002). The advancement of genomic technology and molecular information in recent years has made it possible to develop high-density SNP chips for livestock. The use of high-density SNP panels in farm animals has opened up the possibility of implementing genomic selection (Bertolini et al., 2017b; Rupp et al., 2016). The development of the **50K** ovine SNP chip in 2009 made genomic selection possible in small ruminants for the first time (Rupp et al., 2016). According to (Auvray et al., 2014); Nicolazzi et al. (2015), Illumina developed the Ovine **50K** SNP chip, containing 54,241 SNPs, and the Goat **SNP50** BeadChip, containing 53,347 SNPs.

1.7.3 Use of molecular markers in the prediction of breeding value

Even though traditional genetic evaluation methods have made some progress, the recent development of genomic research and technologies has led to the successful use of new tools and methods in the livestock industry. Marker-assisted selection (MAS) is one of these techniques, which depends on utilizing genetic markers to investigate any QTL associations with these markers. MAS refers to the use of breeding values in conjunction with genetic marker information in the selection of animals in a breeding programme on the basis of linkage analysis (Mrode, 2014; Simm et al., 2020). The utilisation of marker loci that are linked to QTLs has the potential to enhance genetic progress through the increase of selection accuracy and the minimization of generation intervals (Fernando & Grossman, 1989). However, because many genes usually influence quantitative characteristics, the expected gain from MAS is limited by the fraction of genetic variance of the target trait, which may be explained by the segregation of marker alleles (Ibtisham et al., 2017; Mrode, 2014). In addition, the linkage between the interested marker and the QTL is probably not close enough to sustain across the population, which involves structuring a linkage phase within each family (Mrode, 2014).

As a typical form of MAS evaluation of quantitative genetic variation, Meuwissen et al. (2001) developed genome-wide selection, usually known as genomic selection (GS). They theoretically demonstrated a possible accuracy in selection of up to 80%. This approach selects animals by combining pedigree and phenotypic data with all possible genomic information from the whole genome. Genomic selection is advantageous when traits, such as carcass quality, can be phenotyped in late life or are very difficult or expensive to phenotype. It enables breeders to select animals early

in life, thus reducing the generation interval (Oldenbroek & van der Waaij, 2014). In addition, animal breeders can potentially predict breeding values with higher accuracy than classical methods (Blasco & Toro, 2014). In dairy cattle, for instance, the prediction accuracy for production traits exceeds 0.80 (Weigel et al., 2012). Consequently, GS can substantially improve genetic gain with a much shorter time span and lower effective labour costs.

Genomic selection involves the use of all available genomic markers, i.e., SNPs, which are scattered across the genome. Potentially, they explain the total additive genetic variance caused by QTLs. So that all QTLs are assumed to be in linkage disequilibrium with at least one marker (Goddard & Hayes, 2007). Since all QTLs must be in linkage disequilibrium with at least one marker, the marker density must be high enough to achieve this (Mrode, 2014). To determine each animal's genomic estimated breeding value (GEBV), the effects explained by all markers throughout the entire genome associated with the trait variation are used. GS involves estimating the markers' effects in a reference population whose individuals are genotyped and phenotyped for the trait. Afterwards, selected candidates only need to be genotyped, and GEBV for them is computed by associating their genotypes of the markers with their predicted effects (Meuwissen et al., 2016; Mrode et al., 2018).

1.7.4 Methods of predicting genomic breeding values

Recently, the advancement in SNP typing and the huge amount of SNP chips produced for livestock have helped animal breeders utilize markers' information to estimate the genetic merit of animals. By this, it is expected that the genetic improvement will be enhanced through a more accurate estimation and a decrease in the generation interval. Utilizing the information of SNP markers in the prediction of genomic estimated breeding value (GEBV) is called genomic prediction, and the selection of candidates by this method is called genomic selection. Genomic selection (GS) basically involves the estimation of SNP effects by solving linear equations in a group of animals, i.e., the reference population in which the animals have genotypes for these SNPs and phenotypes. Then, these SNP estimates are used to predict GEBV when selecting candidates. The estimation of the accuracy of the prediction might be conducted by correlating the predicted EGBV and the true breeding value (TBV) in the validation set (Simm et al., 2020).

1.7.4.1 SNP-BLUP

This methodology relies on the utilisation of the same principles used by the BLUP estimator approach to estimate the effects of all SNPs throughout the entire genome in a reference population, typically consisting of several thousand individuals who have undergone phenotyping and genotyping. It has been shown that in the setting of classic BLUP, the number of equations formed for obtaining the solutions for the random additive effects is equivalent to the number of animals for which breeding values are being estimated. In the context of SNP-BLUP, equations are constructed for each of the SNPs, taking into account the genotypes of these SNPs across all

genotyped animals. Consequently, the solutions obtained correspond to the SNPs themselves rather than the animals (Meuwissen et al., 2016).

This method assumes that the effects of all SNPs are normally distributed and that they have common genetic variance. The typical general linear model, which explains the phenotypes of individuals, can be formulated as follows:

$$y = Xb + Zg + e, \quad (19)$$

where:

y is the vector of phenotypic records ; b and g are environmental fixed effects, and the additive genetic effect for each i th SNP genotype, respectively; X and Z are design matrices relating records to fixed effects and additive genetic effects of SNPs , respectively e is the error.

The Z matrix in (19) is a scaled matrix that was generated from a matrix called the M matrix. The M matrix includes the genotype of each genotyped SNP for each individual (It may be coded as 2, 0, and 1 for the homozygous, alternative homozygous, and heterozygous individuals for the SNP, respectively). Then, the Z matrix can be obtained by subtracting the P matrix from M , as follows:

$$Z = M - P, \quad (20)$$

where:

The matrix P consists of $2p_j$ elements, where p_j represents the frequency of the alternative allele of the SNP at locus j .

According to Mrode (2014), scaling the M matrix into a Z matrix is suggested to account for possible differences between various allelic frequencies of SNP and to set the allelic SNP effects of an average equal to zero.

The solutions of b (fixed effects) and g (random SNP effects) in (19) can be obtained by the *MME* equations as same as happened with *BLUP* in (18) as follows :

$$\begin{pmatrix} X'X & X'Z \\ Z'X & Z'Z + I\alpha \end{pmatrix} \begin{pmatrix} \hat{b} \\ \hat{g} \end{pmatrix} = \begin{pmatrix} X'y \\ Z'y \end{pmatrix}, \quad (21)$$

where:

$$\alpha = \frac{\sigma_e^2}{\sigma_g^2}.$$

However, because the genetic variance σ_g^2 practically is unknown, σ_g^2 can be estimated approximately from σ_a^2 by the following equation:

$$\sigma_a^2 / 2\sum p_j(1 - p_j), \quad (22)$$

where:

p_j is the allelic frequency of j th SNP.

After obtaining the additive genetic effects of SNPs by solving for g , the genomic estimated breeding value (*GEBV*) for all individuals in the reference and validating animals can be estimated by multiplying Z matrix (Fixed matrix of SNPs genotypes of all individuals) by g (the estimated genetic effects of SNPs) as follow :

$$GEBV = Zg \quad (23)$$

1.7.4.2 Genomic best linear unbiased prediction (GBLUP)

The genomic best linear unbiased prediction (*GBLUP*) has been developed by the use of constructing the G matrix which defines the genomic relationships between the individuals (Habier et al., 2007; VanRaden, 2008). This technique is comparable to Henderson (1976) with *MME (BLUP)*. Nevertheless, rather than using the additive numerator relationship (A), it makes use of the genomic relationship (G) matrix, which is derived from the SNPs marker information (Prince & Gowane, 2017).

The conventional *BLUP* approach involved the utilisation of the A matrix inside the Mixed Model Equations (*MME*) framework to solve the equations and obtain estimates for the breeding values (a). Given that parents pass on half of their genes exactly to all of their offspring, it defines a predicted percentage of shared genes between a pair of individuals. This implies that siblings who share both parents inherit precisely 50% of their genetic material from each parent, but this may not always hold true in practise due to the inherent variability in Mendelian sampling. In contrast, the G matrix serves to distinguish the observable genetic relationships among individuals via the utilisation of genotyped markers (Simm et al., 2020). As a result, it may be inferred that it offers a higher degree of accuracy compared to matrix A . However, this needs the utilisation of an extensive amount of markers in order to adequately represent the relationships between individuals, hence enhancing its accuracy precision.

Let us consider the following general model:

$$y = Xb + Ba + e, \quad (24)$$

where:

y is the vector of phenotypic records; b and a are vectors of fixed effects and genomic additive effects, respectively; X and B are the incidence matrices which relate records to b and a vectors, respectively; and e is the random residuals.

The genomic breeding values (*GBV*) of the animals which are equivalent to the additive genomic effects (*a*) are computed directly via the *MME* equations, wherein $a = Zg$ as we saw that in the SNP-BLUP method. This means that:

$$\text{var}(a) = ZZ' \sigma_g^2,$$

and given that the $\sigma_g^2 = \sigma_a^2 / 2\sum p_j(1 - p_j)$ as in equation (22), then the scaled matrix of *G* can be obtained as follows:

$$G = \frac{ZZ'}{2\sum p_j(1 - p_j)}, \quad (25)$$

which means that the $\text{Var}(a) = G\sigma_a^2$.

Then, the predicted genomic breed value (**GEBV**) can be obtained by the *MME* procedure using for example the animal model, by replacing the *A* matrix with the matrix **G** as illustrated in (26):

$$\begin{pmatrix} X'X & X'B \\ B'X & B'B + G^{-1}\alpha \end{pmatrix} \begin{pmatrix} \hat{b} \\ \hat{a} \end{pmatrix} = \begin{pmatrix} X'y \\ B'y \end{pmatrix}, \quad (26)$$

where α equals $\frac{\sigma_e^2}{\sigma_a^2}$.

The GBLUP approach offers advantages in terms of utilising the same software used for standard BLUP, with the key modification of substituting the *A* matrix with the *G* matrix. Additionally, the utilisation of molecular information enables the capture of

variations among similar individuals which rise as a result of Mendelian sampling variance. An accurate estimation of the relationships among individuals can be obtained even in a population with a poor pedigree (Mrode, 2014). However, the inversion of the G matrix could not be feasible as the population gets larger. In addition, the above genomic assessment approaches, *i.e.*, SNP-BLUP and GBLUP could only evaluate the genotyped animals (Weigel, 2017), and they are not straightforward to evaluate the ungenotyped animals.

Due to the cost of genotyping or the unavailability of DNA samples for some animals, especially the older animals, the $GEBVs$ of the younger animals may not contain information from their parents. In order to overcome this issue, a two-step procedure for selecting candidates can be implemented. Initially, $BLUP$ estimation is done for all the animals with the help of phenotypes and pedigrees. Then, $GEBVs$ estimated by the mentioned genomic methods for genotyped animals can be combined with the averaged-BLUP of their parents to obtain $EBVs$ (Simm et al., 2020).

1.7.4.3 *The single-step GBLUP (ssGBLUP)*

Misztal et al. (2010) proposed a technique that estimates $GEBVs$ for genotyped animals and $EBVs$ for ungenotyped animals by integrating EBV and $GEBVs$ in a single step. The underlying basis for employing this approach lies in the utilisation of genomic data from genotyped animals to make inferences about the possible genomic information of non-genotyped animals, exploiting the pedigree relationships that exist between the two groups. The integration of genomic (G) and pedigree (A) relationships among individuals into a single matrix, referred to as (H), is a fundamental aspect of

this approach. Therefore, the single-step genomic best linear unbiased prediction (*ssGBLUP*) method has the capability to calculate breeding values for both genotyped animals, known as genomic estimated breeding values (*GEBVs*), and non-genotyped animals, referred to as estimated breeding values (*EBVs*) (Bermann et al., 2022; Lourenco et al., 2020).

The utilisation of *ssGBLUP* is recommended, especially in cases where the reference population size is limited, referring to individuals that have been both genotyped and phenotyped. The utilisation of this approach has the potential to minimise bias in the estimation of *GEBV*, as demonstrated by Rupp et al. (2016). Additionally, it has been shown to enhance the accuracy of predicting candidates, as evidenced by the findings of Carillier et al. (2013). The following linear mixed model can explain the quantitative trait:

$$y = Xb + Ba + e \quad , \quad (27)$$

where:

The breeding value of the animals (a) here is assumed to be partitioned into (a_1) for ungenotyped individuals, and (a_2) for genotyped one.

So, the assumed variances for both breeding values would be as follows:

$$\text{Var} \begin{pmatrix} a_1 \\ a_2 \end{pmatrix} = \begin{pmatrix} A_{11} & A_{12} \\ A_{21} & G \end{pmatrix} \otimes \sigma_a^2,$$

or by taking A as a common factor, $\text{Var} \begin{pmatrix} a_1 \\ a_2 \end{pmatrix} = A + \begin{pmatrix} 0 & 0 \\ 0 & G - A_{22} \end{pmatrix} \otimes \sigma_a^2$

where:

A_{22} is the pedigree relationship of the genotyped animals; G is the genomic relationships between genotyped animals.

Because of that $a_2 = Zg$ (23), and the $\text{Var}(a_2) = G\sigma_a^2$ (25), so a_1 can be estimated from the genotyped animals by the following equation:

$$a_1 = A_{12}A_{22}^{-1}Zg + e \quad (28)$$

So that:

$$\text{Var}(a_1) = A_{12}A_{22}^{-1}GA_{22}^{-1}A_{21} + A_{11} - A_{12}A_{22}^{-1}A_{21}$$

It can be shortened to:

$$\text{Var}(a_1) = A_{11} + A_{12}A_{22}^{-1}(G - A_{22})A_{22}^{-1}A_{21},$$

$$\text{and } \text{Cov}(a_1, a_2) = A_{12}A_{22}^{-1}G$$

The (Co)variance matrix of both genotyped and non-genotyped animals is combined together in one matrix called (H):

$$H = \begin{pmatrix} H_{11} & H_{12} \\ H_{21} & H_{22} \end{pmatrix}$$

$$H = \begin{pmatrix} A_{11} + A_{12}A_{22}^{-1}(G - A_{22})A_{22}^{-1}A_{21} & A_{12}A_{22}^{-1}G \\ GA_{22}^{-1}A_{21} & G \end{pmatrix}$$

Because the inverse of H matrix is involved in the *MME* equations, The inverse of H can be constructed as proposed by (Aguilar et al., 2010; Christensen & Lund, 2010) by following:

$$H^{-1} = A^{-1} + \begin{pmatrix} 0 & 0 \\ 0 & G^{-1} - A_{22}^{-1} \end{pmatrix}$$

Then, the solutions of a values can be estimated by the MME as follows:

$$\begin{pmatrix} X'X & X'B \\ B'X & B'B + H^{-1}a \end{pmatrix} \begin{pmatrix} \hat{b} \\ \hat{a} \end{pmatrix} = \begin{pmatrix} X'y \\ B'y \end{pmatrix}$$

1.7.5 Challenges to implement genomic selection in small ruminants

Potential advantages of implementing genomic selection (GS) instead of traditional selection methods in small ruminants (namely sheep and goats) may arise from the potential increase in the accuracy of predictions. Nevertheless, the expense associated with SNP genotyping may exceed the economic worth of the animals, posing a significant challenge. Multiple factors play a significant role in the precise estimation of genomic breeding values in small ruminants (SR). These factors mostly include the size of reference populations, the heritability of the trait, the density of markers, the linkage disequilibrium (LD) existing between markers and quantitative trait loci (QTLs), and the specific method employed for genomic prediction (Goddard & Hayes, 2007; Hayes & Goddard, 2010; Yan et al., 2022). Thus, the expected advantages of genomic selection (GS) in SR may be comparatively lower than those observed in the field of cow breeding. As an illustration, it is commonly observed that the generation interval in SR is typically short, with economic traits being manifested in both sexes prior to reaching maturity. Additionally, an important number of production traits exhibit moderate to high heritability. This means that we can expect superiority of genomic selection over traditional selection in terms of prediction accuracy, particularly with low heritable traits.

One of the most critical limitations to implementing GS is the reference population's size, particularly in SR. As mentioned in the literature, genomic selection relies on linkage disequilibria between markers and QTLs (*i.e.*, the non-random association). The accuracy of marker-assisted evaluation of breeding values is largely affected by the number of genotyped animals and by the genomic relationships of the animals between the training and reference populations (Oldenbroek & van der Waaij,

2014). Besides, if the heritability of the trait is low, it needs a large number of genotyped animals and recorded phenotypes to obtain acceptable accuracy. Daetwyler et al. (2012) showed that the accuracy of *GEBV* is well correlated with the size of the reference population and the trait's heritability. However, Blasco and Toro (2014) stated that this issue might be minimized by using information from multiple breeds whose individuals are genetically related or by using information from several generations.

The method used for estimating *GEBVs* is another factor that can impact the accuracy of the estimation (Legarra *et al.*, 2009; Misztal *et al.*, 2013). In such a small reference population, the *ssGBLUP* method is preferable over other genomic methods because it integrates all available information from phenotypes, pedigrees, and genomic relationships in a single step.

Marker density and linkage disequilibrium (LD) between markers and QTLs are essential determinants of *GEBV* accuracy. A low level of LD involves high-density markers to capture most of the genetic variation in the population. With high LD, the marker effects are more precisely estimated, resulting in a more accurate estimation (Sadan & Valsalan). Rupp et al. (2016) discussed another issue: the higher cost of genotyping relative to the animal production value is still an economic barrier to implementing genomic selection in sheep and goat breeding schemes. Further, many economic traits, like growth traits, are feasible to record before the reproductive stage.

1.8 Inbreeding

1.8.1 Introduction

Adopting *BLUP* and advanced *GBLUP* approaches to estimate animals' *EBVs* and subsequently rank them upon their *EBVs* would usually favour related animals for selection (Mrode, 2014). The implementation of intensive selection, which means using a limited number of sires and dams for breeding, along with the closed nature of populations in breeding programmes, can result in a rise in inbreeding and a decline in genetic variation (Venkataraman et al., 2016).

Animal breeding programmes are expected to be coupled with the development of inbreeding. Evaluation of inbreeding's level within animal populations, particularly in the context of a closed breeding programme, is crucial due to its potential impact on reducing genetic variation and inducing inbreeding depression. In practice, the avoidance of inbreeding is unattainable due to the inherent impossibility of preventing mating among closely related individuals within a finite population. However, the level of inbreeding can be appropriately controlled and managed through the implementation of a well-designed breeding programme that takes into account a number of factors that have the potential to limit the degree of inbreeding (Kristensen & Sørensen, 2005). In order for animals to respond to future selection and to reduce the detrimental effects of inbreeding depression, inbreeding levels should be kept to a minimum in order to retain appropriate levels of genetic variability.

The amount of inbreeding is typically expressed through the calculation of the inbreeding coefficient *F*. This coefficient represents the probability of an individual has two identical alleles by descent (IBD) at any locus, in relation to a base population

(Falconer, 1996; Mrode, 2005). The two alleles are called IBD when they originate from a single replicated allele inherited from a shared ancestor. We refer to the locus that have IBD alleles as autozygous genotype. In contrast, a pair of alleles in any locus that share the same DNA nucleotide sequence but are not descended from a common ancestor is referred to as identical by state (IBS), and the genotype is known as allozygous(Hartl, 2020).

The assessment of inbreeding level may be better indicated by the computation of Inbreeding rate (ΔF) rather than relying just on the F value. According to Falconer (1996), the F value is influenced by the pedigree depth which may be overestimated or underestimated. The increase in inbreeding ΔF can consider the variation in pedigree information. Inbreeding depression and genetic variation can be effectively monitored using this indicator. Using this indication, one may determine how long can keep the flock until critical levels of inbreeding occur (Ceyhan et al., 2009). The rate can be regarded as the difference between the mean inbreeding coefficients of animals on an annual basis or generation interval (Oldenbroek & van der Waaij, 2014) .

According to Falconer (1996), levels of inbreeding can be considered acceptable and non-detrimental if they remain below 10%. In the context of inbreeding rate, Nicholas et al. (1989), proposed that a yearly inbreeding rate of no more than 0.5% would be considered acceptable. As per Tahmoorespur and Sheikhloo (2011), the FAO recommends that the rate of inbreeding should not surpass 1% every generation in order to prevent or mitigate the severe effects of inbreeding depression. As a result, it is of the utmost significance to closely monitor the level of inbreeding within a population and implement strategies to control it, as this is essential for the development and maintenance of an efficient selection programme.

1.8.2 Consequences of inbreeding

The ongoing maintenance of adequate levels of genetic variability is necessary in order to maintain an effective response to selection within breeding programmes (Howard et al., 2017). Inbreeding is a determinant factor in the reduction of genetic variability within a population, because it increases the frequency of homozygotes relative to the frequency of heterozygotes. Hence, it is emerging as an essential consideration in genetic improvement projects. According to the review of Kristensen and Sørensen (2005), an increase in the average inbreeding coefficient within a population has been demonstrated to result in a subsequent decrease in the additive genetic variance (V_A). This decrease in V_A is a matter of great concern for animal breeders because it limits the response to selection of a trait under selection. Generally, it is expected that the genetic variance decreases in the long term, while the additive genetic variance may increase in the short term due to the conversion of nonadditive effects to additive effects (Howard et al., 2017).

Within a population, inbreeding tends to increase the homozygosity status of genotypes, allowing an equal chance for either recessive or dominant alleles to set in a paired form. This implies that the originally concealed alleles in the heterozygous state are now exposed and capable of being expressed. The manifestation of recessive alleles usually leads to a range of detrimental outcomes in animals, including weakened or nonviable offspring, reduced animal performance, and reduced fertility. Conversely, inbreeding results in a decrease in heterozygosity within the population, which in turn reduces genetic variation (Howard et al., 2017).

Inbreeding depression is another detrimental outcome characterised by a decrease in the average phenotypic value of a characteristic as a result of inbreeding.

Many economic traits in farm animals exhibit significant susceptibility to the influence of inbreeding, including but not limited to milk production, growth characteristics, survival rates, reproductive success, onset of sexual maturity, and sperm quality. Research findings indicate that reproductive traits might be more susceptible to influence compared to production characteristics, but meat quality traits are minimally or not impacted at all (Mandal et al., 2004; Wakchaure & Ganguly, 2015). **Table 3** shows numerous studies investigating the effect of inbreeding on some growth traits in sheep and goats.

The extent of inbreeding depression can vary throughout populations, as it is conditional upon the frequency of alleles, which is influenced by both genetic drift and the intensity of selection (Howard et al., 2017). It is also influenced by the degree of dominance. According to Crow (2017), the change in the mean phenotypic value of a trait due to inbreeding is expected by the formula:

$$2F \sum_{i=1}^n p_i q_i d_i, \quad (29)$$

where:

F is the coefficient of inbreeding, p_i , q_i , and d_i , are dominant and recessive allele frequencies, and degree of dominance, respectively for the i th locus.

Table 3. Estimates of inbreeding depression on some growth traits in various breeds of sheep and goats.

BW (birth weight), **WW** (weaning weight), **W6** (six-months weight), **W12** (yearling weight).

Name of breed	Growth trait	% of inbreeding depression per 1% increased inbreeding	Reference
Iran-Black sheep	BW	-3.4 (g)	(Baneh et al., 2019)
	WW	-32.1 (g)	
	W6	-14.4 (g)	
	W12	-23.7 (g)	
Sakiz sheep	BW	-0.02 (kg)	(Ceyhan et al., 2011)
	WW	Not significant	
Kenya goats	BW	-0.04 (kg)	(Muasya et al., 2006)
	WW	Not significant	
	W12	-0.22 (kg)	
Baluchi sheep	BW	Not significant	(Gholizadeh & Ghafouri-Kesbi, 2016)
	WW	Not significant	
	W6	-0.02 (kg)	
	W12	-0.13 (kg)	
Nilagiri sheep	BW	Not significant	(Venkataraman et al., 2016)
	WW	-0.05 (kg)	
	W6	Not significant	
	W12	-0.07 (kg)	
Thalli sheep	BW	-0.05 (kg)	(Hussain et al., 2006)
	WW	-0.05 (kg)	
Iranian Moghani sheep	BW	-0.01 (kg)	(Dorostkar et al., 2012)
	WW	-0.29 (kg)	
	W6	-0.03 (kg)	
	W12	-0.04 (kg)	

1.8.3 Control of inbreeding level

The level of inbreeding can be influenced by the practice of breeding strategies like artificial insemination and the application of high selection intensity (Mandal et al., 2004). Additionally, the level of inbreeding in a population is influenced by factors such as the mating system, population size, reproductive efficiency, and the ratio of sex to females (Ceyhan et al., 2011). According to Pedrosa et al. (2010), a reduction in the number of animals utilised in breeding programmes leads to a higher intensity of selection, resulting in a rise in inbreeding. Therefore, increasing the number of males accessible to mating can be considered an effective strategy for reducing the level of inbreeding.

There are a number of actions that animal breeders can take to avoid inbreeding or at least maintain it below the threshold. According to Wakchaure and Ganguly (2015), several strategies can be employed to minimise inbreeding or reduce its rate. These include the avoidance of mating between closely related animals, the utilisation of computer programmes specifically designed for mating purposes, the introduction of new genetic material through the purchase of new animals, and an increase in population size. When the population effective size is less than fifty, the inbreeding curve increases rapidly (Oldenbroek & van der Waaij, 2014).

1.8.4 Methods of estimating inbreeding coefficient (F)

In order to calculate the coefficient of inbreeding (F) using a pedigree, it is necessary to first identify a common ancestor between the parents of individual i . This is because the only way for individual i to receive alleles that are identical by descent (IBD) is if its parents had a common ancestor. Afterwards, every path originating from the individual i are followed in an upward direction towards the shared ancestor and then downwards towards the same individual, as depicted in **Figure 2**. Next, the probability of passing on an allele to the offspring is determined, which is 50% as dictated by Mendel's law of gamete segregation. Nevertheless, the probability of the common ancestor transmitting an allele (IBD) is $0.5(1 + F)$, where F represents the inbreeding coefficient of the common ancestor.

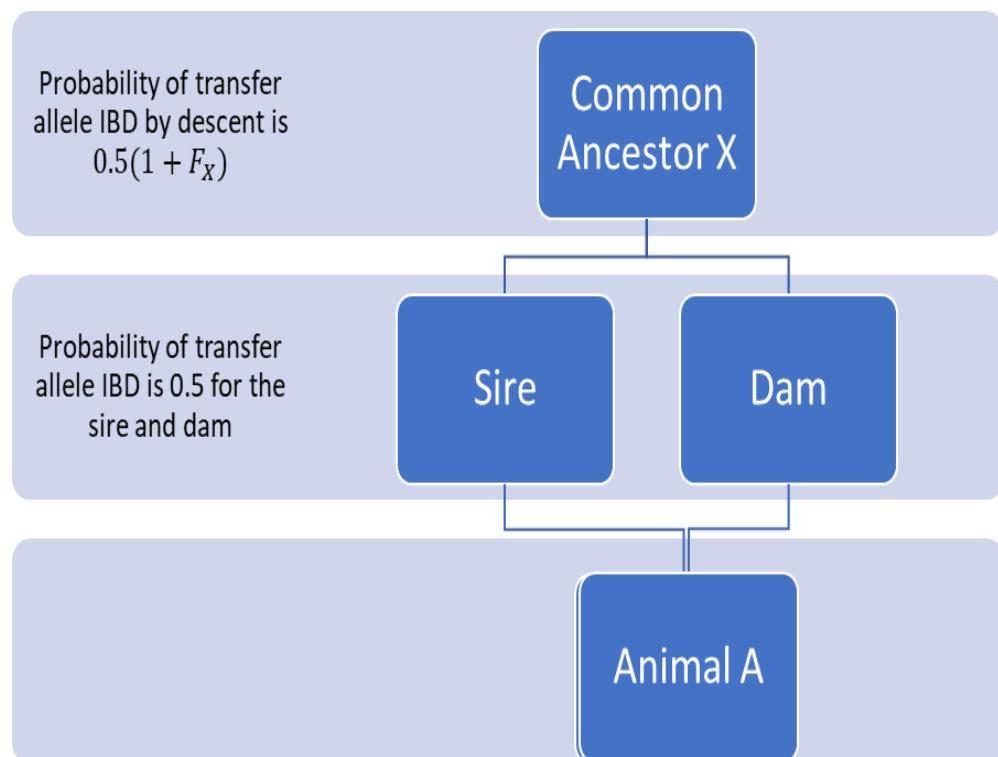


Figure 2. Calculation of the inbreeding coefficient through the ancestral path.

Mathematically, the F_i value of individual i can be calculated as proposed by Hartl (2020) by the following:

$$F_i = (0.5)^n(1 + F_{CA}), \quad (30)$$

where:

n is the number of i th ancestors leading to the common ancestor, F_{CA} is the inbreeding coefficient of the common ancestor CA .

If there are more than one common ancestor, then the F_i equals:

$$\sum_{all\ paths} (0.5)^n(1 + F_{CA}), \quad (31)$$

The utilisation of the pathways approach for computing the inbreeding coefficient may become unfeasible and complex when dealing with a larger number of population, resulting in the challenge of tracing all paths for every ancestor. Henderson (1976) established a recursive method for computerization compatibility whereby builds additive genetic relationships among individuals in a matrix known as the numerator relationship matrix (A). The matrix is symmetrical, with the diagonal elements (a_{ii}) equal to $1 + F_i$, where F_i represents the inbreeding coefficient of individual i . The off-diagonal elements (a_{ij}) reflect the additive genetic relationship between individuals i and j . Estimation of variance components and breeding values is utilising the A matrix, as it is assumed that the variance of the additive genetic effects

$$V_a = A\sigma_a^2.$$

The above approach of computing F values involves assigning numerical codes to the animals, ranging from 1 to n , in a particular order where the parents come before their offspring. It has the following rules to estimates the elements of A matrix:

1. If both parents the sire and the dam of animal i are known, then the additive genetic relationship between animal i and animal j is calculated as:

$$(a_{ji} = a_{ij}) = 0.5(a_{j,sire\ of\ i} + a_{j,dam\ of\ i}), \text{ and } a_{ii} = 1 + 0.5(a_{sire,dam}).$$

2. If only one parent is known, then:

$$(a_{ji} = a_{ij}) = 0.5(a_{j,sire\ of\ i}), \text{ and } a_{ii} = 1.$$

3. If both parents are unknown, then:

$$(a_{ji} = a_{ij}) = 0, \text{ and } a_{ii} = 1.$$

Several algorithms have been developed to calculate the F value with greater computation efficiency, especially for large populations. The techniques primarily relied on adaptations to the tabular method or Henderson (1976) findings, who demonstrated that the A matrix may be decomposed into three matrices as following:

$$A = LDL', \quad (32)$$

where:

The L matrix is a lower triangular matrix that represents the genetic contribution of parents to offspring; the D matrix, on the other hand, is a diagonal matrix that represents the variance in Mendelian sampling.

This method involves the calculation of L matrix column by column at a time, and then accumulates the summation of L elements for each row of i th animal, wherein the diagonal elements of A matrix which equals $1 + F$ can be expressed as:

$$a_{ii} = \sum_j^i l_{ij}^2 d_{jj}, \quad (33)$$

A comparison study conducted by (Sargolzaei & Iwaisaki, 2005) using simulated data compared between four common algorithms to compute inbreeding coefficient (F). They compared Tier (1990), Meuwissen and Luo (1992), Quaas (1995),

and Sargolzaei and Iwaisaki (2004). The algorithm used by Tier (1990) is an adaptation for the tabular method. The numerator relationship A is only used partially. This method utilises a recursive process to identify and mark only what is needed for calculating the diagonal elements of matrix A . Subsequently, the flagged elements are computed using the tabular method.

The algorithm used by Meuwissen and Luo (1992) was faster and superior computationally to that used by Tier (1990), when the average number of generations is not too large, and when a new patch of animals added to be estimated. They proposed a method that computes the elements of the lower triangular matrix L row by row at a time, rather than by columns, using the principles of Henderson's (1976) decomposition of matrix A in equations 41 and 42. This feature allows to use previously calculated inbreeding coefficients, for the estimation of newly added animals. It entails creating of ancestral list for every animal. The L elements are calculated as follows:

$$l_{ij} = \sum_{k \in ANC_i \cap P_j} 0.5l_{ik}, \quad (34)$$

where:

ANC_i is the ancestors list of animal i including the i th itself, and P_j includes the progeny of ancestor j .

However, this approach requires tracing the complete pedigree of the animal being estimated, including all ancestors, regardless of whether they are common or not, which involves summing all the diagonal elements of that animal row of matrix A , which can be a time-consuming process (Mrode, 2014). What is really needed is just the common ancestors, considering that the F value of animal i equals $1/2 a_{sire_i, dam_i}$. Accordingly, in 1995, Quaas developed modifications to the Meuwissen and Luo

algorithm, requiring the creation of two lists of ancestors for sire and dam of the animal, which involves the simultaneous developing of two rows of matrix L. Which means only computing the non-zero elements of the two rows of the sire and dam.

1.9 Objectives of the thesis

Genetic improvement programmes serve as an important tool to improve animals' performance, including growth traits. These programs rely on the accurate estimation of key genetic parameters that define the population, such as the heritability of the trait and the genetic correlations between traits. WQLRS is a station in Oman that keeps local sheep and goats for breeding programme, i.e., genetic improvement through within-breed selection, with the goal of improving the animals' performance and focusing on their growth potential to enhance meat output.

Thus, the chief objective of this thesis (Chapter 4) was to estimate genetic parameters that include heritability of growth traits and the genetic correlations, as well as the genetic trend for each trait from 2008 to 2020, focusing on the most common goat and sheep breeds exist in Oman: Omani sheep (OS), Jebel Akhdar (JA), and Batinah (BA) goats. The weights at birth (BW), weaning (WW), six months (W6), and yearling (W12) were the targeted traits.

The efficiency of breeding programmes can be impacted by inbreeding level within population since it reduces genetic variability (Ceyhan et al., 2011; Mandal et al., 2020) and can cause inbreeding depression (Falconer, 1996). Increased levels of inbreeding are typically associated with genetic improvement programmes, particularly in closed-population programmes that prioritise within-breed selection. The investigation of the level of inbreeding in the three populations, tracking how it changed from 2008 to 2020, and suggesting a number of strategies to control it was the second goal of this thesis (Chapter 3).

In chapter 5, I conducted a simulation study using Omani sheep as a case study in order to investigate if genomic methods that include Genomic Best Linear Unbiased Prediction (GBLUP) and Single Step Genomic Best Linear Unbiased Prediction (ssGBLUP) could be used to predict breeding values of selected animals more accurately than the traditional BLUP approach. The simulation used the real pedigree and heritability level described in Chapter 4. As a result, theoretical guidelines have been proposed for the possibility of implementing genomic selection in Omani populations of sheep and goats.

CHAPTER TWO

MATERIALS AND METHODS

2.1 The study populations

Three populations were considered for the research of this thesis, including two indigenous breeds of Omani goats, namely Jebel Akhdar (JA) and Batinah (BA), as well as one breed of sheep called Omani sheep (OS). They are primarily used for the production of meat (Shaat and Al-Habsi, 2016). Although raw goat milk is infrequently consumed, it could be used to make byproducts like butter and cheese for household consumption only. Sheep milk is rarely used, and the fibre may be used by Bedouins to make rugs and household artifacts (Mahgoub et al., 2010).

The choice of these particular breeds for the study was primarily based on three factors. Firstly, they are relatively more productive than other small ruminants available in the country. Secondly, they are common and widely raised by farmers in Oman. Thirdly, they have been housed and subjected to breeding programs for genetic improvement at the Wadi Qurayyat livestock research station (WQLRS), where I am employed.

The investigated flocks were managed in a semi-intensive production system at the WQLRS. The animals were fed with a concentrated feed ration that contained a minimum of 14% crude protein, along with dry Rhodes grass hay. The amount of concentrate feed varied depending on the age and physiological state of the animals, from 250 g/head to a maximum of 700g/head. The growing animals were gradually fed concentrate until they reached a maximum of 600 g per head at approximately six months of age, and this amount continued until they reached maturity. The adult females were provided with the highest possible quantity of concentrate during the final trimester of pregnancy and for flushing during the early stage of lambing/kidding. The

dry grasses were frequently provided ad libitum, with occasional restricted amounts based on resource availability from year to year.

2.1.1 Jebel Akhdar (JA) goats

The breed is typically medium-sized and brown in colour (Shaat & Al-Habsi, 2016) as shown in **Figure 3** and **Figure 4**. It is characterised by its considerable size and weight, making it one of the largest and heaviest breeds among the various indigenous goat breeds found in the country. Its distribution is extensive, primarily concentrated in the interior regions of Oman, particularly in the Jebel Akhdar mountain area. Animals of this breed usually have twisted horns and pendulous ears (Mahgoub et al., 2005).

According to the recent findings published by the Ministry of Agriculture and Fisheries in Oman (MAF (2019), it was observed that JA goats, which underwent genetic improvement at the research station of WQLRS, exhibited an excellent fertility rate of 94%. The average litter size (LS) was recorded as 1.47, meaning that for every 100 mated female goats, almost 147 kids were produced.

2.1.2 Batinah (BA) goats

The animals belonging to this particular breed possess a coat containing hair that ranges in colour from dark brown to black. Notably, these animals also possess distinct white markings on their face, abdomen, and lower legs, as depicted in **Figure 5**. They are reared mainly for meat production (Shaat & Al-Habsi, 2016). The breed

under consideration has an excellent fertility rate of 94% and a LS rate of 1.43, which is comparable to the JA goat breed (MAF, 2019).



Figure 3. An adult male of Omani Jebel Akhdar goat.



Figure 4. An adult female of Omani Jebel Akhdar goat.



Figure 5. Adult female of Omani Batinah goat.



Figure 6. Ewe dam of Omani sheep raising its offspring.

2.1.3 Omani sheep (OS)

This particular breed is well recognised as one of the foremost indigenous sheep breeds in Oman. They are primarily found in the north, and producing meat is the primary objective of their breeding. The dominant colour exhibited by this breed is black, with a relatively small proportion displaying white or brown coloration, potentially attributable to the presence of recessive genetic segregations. The fleece of these animals exhibits a short and coarse nature. The individuals feature a cranial structure that exhibits elongation, accompanied by a nasal region that is characterised by a curved shape (al-Subeih et al., 2018). **Figure 6** illustrates an Omani ewe nursing its lambs. The fertility rate stands at around 90%. The breed is characterised by a comparatively greater rate of LS (1.70) compared to goat breeds, following the implementation of breeding improvements (MAF, 2019).

2.2 The breeding programme at WQLRS station

The station is staffed with technical and veterinary specialists. The technicians are responsible for supervising feed management, collecting and recording data, and shearing animals. All the animals at the station undergo the process of dipping and shearing during the late summer season. They get regular vaccinations based on governmental recommendations and deworming treatments administered by the veterinary staff.

Without the use of a selection index, the breeding program at WQLRS was developed using a multiple trait selection strategy. It was suggested that birth type (BT) and weight at six months (W6) would be the selection criteria for replacement males. The male twins with good W6 were kept as future sires, and the other males were either sold or given to the local farmers. One main purpose of the breeding program was to increase the litter size of the breeds under investigation, which is why BT was prioritised. While the selection of the W6 trait was based on literature that shows that it usually is moderate to high heritable and it has a strong correlation with other growth traits, particularly with W12. Therefore, enhancing W6 would enhance other growth traits. To maintain as many of the replacement females as possible for breeding, the selection process for them was less intensive than that for the males. Priorities for selecting females were set by the following: mothering ability, BT, W6, yearling weight (W12), and weight at 18 months.

The rams and bucks (adult males of sheep and goat, respectively) were usually retained in service for a maximum of two years during a one-year mating season, while the female was kept in service until it reached eight years old, unless it was culled. Generally, the flocks were in a closed breeding program, except that three bucks of JA

were introduced from outside the station in 2011 and 2014, one buck of BA in 2010, and three OS rams in 2014.

The goats went into their mating season in mid-September, following the summer season, while the sheep's mating season occurred in October. The females chosen for breeding should have a minimum weight of 30 kg. The selected rams/bucks were distributed at random to different pens, which included randomly assigned females. The males were kept with the females for a duration of 45 days for goats and 30 days for sheep. This is because ewes have a shorter oestrous period compared to does. Most of the animals' pens were located in a separate barn with one animal keeper for each breed, with the exception of one barn that included pens for the three different breeds.

To ensure optimal management, the kidding season for goats was scheduled to commence in February and end in March, while the lambing season for sheep was set to begin in March and end in April. Both kids and lambs were kept with their dams until they were weaned. Because the animals were born on various dates, weaning took place at two different intervals to ensure that they roughly reached three months of age at weaning. The majority of the kids were weaned in early June, while the others were weaned in July. The majority of lambs were weaned in late June, with the remaining lambs being weaned in July. At birth, the animal was immediately weighed and ear-tagged with its unique identification number. The data recording covered the animal's identification, paternal and maternal identities, sex, date of birth, type of birth, pen, and measurements of weight at birth (BW), two months (WW), 6 months (W6), and 12 months (W12) as illustrated by **Figures 7 and 8**. Afterwards, kids/lambs were

separated and distributed into different groups according to their sex, body weights, and type of birth.

Figure 7. Recording book of the newly born animals for each breed at WQLRS.

It contains, starting from the left side, Dam ID, Progeny ID, Sex, Birth weight, Date of birth, Type of birth, and Remarks.

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
SR	ID	SID	DID	Breed	Pen No	B Date	Sex	YRP	Brth Typ	BW	WW	DWW	W6	DW6	W12	DW12
1	32759	31763	30429	sheep	1	10/03/2019	2	2019	2	3.155	9	22/07/2019	14.3	07/09/2019	.	.
2	32760	31763	30429	sheep	1	10/03/2019	2	2019	2	2.845	13.1	20/06/2019	19.6	07/09/2019	30	31/03/2020
3	32595	31763	30583	sheep	1	25/02/2019	1	2019	2	2.300	8.1	22/07/2019
4	32596	31763	30583	sheep	1	25/02/2019	2	2019	2	2.000
5	32870	31763	30613	sheep	1	28/03/2019	2	2019	2	3.100	15.4	20/06/2019	23.8	07/09/2019	37	31/03/2020
6	32871	31763	30613	sheep	1	28/03/2019	2	2019	2	2.500	6.2	22/07/2019
7	32605	31763	30818	sheep	1	02/03/2019	1	2019	2	2.500	13.7	20/06/2019	20.2	08/10/2019	31	01/04/2020
8	32606	31763	30818	sheep	1	02/03/2019	1	2019	2	2.420	16	22/07/2019	23.2	08/10/2019	35	01/04/2020
9	32704	31763	30984	sheep	1	07/03/2019	1	2019	1	3.200	13.8	20/06/2019	16.4	08/10/2019	.	.
10	32676	31763	31047	sheep	1	05/03/2019	2	2019	2	3.700	12.1	20/06/2019	21.6	07/09/2019	.	.

Figure 8. A database of the live body weights of lambs belonging to the OS breed at WQLRS.

This example illustrates how animal weights are digitally recorded in an Excel spreadsheet. From left to right, the sheet provides information on serial numbers, animal IDs, sire IDs, dam IDs, breeds, pen numbers, birth dates, animal sex, birth year, birth type, BW, WW, date of WW recording, W6, date of W6 recording, W12, and date of W12 recording.

2.3 Collected data

Records of pedigreed animals made up of 2,826 records, 2,609 records, and 3,530 records for JA goats, BA goats, and OS sheep, respectively, were included in the data collection. The total number of individuals in the pedigree for the JA, BA, and OS breeds was 3,128, 2,947, and 3,931, respectively. Tables 4 and 5 summarize the data structure for each recorded trait of the three breeds and the pedigree structure, respectively. Data was collected from the WQLRS station over a 13-year period, from 2008 to 2020. The data used for analysis comprised the live body weights of animals at birth (BW), weaning (WW), six months (W6), and one year (W12). Besides, it included the animal's identification, paternal and maternal information, date of birth, age of the dam, sex, type of birth (BT), year of birth, pen, and the dates when weights were recorded.

Table 4. Number of records for each growth trait in JA goats, BA goats, and OS sheep.

BW (birth weight), **WW** (weaning weight), **W6** (six-months weight), and **W12** (yearling weight).

Trait	JA goats	BA goats	OS sheep
BW	2,826	2,609	3,530
WW	2,342	2,186	3,120
W6	1,706	1,689	2,374
W12	1,265	1,208	1,745

Table 5. Pedigree structure of the three breeds of JA goats, BA goats, and OS sheep.

Item	JA	BA goats	OS sheep
No. of animals without offspring	2,231	2,091	2,782
No. of animals with offspring	897	791	1,149
No. of animals with unknown sire	235	273	401
No. of animals with unknown dam	299	338	401
No. of animals with both parents' known	2,826	2,610	3,530
No. of sires with progeny	129	116	134
No. of dams with progeny	768	675	1,015

2.4 Statistical analysis

2.4.1 Estimating inbreeding levels in the three breeds (Chapter 3)

Initially, all existing relationships between individuals were reviewed and checked. The checking process included the following considerations:

- There are no duplicate numbers in the column of animal IDs.
- The animal's date of birth is more recent than that of its parents.
- The identification number of the offspring is greater than the numbers of its father and mother.
- Matching the animal to its sex is necessary in order to prevent the female animal from being listed as the sire and vice versa.
- Reviewing that the sire number is not found in the dams' column, and vice versa.

To facilitate the analysis computationally, all animals were initially assigned new numerical identifiers in ascending order, commencing from 1 to n animals (n is the overall animals in the pedigree). The renumbering process was undertaken to be formatted for the subsequent analysis involved by the analysis algorithm. The calculation of inbreeding coefficients (F) for each animal was performed using Fortran source code, following the algorithm proposed by Meuwissen and Luo (1992). The algorithm utilises the decomposition principles of the additive genetic relationship matrix (i.e., numerator relationship matrix (A)) as described by Henderson (1976). The A matrix can be expressed as a result of three main matrices as follow:

$$A = LDL^T, \quad (35)$$

Where:

L is a triangular matrix that contains l elements which explains the proportion of the genes contributed by the ancestors for a given animal considering that half of the genes are passed to offspring; D is a diagonal matrix which explains the within-family variance (i.e., Mendelian sampling variance), which is calculated by the following equation:

$$D_{ii} = 0.5 - 0.25(F_{Sire_i} - F_{Dam_i}), \quad (36)$$

where:

D_{ii} is the diagonal element of i th animal; F_{Sire_i} and F_{Dam_i} are the inbreeding coefficients of i th sire and dam, respectively.

Quaas (1976) has shown that from the A decomposition as in *equation (35)* that:

$$(a_{ii}) = \sum_{j=1}^i l_{ij} l_{ij} d_{jj}, \quad (37)$$

where:

a_{ii} is the diagonal elements of the A matrix that equals $1+F$, where F is the animal's inbreeding coefficient.

The algorithm suggested by Meuwissen and Luo (1992) for the calculation of F is considered a fast method, and more adaptable to be updated when new group of animals are added, because of that it calculates the elements of L matrix row by row at a time instead of column by column as previous algorithm presented by Tier (1990). This enabled it to get benefits of the utilisation of previous computed F values (Sargolzaei & Iwaisaki, 2005). It entails creating of ancestral list for every animal. The L elements are calculated as follows:

$$l_{ij} = \sum_{k \in ANC_i \cap P_j} 0.5l_{ik}, \quad (38)$$

where:

ANC_i is the ancestors list of animal i including the i th itself, and P_j includes the progeny of ancestor j .

The overall mean inbreeding level (\bar{F}) of the population was determined by averaging the F values of all individuals in the study course. The trend of inbreeding over the course of 13 years (2008-2020) was determined by conducting a regression analysis, where \bar{F} of each year was regressed against the corresponding year of production.

Pedigree quality was assessed using two measurements: the proportion of animals having known parents for both sire and dam, and the number of equivalent complete generations (Mandal et al., 2020; Rashidi et al., 2015). Number of equivalent complete generations for each i th individual (EqG_i) were computed following Maignel et al. (1996) as follows:

$$EqG_i = \sum \left(\frac{1}{2} \right)^n, \quad (39)$$

Where:

n is the number of generations which separate the individual i from each known ancestor.

Then, EqG_i of all animals were averaged \bar{EqG}_i to be used in the quality assessment.

2.4.2 Estimation of genetic parameters of the growth traits in the three breeds (Chapter 4)

2.4.2.1 Records adjustment

The data underwent a preliminary inspection and adjustment to avoid any potential biases. Initially, outliers were removed from the analysis. Outliers were defined as values that exceeded the mean by three times the standard deviation. In addition, the weights corresponded to the WW, W6, and W12 traits were adjusted to 90, 180, and 360 days, respectively. This adjustment was implemented to decrease the variation in results from weighing animals at different ages, as there were differences in age at the time of weighing. The adjustment of weights was based on the following equation, as suggested by Inyangala et al. (1992) as follows:

$$\left[\left(\frac{\text{animal's weight of trait} - \text{animal's weight at birth}}{\text{Date of animal's weighing} - \text{Date of birth}} \times \text{adjusted days} \right) + \text{weight of BW} \right] \quad (40)$$

2.4.2.2 Significance of fixed effects

Initially, the significance of environmental fixed factors was assessed using ANOVA by fitting a general linear model in the Minitab software (Minitab, 2021). This was done to determine which fixed components should be included in the final animal model, which was used to estimate the genetic parameters. The factors considered in the analysis were year of birth (categorised into 13 levels), pen (categorized into 18 levels), sex (categorized into two levels: male and female), type of birth (categorized into three levels: single, twin, and multiple), and age of the dam, which was included as a covariate equation (41). All possible two-way interactions were examined, and only the interaction with a *P*-value less than 0.05 was retained in the model. The Tukey-Kramer method was employed to examine differences among pairs of levels of the fixed variables. Only the components with a significance level (*P*-value) of less than

0.05 were selected to be included in the animal model for the estimation of the genetic parameters.

$$Y_{abcd} = \mu + Year_a + Sex_b + Type\ of\ birth_c + CovAge\ of\ dam_d + e_{abcd} \quad , \quad (41)$$

where:

Y_{abcd} is the animal's observation in a^{th} year, b^{th} sex, c^{th} type of birth, d^{th} age of dam; μ is the population's mean; e_{abcd} is the random error associated with $abcd^{\text{th}}$ observation.

2.4.2.3 Estimating (Co)variance components and corresponded genetic parameters

The (Co)variance components and their corresponding genetic parameters were estimated by the restricted maximum likelihood estimator REML by fitting six various univariate animal models with the WOMBAT software (Meyer, 2012). All models fit the animal's additive genetic effect, while they differ in including or excluding maternal genetic and environmental effects. Then, the best model will only be determined for the estimations. The six animal models were as follows:

$$(1) \quad y = Xb + \beta a + e$$

$$(2) \quad y = Xb + \beta a + Zm + e, \quad Cov(a, m) = 0$$

$$(3) \quad y = Xb + \beta a + Zm + e, \quad Cov(a, m) = A\sigma_{a,m}$$

$$(4) \quad y = Xb + \beta a + Wc + e$$

$$(5) \quad y = Xb + \beta a + Zm + Wc + e, \quad Cov(a, m) = 0$$

$$(6) \quad y = Xb + \beta a + Zm + Wc + e, \quad Cov(a, m) = A\sigma_{a,m}$$

Where:

y is a vector of records; b is a vector of the fixed effects; a , m , c and e are vectors of animal's additive genetic effect, maternal additive genetic effect, maternal permanent environmental effect and residual effect, respectively; X , β , Z and W are design matrices relating records to the effects of b , a , m and c , respectively; A is the numerator genetic relationship matrix.

It was assumed that all the effects of the random factors follow the normal distribution and that the mean equals zero, with variances equal to:

$$V_{(a)} = A\sigma_a^2,$$

$$V_{(m)} = A\sigma_m^2,$$

$$V_{(c)} = I\sigma_c^2,$$

$$V_{(e)} = I\sigma_e^2,$$

Where:

A and I are the numerator relationship matrix and identity matrix (order equal to the number of dams and number of records), respectively; σ_a^2 , σ_m^2 , σ_c^2 , and σ_e^2 are animals' additive genetic variance, maternal genetic variance, maternal permanent environmental variance, and residual variance, respectively.

Choosing the best-fitted model was based on both the likelihood ratio test LRT (Wilson et al., 2010) and the Akaike information criterion AIC (Akaike, 1974). The LRT estimates the goodness of fit, and it can compare the models that differ by at least one parameter. While the AIC method was used, it estimates the prediction error and can compare models with the same or different number of parameters. The LRT tests the significance of the random effect by comparing the loglikelihoods ($LogL$) between the model that fitted the random effect and the model that ignored it. It is assumed that the twice-difference of these loglikelihoods between the models follows a chi-square (χ^2) distribution with one degree of freedom, so it is calculated as follows:

$$LRT = 2(LogL(Full\ model) - LogL(Reduced\ model))$$

The effect was considered significant if the value of χ^2 corresponded to $P < 0.05$.

The AIC was calculated as:

$$AIC = 2(LogL) + 2K,$$

Where:

K represents the number of fitted parameters, and **LogL** represents the maximum loglikelihood of the model.

Estimates of direct heritability h_a^2 , maternal heritability h_m^2 , and proportional maternal permanent environmental effects c^2 were calculated as follows:

$$h_a^2 = \frac{\sigma_a^2}{\sigma_P^2},$$

$$h_m^2 = \frac{\sigma_m^2}{\sigma_P^2},$$

$$c^2 = \frac{\sigma_c^2}{\sigma_P^2},$$

Where:

σ_a^2 , σ_m^2 , σ_c^2 and σ_P^2 are the variances of animal's additive genetic effects, maternal additive genetic effects, maternal permanent environmental effects and phenotypic values, respectively.

The genetic r_a and phenotypic r_P correlations were estimated using four trait multi-variate animal model as explained in equation (42), by fitting the most appropriate model specified in the univariate analysis for each trait. The fixed effects fitted in the multi-trait animal models were the same as those in the single-trait analysis for each trait.

$$\begin{pmatrix} y_1 \\ y_2 \\ y_3 \\ y_4 \end{pmatrix} = \begin{pmatrix} X_1 & 0 & 0 & 0 \\ 0 & X_2 & 0 & 0 \\ 0 & 0 & X_3 & 0 \\ 0 & 0 & 0 & X_4 \end{pmatrix} \begin{pmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{pmatrix} + \begin{pmatrix} \beta_1 & 0 & 0 & 0 \\ 0 & \beta_2 & 0 & 0 \\ 0 & 0 & \beta & 0 \\ 0 & 0 & 0 & \beta_4 \end{pmatrix} \begin{pmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \end{pmatrix} +$$

$$\begin{pmatrix} Z_1 & 0 & 0 & 0 \\ 0 & Z_2 & 0 & 0 \\ 0 & 0 & Z_3 & 0 \\ 0 & 0 & 0 & Z_4 \end{pmatrix} \begin{pmatrix} m_1 \\ m_2 \\ m_3 \\ m_4 \end{pmatrix} + \begin{pmatrix} W_1 & 0 & 0 & 0 \\ 0 & W_2 & 0 & 0 \\ 0 & 0 & W_3 & 0 \\ 0 & 0 & 0 & W_4 \end{pmatrix} \begin{pmatrix} c_1 \\ c_2 \\ c_3 \\ c_4 \end{pmatrix} + \begin{pmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \end{pmatrix}, \quad (42)$$

Where:

y_1 , y_2 , y_3 and y_4 are vectors of records for the traits of BW, WW, W6 and W12, respectively; \mathbf{b}_1 , \mathbf{b}_2 , \mathbf{b}_3 and \mathbf{b}_4 are vectors of the fixed effects for the traits of BW, WW, W6 and W12, respectively; \mathbf{a}_1 , \mathbf{a}_2 , \mathbf{a}_3 and \mathbf{a}_4 are vectors of animals' additive genetic effects for the traits of BW, WW, W6 and W12, respectively; \mathbf{m}_1 , \mathbf{m}_2 , \mathbf{m}_3 and \mathbf{m}_4 are vectors of maternal additive genetic effects for the traits of BW, WW, W6 and W12, respectively; \mathbf{c}_1 , \mathbf{c}_2 , \mathbf{c}_3 and \mathbf{c}_4 are vectors of maternal permanent environmental effects for the traits of BW, WW, W6 and W12, respectively.

X_1 , X_2 , X_3 , X_4 , β_1 , β_2 , β_3 , β_4 , Z_1 , Z_2 , Z_3 , Z_4 , W_1 , W_2 , W_3 and W_4 are the incidence matrices which relates the records to the fixed effects, animal's additive genetic effect, maternal additive genetic effect and maternal permanent environmental effect for the traits of BW, WW, W6 and W12, respectively.

It was assumed that all the effects of the random factors follow the normal distribution and that the mean equals zero, with (Co)variances structure as follows :

$$\begin{aligned} \text{Var} \begin{pmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \end{pmatrix} &= A \otimes \begin{pmatrix} \sigma_{a1}^2 & \sigma_{a1a2} & \sigma_{a1a3} & \sigma_{a1a4} \\ \sigma_{a1a2} & \sigma_{a2}^2 & \sigma_{a2a3} & \sigma_{a2a4} \\ \sigma_{a1a3} & \sigma_{a2a3} & \sigma_{a3}^2 & \sigma_{a3a4} \\ \sigma_{a1a4} & \sigma_{a2a4} & \sigma_{a3a4} & \sigma_{a4}^2 \end{pmatrix}, \\ \text{Var} \begin{pmatrix} m_1 \\ m_2 \\ m_3 \\ m_4 \end{pmatrix} &= A \otimes \begin{pmatrix} \sigma_{m1}^2 & \sigma_{m1m2} & \sigma_{m1m3} & \sigma_{m1m4} \\ \sigma_{m1m2} & \sigma_{m2}^2 & \sigma_{m2m3} & \sigma_{m2m4} \\ \sigma_{m1m3} & \sigma_{m2m3} & \sigma_{m3}^2 & \sigma_{m3m4} \\ \sigma_{m1m4} & \sigma_{m2m4} & \sigma_{m3m4} & \sigma_{m4}^2 \end{pmatrix}, \\ \text{Var} \begin{pmatrix} c_1 \\ c_2 \\ c_3 \\ c_4 \end{pmatrix} &= I \otimes \begin{pmatrix} \sigma_{c1}^2 & \sigma_{c1c2} & \sigma_{c1c3} & \sigma_{c1c4} \\ \sigma_{c1c2} & \sigma_{c2}^2 & \sigma_{c2c3} & \sigma_{c2c4} \\ \sigma_{c1c3} & \sigma_{c2c3} & \sigma_{c3}^2 & \sigma_{c3c4} \\ \sigma_{c1c4} & \sigma_{c2c4} & \sigma_{c3c4} & \sigma_{c4}^2 \end{pmatrix}, \text{ and} \end{aligned}$$

$$\text{Var} \begin{pmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \end{pmatrix} = I \otimes \begin{pmatrix} \sigma_{e1}^2 & \sigma_{e1e2} & \sigma_{e1e3} & \sigma_{e1e4} \\ \sigma_{e1e2} & \sigma_{e2}^2 & \sigma_{e2e3} & \sigma_{e2e4} \\ \sigma_{e1e3} & \sigma_{e2e3} & \sigma_{e3}^2 & \sigma_{e3e4} \\ \sigma_{e1e4} & \sigma_{e2e4} & \sigma_{e3e4} & \sigma_{e4}^2 \end{pmatrix},$$

Where:

\mathbf{A} is the numerator relationship matrix and I is an identity matrix; $\sigma_{a1}^2, \sigma_{a2}^2, \sigma_{a3}^2, \sigma_{a4}^2, \sigma_{m1}^2, \sigma_{m2}^2, \sigma_{m3}^2, \sigma_{m4}^2, \sigma_{c1}^2, \sigma_{c2}^2, \sigma_{c3}^2, \sigma_{c4}^2, \sigma_{e1}^2, \sigma_{e2}^2, \sigma_{e3}^2$ and σ_{e4}^2 are variances of the animal's additive genetic effects, maternal additive genetic effects, maternal permanent environmental effects and residual effects for the traits of BW, WW, W6 and W12, respectively; $\sigma_{a1a2}, \sigma_{a1a3}, \sigma_{a1a4}, \sigma_{a2a3}, \sigma_{a2a4}, \sigma_{a3a4}, \sigma_{m1m2}, \sigma_{m1m3}, \sigma_{m1m4}, \sigma_{m2m3}, \sigma_{m2m4}, \sigma_{m3m4}, \sigma_{c1c2}, \sigma_{c1c3}, \sigma_{c1c4}, \sigma_{c2c3}, \sigma_{c2c4}, \sigma_{c3c4}, \sigma_{e1e2}, \sigma_{e1e3}, \sigma_{e1e4}, \sigma_{e2e3}, \sigma_{e2e4}$ and σ_{e3e4} are the covariances of the animal's additive genetic effects, maternal permanent environmental effects and residual effects between the traits of BW, WW, W6 and W12, respectively.

The genetic r_a and phenotypic r_p correlations between the four traits were calculated by following equations:

$$r_a = \frac{\sigma_{a \text{ of trait 1, } a \text{ of trait 2}}}{\sqrt{\sigma_{a \text{ of trait 1}}^2 \times \sigma_{a \text{ of trait 2}}^2}}$$

$$r_p = \frac{\sigma_{P \text{ of trait 1, } P \text{ of trait 2}}}{\sqrt{\sigma_{P \text{ of trait 1}}^2 \times \sigma_{P \text{ of trait 2}}^2}}$$

In order to test the statistical significance of genetic correlations among traits, the *LRT* was employed to compare the model fitted with the covariance to a model with a covariance of zero (Wilson et al., 2010). The phenotypic correlations were tested by doing a hypothesis test to determine if the correlation coefficient differs from zero (Rajkumar et al., 2021).

The estimated breeding values EBVs of animals were calculated using the BLUP method, as described by Henderson (1973). They were generated by WOMBAT software by-product (solutions of animals' effects a) from REML estimations of (Co) variance estimates via the multivariate analysis. Subsequently, the mean breeding values \bar{EBVs} of the animals born in the same year were regressed to the year of birth in order to determine the genetic trend. Following the standardisation of the collected body weight data based on the fixed effects, the phenotypic trend was determined by calculating the linear regression of the adjusted means for a specific body weight in relation to the birth years (Elsayed, 2013).

2.5 The simulation study of implementing genomic selection in Omani sheep (Chapter 5)

The Omani sheep breed was selected as a case study to investigate the potential benefits of using genomic selection compared to traditional selection. The study focused on three specific growth traits: BW, W6, and W12. These traits correspond to three different categories of heritability: low, moderate, and high, respectively. The simulated heritability estimates of the three traits were the same as those obtained in Chapter 4 (genetic parameter estimation) in order to represent the realized genetic characteristics of this population. The phenotypes of individuals were generated by simulating the sheep genome of pedigreed animals, which was the same real pedigree of this population used in Chapter 3. The EBVs of the animals were predicted using three methods: BLUP, GBLUP, and ssGBLUP. The correlation coefficient r was used to calculate the accuracy of the prediction by assessing the relationship between the true breeding value (TBV) and the EBV.

2.5.1 Simulation of sheep genome

Steps of the genome simulation involved setting up simulated genetic loci, including markers and QTLs, in simulated sheep individuals. The simulation was written in Fortran source code (Appendix A), and it has been verified by checking the output files of marker alleles and their corresponding genotypes (Appendix B), and the simulated heritability was verified by WOMBAT analysis (Appendix C). It was based on two sources of real datasets: the structure of the sheep genome and the real pedigree of the Omani sheep breeding cohorts under study. The genome was defined by species ploidy, the number of ovine chromosomes, the chromosomes' length in cM units, the

number of total simulated loci (markers and QTLs), and the assignment of markers and QTL positions and their genetic effects.

The sheep's genome was simulated to have 5 pairs of chromosomes with a total length of about 400 cM. Reducing the simulation from the real number of ovine chromosomes to only 5 chromosomes was because of computer efficiency limitations and the limitation of array dimension in the Fortran language. Each chromosome was evenly allocated 1,010 biallelic genetic loci (taking the codes of 1 for the dominant allele and 0 for the recessive allele) totalling 5,050 loci, of which 50 distributed QTLs and the rest were considered markers. **Tables 6 and 7** illustrate the simulated genome structure and the genetic parameters of the simulated traits.

Alleles of different loci on same chromosome may co-segregate more frequent than normal. The frequency of this association between alleles of different loci depends on the genetic distance between loci, which can be estimated by the recombinant gametes. Therefore, in the simulation process, the allele's type at first locus of the formed gamete was determined to follow uniform distribution with frequency $x = 0.5$, so that both alleles (1 and 0) have equal probability 50% of being picked. For the rest loci of the formed gamete, they were determined taking into account the recombination frequency among the adjacent loci, where x here follow, the uniform distribution is adjusted to the recombination frequency as follow:

$$x \leq \text{recombination frequency (between the two adjacent loci)},$$

So, the frequency of co-segregated alleles of the different loci would appear more frequent than normal.

Table 6. Lengths in centiMorgan (cM) of the simulated five ovine chromosomes

Number of chromosome	Length in cM
1	80.72
2	70.63
3	100.90
4	70.63
5	70.63
Total	393.51

Table 7. Description of the simulated genome and genetic model of the ovine simulation study.

BW = birth weight, **W6** = six-months weight, and **W12** = yearling weight.

The genome	The simulation
No of chromosomes	5
Total of genome length	~400 cM
Number of markers	5,000 bi-allelic
Distribution of markers	Evenly spaced
Number of QTLs	50 bi-allelic
QTL distribution	User-specific allocations
QTL effects	one with large effects (20% of total genetic variance) Two with medium effects (each with 10% of total genetic variance) Remaining 47 (1% or 2% of total genetic variance)
The genetic model	Parameters
Genetic effects	Additive genetic effects only
Heritability	BW, W6 and W12 (0.16, 0.28, 0.48, respectively)
Population means	BW, W6 and W12 (3.05 kg, 20.03 kg and 32.44 kg, respectively)

Genotypes of the founder animals for all loci were determined according to the distribution of allelic frequencies (0.50). While the genotypes of their progenies were generated from the union of the gametes randomly sampled from their parents specified in the pedigree. The gametes are always haploid (n chromosomes) created from a diploid parental cell. The two alleles (coded as 1 and 0) of each gene segregate randomly to form the gamete (i.e., 50% probability).

2.5.2 The genetic model of the simulation

The investigation of genetic variation (V_G) among population's individuals that associated with a particular quantitative trait can be studied with the help of formulating genetic models, the most common of which is the QTL model. The QTL model assumes that a limited number of genes exhibit major effects on the trait explaining significant part of the phenotypic variance (V_P), whereas the remaining V_P is explained by remaining numerous genes, of each have a minor impact (Clark et al., 2011). The suggested genetic model for this simulation assumed that QTLs have only the additive genetic effects (a), ignoring dominance (d) and epistasis (I) effects. The additive genetic effect (a) of a certain QTL was computed based on the relationship between the QTL allelic frequency (p) and its variance (V_{QTL}) as explained by Falconer (1996) following the steps 1 and 2:

$$V_{QTL} = 2p(1 - p)a^2 \quad (1)$$

If the allelic frequency p of a QTL is 0.50, then (1) can be reduced to become:

$$V_{QTL} = \frac{1}{2} \cdot a^2 \quad (2)$$

So, in order to calculate the additive genetic effect (a) of that QTL, from (2):

$$a = \sqrt{2 \cdot V_{QTL}} \quad (3)$$

The value of an individual's phenotype was calculated according to the basic quantitative additive genetic model as follows:

$$y_i = \mu + G_i + e_i \quad , \quad (4)$$

where:

y_i is the phenotypic value of individual i , μ is the population's mean, G_i is the genotypic value for individual i , and e_i is a normally distributed error terms with mean = 0 and variance (σ_e^2).

The environmental variance σ_e^2 was estimated based on the relationship of it with the heritability as in (5), considering that the phenotypic variance of the trait equals 1:

$$\sigma_e^2 = \frac{\sigma_G^2(1-h^2)}{h^2} \quad , \quad (5)$$

where:

σ_G^2 is the genetic variance and h^2 is the trait's heritability.

The true genetic value (G) of individual i was calculated by summing all the effects of their genotype on every QTL as following:

$$G_i = \sum_{j=1}^n x_{ij} a_j \quad , \quad (6)$$

where:

x_{ij} is the genotype of individual i at locus j coded as (0, 1, or 2) for QTL genotypes of (homozygous, heterozygous and alternate homozygous, respectively) ; a_j is the additive genetic effect of QTL j ; and n is the number of all QTL loci.

2.5.3 Example for illustration (How to calculate the additive genetic effects)

If we simulate a trait of heritability $h^2 = 0.16$, and the phenotypic variance $V_P = 1$. The defined quantitative genetic model for a putative QTL would be as follows: QTL genotypes at locus Q are QQ, Qq and qq, which have genotypic values of $a - d/2$, $d/2$ and $-a - d/2$, respectively. The V_{QTL} at this QTL is $\sigma_{QTL}^2 = 1/2 a^2$ as illustrated in (2), with the assumption of $d = 0$, (i.e., the additive genic model). If this QTL explains 10% of total V_G , it means that the heritability of it equals 10% $\times h^2$ ($0.10 \times 0.17 = 0.017$). Thus, the additive genic effect (a) at the QTL is calculated based on (3) as follow:

$$a = \sqrt{(2 \times \sigma_{QTL}^2)}$$

$$a = \sqrt{(2 \times 0.017)}$$

Following the same principles, we can calculate the (a) value for each assumed QTL, while the trait's heritability and proportion of variance explained by the QTL are known.

Let us assume that a given trait is influenced by 13 QTLs, of which three have major effects and ten had minor effects. The three major QTLs (QTL_M), which all together explain 40% of the total genetic variance (V_{QTLs}), of which two QTLs (QTL_{M01} and QTL_{M02}) explain 10% for each one, and one QTL (QTL_{M03}) explains 20%.

According to the *equation 11*, the additive genetic effect a of each major QTL would be as follow:

$$a_{QTL_{M01}} = \sqrt{2(V_{QTL_{M01}})} = \sqrt{2(0.10 \times 0.17)} = 0.18$$

$$a_{QTL_{M02}} = \sqrt{2(V_{QTL_{M02}})} = \sqrt{2(0.10 \times 0.17)} = 0.18$$

$$a_{QTL_{M03}} = \sqrt{2(V_{QTL_{M03}})} = \sqrt{2(0.20 \times 0.17)} = 0.26$$

The remaining ten QTLs would explain the remaining 60% of V_{QTLs} , each with 6% equally. Therefore, each one would explain $0.06 \times 0.17 = 0.01$ of V_{QTLs} . Accordingly, The additive genetic effect (a) for each minor QTL_m would be:

$$a_{QTL_m} = \sqrt{2(V_{QTL_m})} = \sqrt{2(0.01)} = 0.14$$

2.5.4 Statistical analysis of predicting animals' breeding values

Three approaches were used to estimate the estimated EBVs of the animals, including BULP, GBLUP, and ssGBLUP. The BLUP method, which was developed by Henderson (1949), is a conventional estimator that integrates pedigree genetic relationships between individuals in the mixed model equation MME. The other two methods benefit from the information provided by the molecular markers. The GBLUP technique utilises the molecular' genotypes across the genome to construct genomic relationships between individuals instead of pedigree information, as outlined by (Habier et al., 2007; VanRaden, 2008). While the ssGBLUP method utilizes data from both molecular markers and pedigree information to build a single matrix for estimating the genetic relationships between animals, as outlined by Misztal et al. (2010). Chapter 1 reviewed comprehensive details about the statistical basics of these methodologies.

The BLUP approach utilised the pedigree records of all available animals in the whole population, as well as the records of all animals except those in the validation group. The GBLUP approach utilised both phenotypic records and genomic information from genotyped reference animals. The ssGBLUP method incorporates the pedigree information of all animals in the population, as well as the records of all animals except for those used for validation, and the genomic information of the reference animals that have been genotyped.

The three methods were compared for accurately predicting EBVs under three different scenarios, and they varied in the population's size used as a reference (The population whose animals have phenotypic records and marker genotypes). The reference population was used to estimate the effects of SNP markers, and their estimates are subsequently used to predict the breeding values of the validation

population. The validation population included only genotyped animals without phenotypic records. These animals were born in the last generation, whereas the reference animals were ones that were born in the years before that.

The reference population consisted of 500, 1000, and 2000 animals for the three varied scenarios. The prediction accuracy of breeding values was determined by the correlation coefficient r between TBV and the predicted EBV of the validation population. Each scenario has been replicated 10 times, and the value of r of these 10 times was averaged to be considered the final accuracy.

CHAPTER THREE

ESTIMATION OF INBREEDING LEVEL IN *JEBEL AKHDAR* AND *BATINAH* GOATS, AND *OMANI SHEEP*

3.1 Abstract

The main objective of this research was to determine the level of inbreeding and its trend across three distinct breeds of livestock in Oman, namely Jebel Akhdar (JA) goats, Batinah (BA) goats, and Omani sheep (OS). The pedigree analysis in this study utilised records of pedigreed animals obtained from the Wadi Qurayyat livestock research station (WQLRS) in Oman, spanning the period from 2008 to 2020. The dataset included records of 2,826, 2,610, and 3,530 animals belonging to the three breeds JA, BA, and OS, respectively. The findings of the study revealed that the average levels of inbreeding within the overall population were observed to be within acceptable levels, with percentages of 0.67%, 0.65%, and 1.52% for the JA, BA, and OS breeds, respectively. While it was 3.88%, 3.39% and 6.49% within inbred animals of the corresponding breeds,. The distribution of inbred animals was 17.34% for JA, 19.31% for BA, and 23.48% for OS. The breeds JA, BA, and OS have annual rates of inbreeding of 0.12%, 0.13%, and 0.27%, respectively. The most frequently found inbred animals among the others were those with an inbreeding level below 6.25%, accounting for 13.45% for JA, 14.98% for BA, and 12.63% for OS of the entire population. Conversely, the animals with higher levels of inbreeding were the least common among the three categories. The low levels of inbreeding observed in the three breeds do not raise any concerns regarding inbreeding depression and the loss of genetic variation. Yet, the apparent rise in levels of inbreeding within the examined breeds, particularly in recent years, necessitates the monitoring of inbreeding levels as a means of controlling and reducing the potential negative effects of inbreeding depression while also ensuring the maintenance of adequate genetic variability.

3.2 Introduction

Animal breeding programmes rely on exploiting the genetic variation present within a population, as animals can respond to selection effectively. Hence, the ongoing maintenance of sufficient levels of genetic variation is a pivotal concern for animal breeders in the development of genetic improvement strategies (de Oliveira et al., 2023; Fernández et al., 2005). Accordingly, successful implementation of an effective and sustainable genetic improvement programme requires maintaining adequate levels of genetic variability (Pedrosa et al., 2010). Genetic improvement programmes, particularly those carried out by within-population selection of superior animals, often end in a reduction in genetic variability and an increase in rates of inbreeding (Ceyhan et al., 2011; Mandal et al., 2020). Hence, the main objective in the management of animal populations is to maintain a high degree of genetic variability while simultaneously reducing rates of inbreeding.

The level of inbreeding can influence the extent of genetic variability within a population by increasing the frequency of homozygous genotypes and decreasing the frequency of heterozygous genotypes (Hartl, 2020). Ultimately, it may lead to complete homozygosity if it is not controlled (Kristensen & Sørensen, 2005). Moreover, it is commonly known that excessive inbreeding usually has a negative impact on the animal's productivity, health, and ability to reproduce. This is explained by a phenomenon called inbreeding depression, which is the term for the decline in a trait's average value driven by inbreeding (Ceyhan et al., 2011; Falconer, 1996; Rashidi et al., 2015; Weigel, 2001). Many characteristics, including growth traits, pregnancy, puberty, and milk production, are susceptible to the effects of inbreeding (Wakchaure & Ganguly, 2015). Thus, it is important to continually monitor and control the rate of

inbreeding in a population to maintain it at acceptable levels. Managing inbreeding is a vital strategy for mitigating the reduction of genetic variability and the associated detrimental consequences. Multiple factors, including the mating system, sex ratio, reproductive ability, and population size, can have a significant impact on the level of inbreeding (Ceyhan et al., 2011).

Pedigree analysis is a straightforward and economical approach for evaluating genetic variation and inbreeding within a population (Mandal et al., 2020). The estimation of inbreeding level within a population involves calculating the inbreeding coefficients (F) for each individual of the population, where F represents the probability of an individual possessing two identical alleles descended from a common ancestor (i.e., IBD) at any randomly selected locus (Ceyhan et al., 2011; Hartl, 2020; Kristensen & Sørensen, 2005). It is the outcome of breeding between pairs of individuals who are closely related and have one or more common ancestors. An inbred animal is the offspring that arises from a union between closely related parents. The amount of the F value is dependent on the coefficient of the relationship between the mated parents.

The objective of this study was to use pedigree analysis of three Omani breeds, including Jebel Akhdar (JA) and Batinah (BA) goats, as well as Omani sheep (OS) to investigate the level of inbreeding and its trend over a span of 13 years (2008-2020). These breeds have been subjected to a close selective breeding program at Wadi Qurayyat Livestock Research Station (WQLRS) to enhance their productive and reproductive performance. Therefore, the estimation of inbreeding levels among these populations is important to assess the success of the breeding program in terms of inbreeding accumulation and genetic variability maintenance.

3.3 Results

3.3.1 The pedigree structure of the studied populations

Table 8 presents a summary of the main characteristics related to the pedigree structure of the three analyzed breeds, namely Jebel Akhdar (JA) goat, Batinah (BA) goat, and Omani (OS) sheep. The proportion of animals in the overall populations of the JA, BA, and OS breeds that had both known parents was 90.35%, 88.53%, and 89.80%, respectively (**Figures 9, 10 and 11**). In succeeding generations, the proportions of known ancestors progressively decreased from 64%, 59%, and 63% in the second generations of JA, BA, and OS, respectively, to 19%, 17%, and 20%, respectively, for the corresponding breeds.

The percentage of animals that had offspring in the populations of JA, BA, and OS were 28.67%, 27.45%, and 29.23% correspondingly. Among these populations, the proportions of sires and dams were 14.38% and 85.62% for JA, 14.66% and 85.34% for BA, and 11.66% and 88.34% for OS. The average number of complete generations (EqG_i) for the entire populations JA, BA, and OS were 2.14, 2.03, and 2.17, respectively.

Table 8. Pedigree structure of Jebel Akhdar (JA) goats, Batinah (BA) goats and Omani sheep (OS).

Item	JA	BA	OS
No. of total animals in the pedigree	3,128	2,948	3,931
No. of animals with records	2,826	2,610	3,530
No. of animals without offspring	2,231	2,091	2,782
No. of animals with offspring	897	791	1,149
No. of sires with progeny	129	116	134
No. of dams with progeny	768	675	1,015
No. of animals with both known parents	2,826	2,610	3,530
Mean maximum generations	2.84	2.89	3.00
Mean complete generations	1.68	1.55	1.58
Average of equivalent complete generations	2.14	2.03	2.17

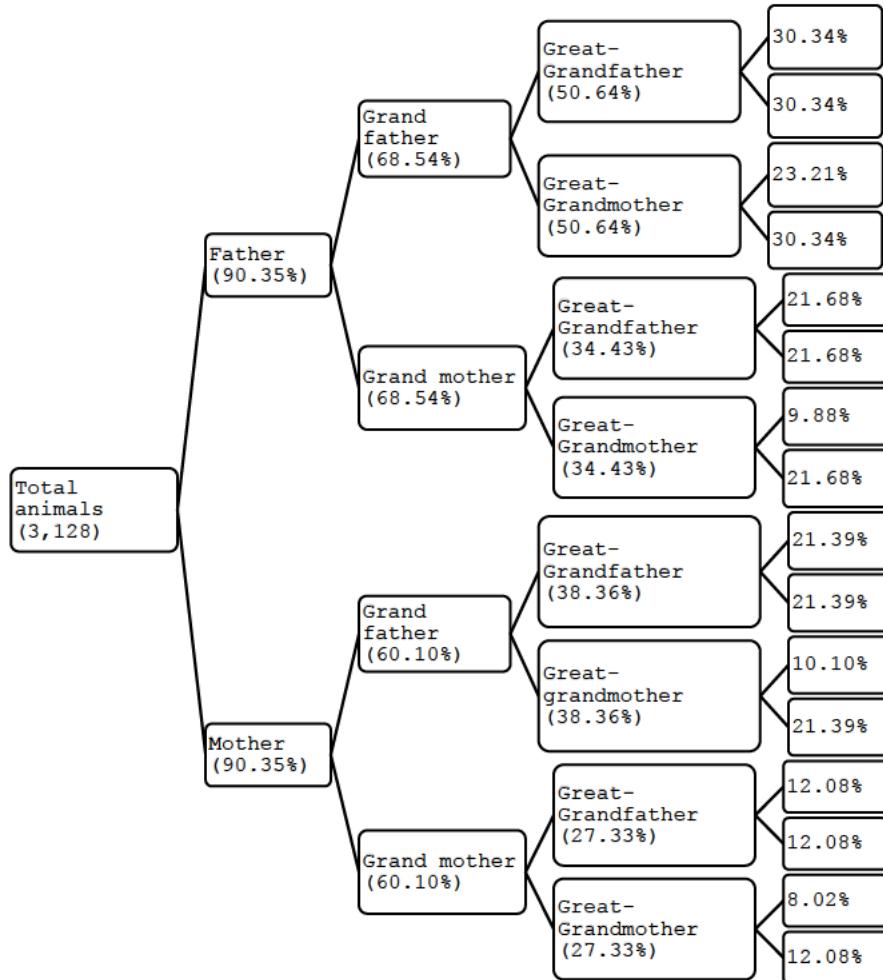


Figure 9. Pedigree content of Jebel Akhdar goats until the fourth generation.

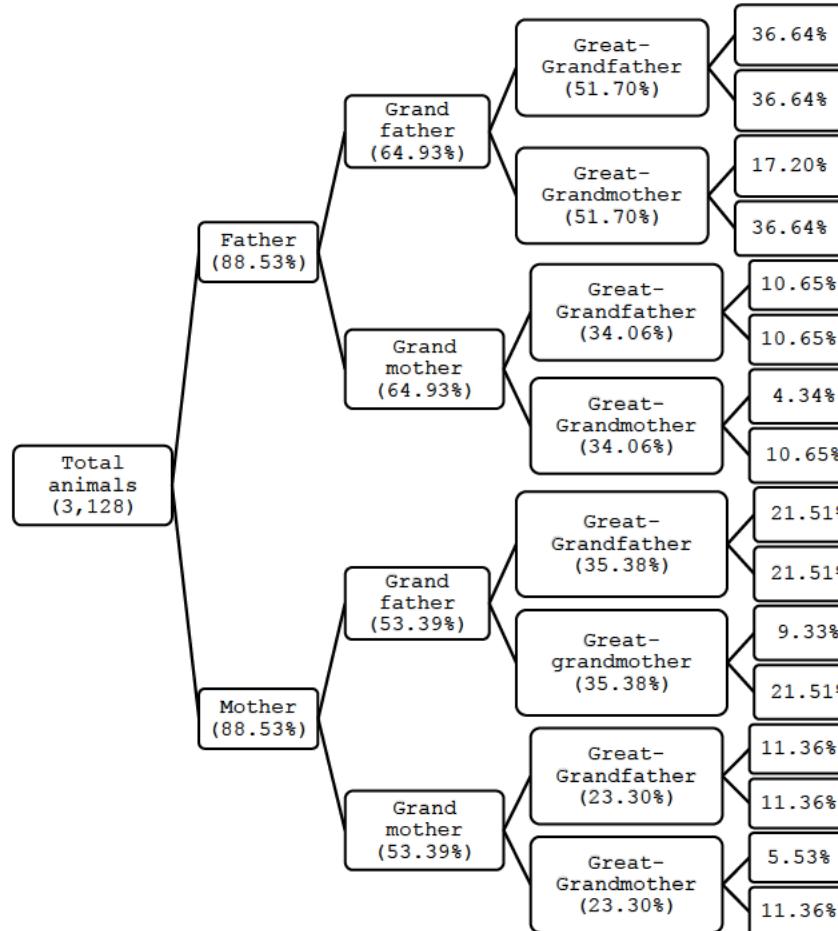


Figure 10. Pedigree content of Batinah goats until the fourth generation.

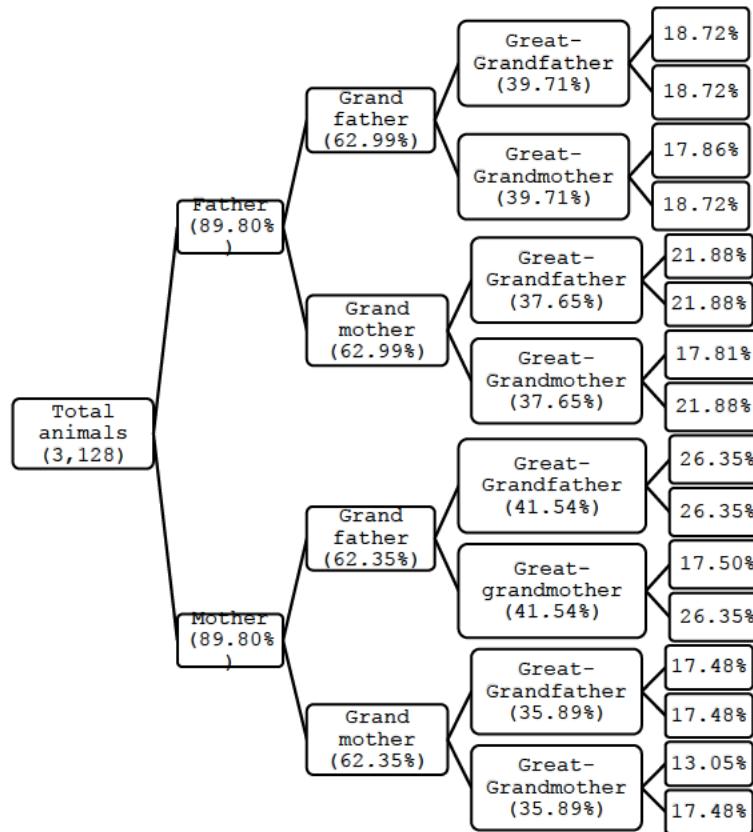


Figure 11. Pedigree content of Omani sheep until the fourth generation.

3.3.2 Average inbreeding coefficient (\bar{F})

A summary of the descriptive statistics for the average inbreeding level (\bar{F}) of the three breeds, as well as the proportions of inbred animals is presented in **Table 9**. The findings derived from the pedigree analysis conducted between 2008 and 2020 revealed that 17.34%, 19.31%, and 23.48% of the overall population of animals were identified as inbred individuals within the respective breeds of JA goats, BA goats, and OS sheep. In contrast, the percentage of individuals that were not inbred among JA goats, BA goats, and OS sheep was 82.66%, 80.69%, and 76.52%, respectively. The mean values of the inbreeding coefficient (\bar{F}) for the three breeds, namely JA goats, BA sheep, and OS sheep, were 0.67%, 0.65% and 1.52%, respectively, when considering the entire population. While it was 3.88%, 3.39% and 6.49% within inbred individuals for the breeds of JA, BA, and OS, respectively. The highest F values were observed in 2017 for OS sheep, reaching 32.03%, while it was 31.25% in JA in the years of 2017 and 2019, and it was 26.56% in BA breed in 2019.

3.3.3 Categorization of animal distribution based on different ranges of F (%) levels.

The inbreeding coefficient of $F = 0\%$ was observed in most animals across all three breeds. Among these breeds, the JA breed showed the highest percentage (82.66%), BA (80.69), while the OS breed indicated the lowest percentage (76.52%), as indicated in **Table 10**. The second largest proportion of animals within the three populations had an inbreeding coefficient F value below 6.25%. More specifically, across the entire population, the proportions of animals with F values below 6.25% were 13.45% in JA, 14.98% in BA, and 12.63% in OS. Less than 1% of the total

population was found in the highest F values ($F \geq 18.75$), which had the lowest frequencies of inbred animals among the three breeds.

Table 9. Summary statistics of inbreeding level from the pedigree analysis of JA, BA, and OS Omani breeds.

(F) is inbreeding coefficient; (\bar{F}) is average inbreeding coefficient.

Item	JA	BA	OS
\bar{F} (%) \pm S.E. of the whole population	0.67 \pm 0.05	0.65 \pm 0.05	1.52 \pm 0.07
\bar{F} (%) \pm S.E. of the inbred animals	3.88 \pm 0.24	3.39 \pm 0.21	6.49 \pm 0.24
Standard deviation of \bar{F}	2.67	2.42	4.30
Maximum F (%)	31.25	26.56	32.03
Proportion of inbred animals (%)	17.34	19.31	23.48
Proportion of non-inbred animals (%)	82.66	80.69	76.52

Table 10. Proportions (%) of animals categorized based on various F (%) ranges.

Breed	$F = 0$	$0 < F < 6.25$	$6.25 \leq F < 12.5$	$12.5 \leq F < 18.75$	$18.75 \leq F < 25$	$F \geq 25$
JA	82.66	13.45	1.88	1.42	0.00	0.60
BA	80.69	14.98	2.41	1.53	0.04	0.34
OS	76.52	12.63	5.35	3.97	0.57	0.96

3.3.4 Trend of inbreeding levels (2008-2020)

Table 11 presents the annual rates of inbreeding for Omani JA goats, BA goats, and OS sheep, which have been found to be 0.12%, 0.13%, and 0.27%, respectively. **Figure 12** illustrates the overall trend of inbreeding for the entire populations of JA and BA goats, as well as OS sheep, in a 13-year interval. The findings demonstrated a predominantly linear trend of annual inbreeding increase during the whole duration of the study for all examined breeds. The level of inbreeding seen in OS was consistently higher than that observed in the goat breeds across the years. The mean level of inbreeding displayed variations ranging from zero to 1.6%, zero to 1.5%, and zero to 3.7% for the JA, BA, and OS, respectively, over the course of the study period.

Table 11. Inbreeding trend in Omani JA goats, BA goats, and OS sheep.

Population	Regression coefficient	P-Value	R ²
JA	0.12	0.0001	78.24%
BA	0.13	0.0000	85.31%
OS	0.27	0.0000	86.08%

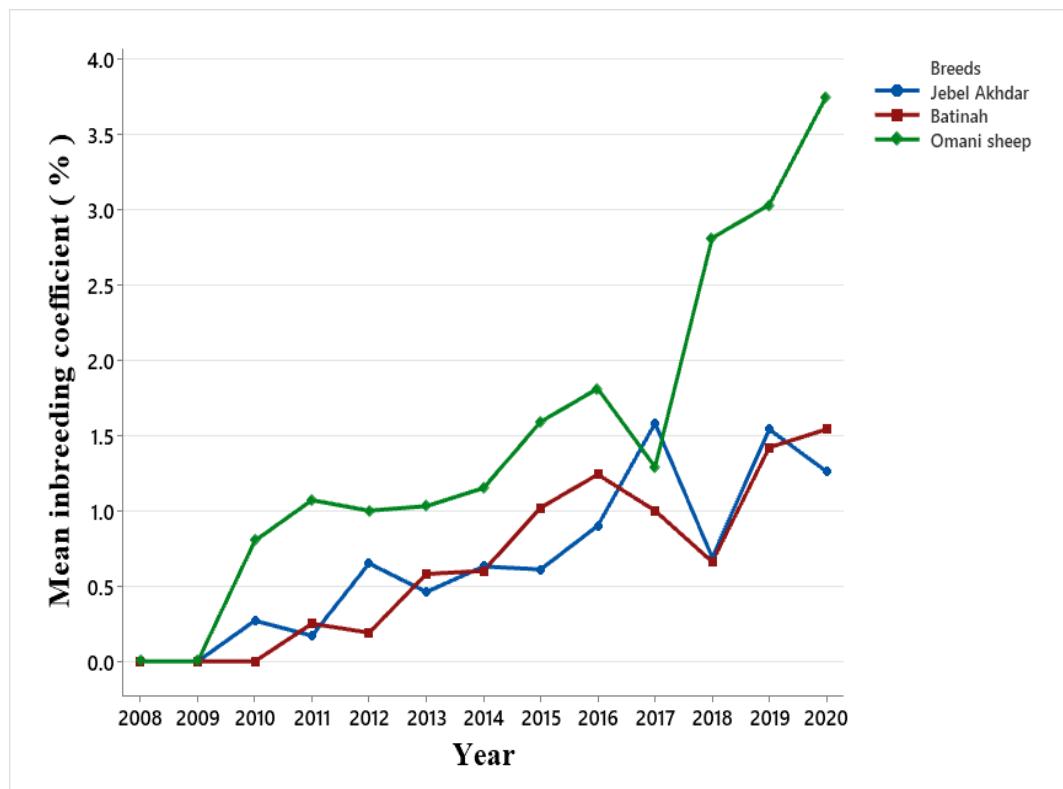


Figure 12. Trend of averaged inbreeding coefficient (%) of the three breeds (2008 - 2020)

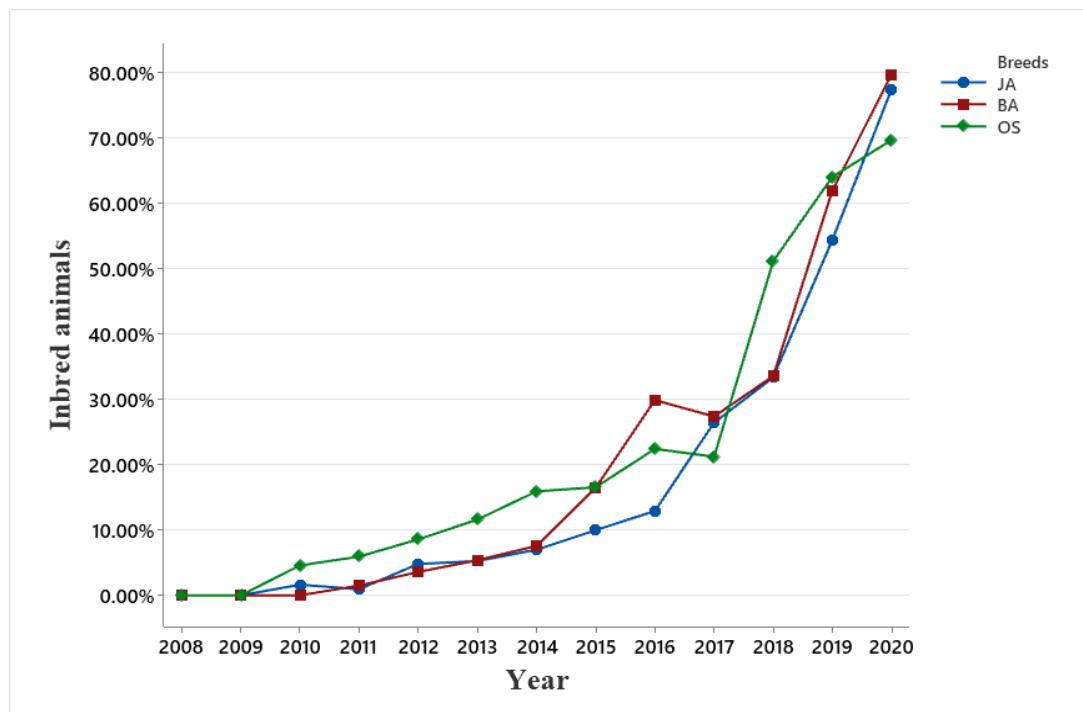


Figure 13. Proportions of inbred animals of the three breeds (2008-2020).

In **Figure 13**, the frequencies (%) of inbred animals for each of the three populations are displayed every year. The proportions exhibited a range of 0% to 77.36%, 0% to 79.62%, and 0% to 69.62% for the JA, BA, and OS, respectively. The trend of inbred individuals across the various breeds had a slightly increasing slope over the initial years. However, in subsequent years, the increase was substantially more significant and progressive, particularly during the final four-year period (2017-2020).

Trends of animal frequencies of the six classes of inbreeding coefficient ($F = 0$, $0 < F < 6.25$, $6.25 \leq F < 12.5$, $12.5 \leq F < 18.75$, $18.75 \leq F < 25$ and $F \geq 25$) of the breeds of JA, BA and OS across the 13 years are illustrated by **Figures 14, 15, and 16**, respectively. The frequency of non-inbred animals ($F = 0$) decreased from being 100% at the base years to become 22.64%, 20.38% and 30.68% for the corresponding JA, BA, and OS breeds. The animals classified in category of $0 < F < 6.25$ were most frequent among the inbred individuals in other categories. Its trend increased dramatically over the last five years for the three breeds reaching its highest frequencies in 2020 at 74.53%, 72.61% and 44.37% for the corresponding breeds of JA, BA, and OS. The remaining categories of moderate to highly inbred individuals were the least frequent across all years, reaching its highest frequency in 2017 (~5%) for JA, in 2019 (~6%) for BA and in 2019 (~14%) for OS.

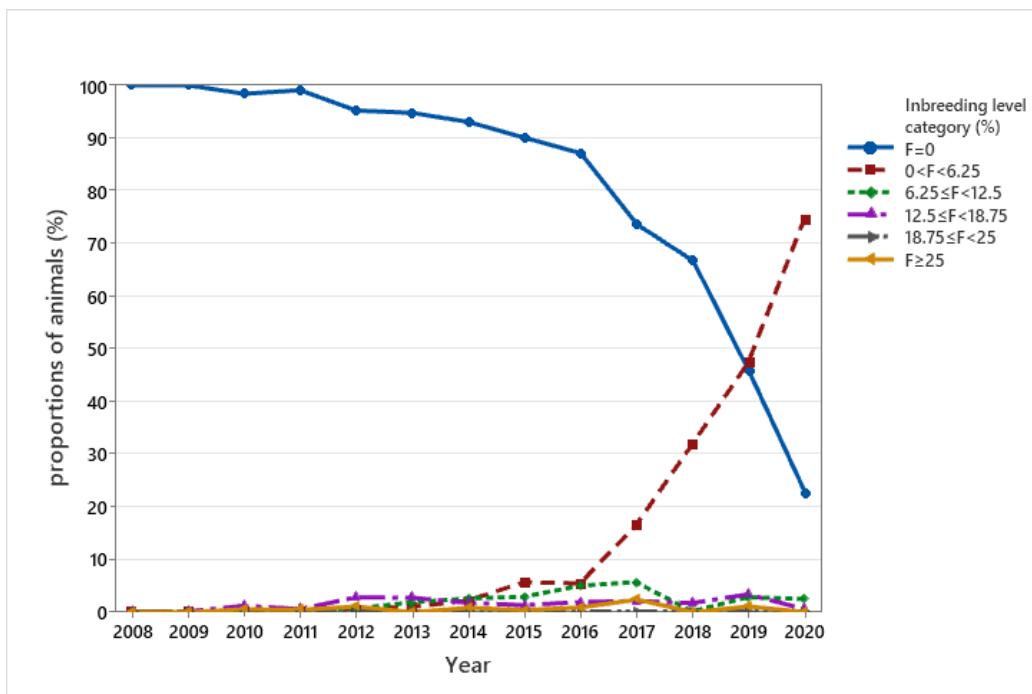


Figure 14. Proportions of animals (%) per category of inbreeding level (F) in Jebel Akhdar Omani goats (2008-2020)

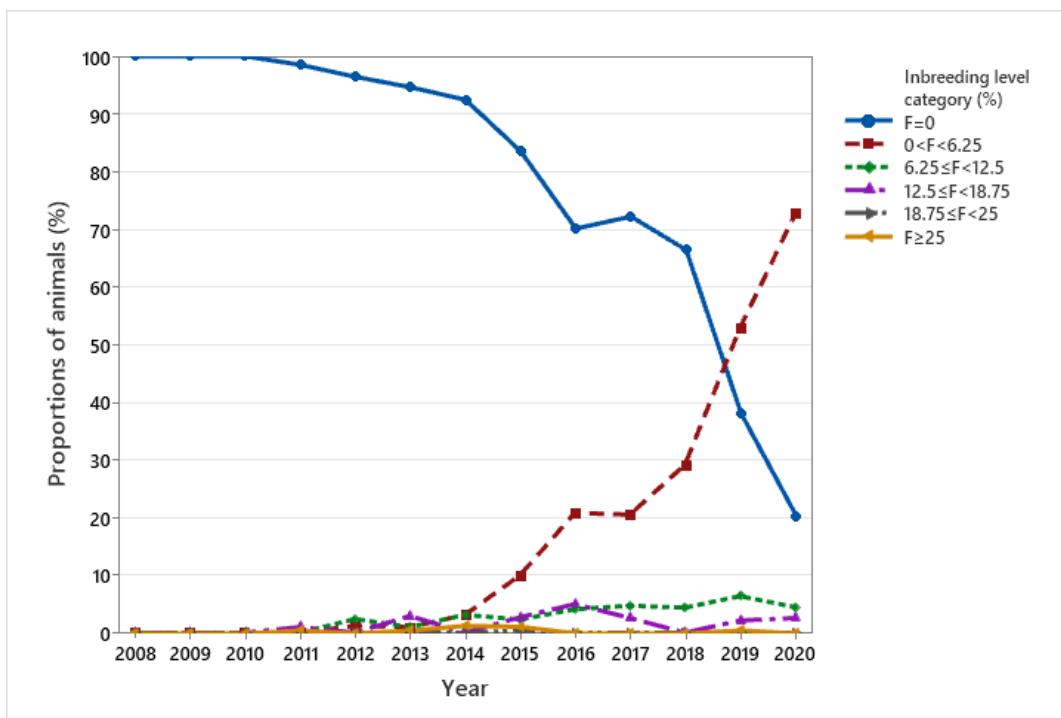


Figure 15. Proportions of animals (%) per category of inbreeding level (F) in Batinah Omani goats (2008-2020)

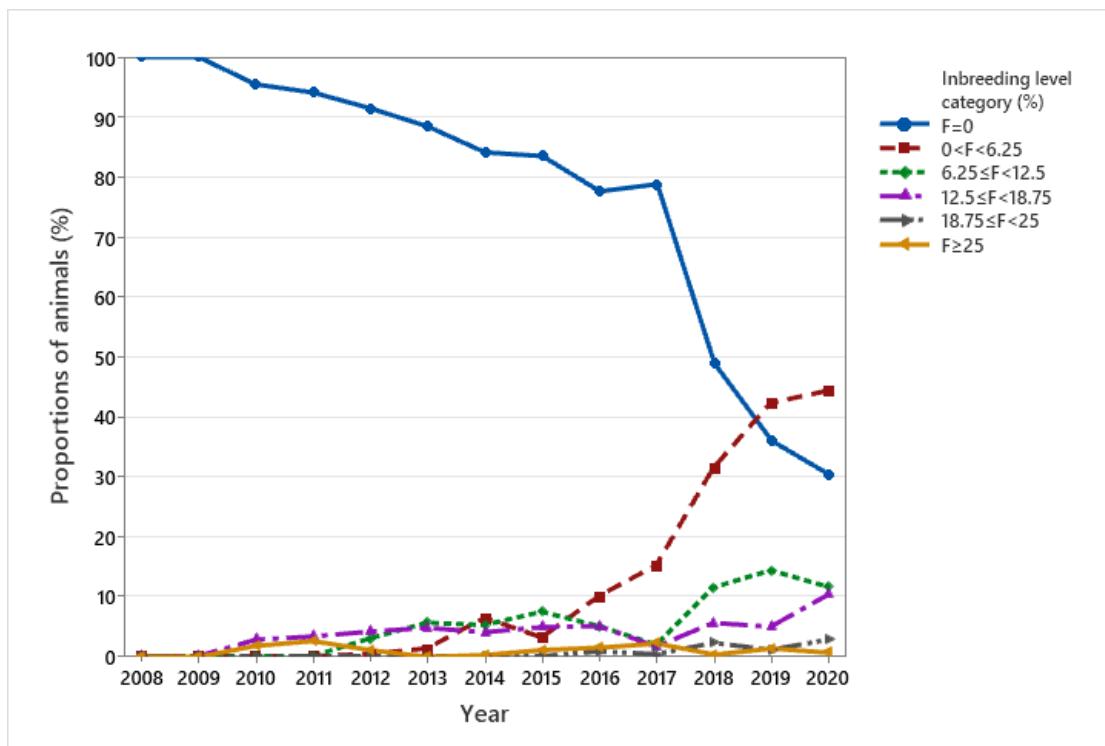


Figure 16. Proportions of animals (%) per category of inbreeding level (F) in Omani sheep (2008-2020).

3.4 Discussion

Inbreeding occurs in any small, closed population, with an increasing rate across subsequent generations. The extent of inbreeding is influenced by the mating strategy and selection methods used (Chaudhari et al., 2023). Monitoring changes in inbreeding levels within a population is an essential step in breeding programmes, as it leads to increased homozygosity and therefore reduced genetic variability (Rafter et al., 2022).

The estimation of the inbreeding coefficient (F) by pedigree analysis can be subject to the influence of pedigree completeness, as highlighted by Mandal et al. (2020). Hence, the depth to which the pedigree of ancestors is complete serves as a measure for the precision in evaluating inbreeding (Jonkus et al., 2023). Pedigree completeness can be assessed by determining the percentage of animals within the entire population that have information on both parents, as well as the equivalent complete generations (EqG_i). This makes sense because any increase in the EqG_i corresponds to a greater probability of finding common ancestors among the paired individuals, and accordingly tracing descended identical alleles as far the common ancestors as possible.

The percentages of animals with known parents which found to be 90.35% in JA, 88.53% in BA, and 89.80% in OS, were consistent with previous studies conducted such as on Markhoz goats (Rashidi et al., 2015), Lori-Bakhtiari sheep (Vatankhah et al., 2019), and Marwari sheep (Vyas et al., 2022). While, they were relatively higher compared to the findings of Mandal et al. (2020) in Muzaffarnagari sheep, Pedrosa et al. (2010) in Santa Ines sheep, and Paiva et al. (2020) in Saanen goats. At first appear, the comparative figures presented with respect to previous studies suggest a good

quality of pedigree. Nevertheless, with respect to the mean EqG_i , it was lower than other studies reviewed in the literature including Rashidi et al. (2015) in Markhoz goats, Mandal et al. (2020) in Muzaffarnagari sheep, Pedrosa et al. (2010) in Santa Ines sheep, and Vatankhah et al. (2019) in Lori-Bakhtiari sheep. They have reported higher EqG_i than our analysis values which were 2.14 in JA, 2.03 in BA, and 2.17 in OS. It is recommended that the value of EqG_i should be at least 3 in order to obtain informative results (Gutiérrez et al., 2009). These lower EqG_i values may have underestimated the F values (Nyman et al., 2022), and ultimately contributed to the low levels of the averaged inbreeding levels of the three populations. In addition, the low rates of inbreeding accumulation might be attributed to little selection and slow genetic gain (Woolliams et al., 2015).

Inbreeding is usually associated with decreased genetic variability within populations, an increase in homozygosity, and the possibility of inbreeding depression (Vyas et al., 2022). The average levels of inbreeding observed in the populations of Omani JA, BA goats, and OS were 0.67%, 0.65%, and 1.52%, respectively. These values are quite low when compared to the findings of Norberg and Sørensen (2007) in three breeds of sheep (6% - 10%) and Mokhtari et al. (2014) in Iran-Black sheep (8.08%). The present results line up with the findings published by Barczak et al. (2009) in a multi-breed sheep population (0.30%), Ajoy et al. (2006) in Muzaffarnagari sheep (3.13%), Paiva et al. (2020) in Saanen goats (1.48%), and Rashidi et al. (2015) in Markhoz goats (2.73%). The average levels of inbreeding reported in this study for the investigated breeds can be considered acceptable and not detrimental, according to Falconer (1996). The author pointed out that inbreeding may become risky if its level

exceeds 10%. Furthermore, the mean inbreeding levels of the inbred animals were below 10%, specifically 3.88% for JA, 3.39% for BA, and 6.49% for OS.

Some strategies that might have helped to keep inbreeding levels low in these populations included maintaining an average good population size, having an appropriate ratio of sires to dams that were 17% in JA and BA goat breeds, and 13% in OS sheep. Besides, avoiding the use of bucks or rams for more than two mating seasons may keep the inbreeding level minimized (Wakchaure & Ganguly, 2015), which might be the most important factor in maintaining and increasing genetic variability within a population, as stated by Vatankhah et al. (2019). Furthermore, during the initial years of the study, specifically (2011-2014), a number of sire individuals (ranging from 2 to 4) were brought into the overall population. This introduction could potentially result in a decline in close relationships within the population. In addition, it should be highlighted that the pedigree completeness may underestimate the estimates of the F values, particularly in the earliest years when there was no pedigree information available for the mates, which results in a 0% mean inbreeding level in those years. This is because as the index of pedigree completeness drops, the probability of finding common ancestors also lowers (Rashidi et al., 2015). Yet when evaluating genetic variability, the annual rate of inbreeding may be considered more effective than the mean inbreeding coefficient (F) itself. This is due to the fact that the calculation of F is relative and can be influenced by the depth and completeness of the pedigree (Falconer, 1996; González-Recio et al., 2007; Paiva et al., 2020).

The three populations showed positive annual rates of inbreeding, with annual rates of 0.12%, 0.13%, and 0.26% for the JA, BA, and OS breeds, respectively. Though

the rates were increasing, they remained below the critical increment. Nicholas et al. (1989) proposed that an annual inbreeding rate of up to 0.5% would be acceptable within the context of animal breeding. The observed trend of gradually increasing levels of inbreeding over time can be explained by the gradual rise in relationships within the population, as mating between related animals gets difficult to avoid over time (Nyman et al., 2022). As generations proceed, the likelihood of identifying common ancestors also increases, which leads to a rise in inbred individuals in the estimation of inbreeding. This could have been another factor in the yearly rise in the level of inbreeding.

It is observed that, despite a rise in the percentage of inbred animals, the mean inbreeding for goat breeds decreased significantly in 2018. This may be because the percentage of inbred animals with high levels of inbreeding has decreased. In JA goats, the proportions of animals with $F \geq 25$ decreased from 2.40% (2017) to 0% (2018), those with $6.25 \leq F < 12.5$ decreased from 5.60% (2017) to 0% (2018), and those with $12.5 \leq F < 18.7$ decreased from 2% (2017) to 1.59% (2018). While in BA goats, the proportions of animals with $6.25 \leq F < 12.5$ decreased from 4.70% (2017) to 4.35% (2018), and those with $12.5 \leq F < 18.7$ decreased from 2.56% (2017) to 0% (2018).

The significant rise in inbreeding observed over the last few years may be attributed to the decrease in population size resulting from the culling of more animals due to financial constraints. In addition, the observed increase in twinning rates over these years may have potentially led to an increase in inbreeding. This occurs because as twinning rates rise, the number of offspring per sire also increases, resulting in a greater likelihood of selecting genetically related animals.

The numbers of inbred animals within the overall populations of the three examined breeds were quite modest, with percentages of 17.34%, 19.31%, and 23.48% for JA goats, BA goats, and OS sheep, respectively. These findings could potentially explain the low mean levels of inbreeding observed across the entire three populations. Besides, it is worth noting that a significant proportion of these inbred animals exhibited low inbreeding levels, which were below 6.25%. The relatively low level of inbreeding may not result in detrimental effects on production performance. However, there has been a significant and rapid increase in the number of inbred animals, particularly in the last four years. More specifically, the proportions of inbred animals for JA, BA, and OS have reached 77.36%, 79.62%, and 69.62% respectively, in few years. This entails paying attention to closely monitoring the inbreeding levels, and implementing practices such as avoiding mating between closely related individuals to limit its increase.

The proportions of inbred animals with a coefficient of inbreeding (F) greater than or equal to 25% were found to be extremely low: 0.60% in JA, 0.34% in BA, and 0.96% in OS. The higher value of F indicates that mating could occur between very closely related individuals, such as a sire mating with its daughter or a son mating with its dam. While the presence of individuals with a range of $18.75 \leq F < 25$ might have been attributed to mating between full or half siblings, such instances were infrequent, which may not be a concern.

Despite the low levels of inbreeding in the three populations, it remains crucial to consistently monitor and control the accumulation of inbreeding within these populations, as there has been a noticeable increase in the degree of inbreeding and the proportion of inbred animals in recent years. Accumulation of inbreeding has

negative consequences for animals' performance, and it can lead to a reduction in genetic variability, which is very important for animal breeding programs (Curik et al., 2014). The introduction of new animals, avoiding interbreeding among closely related mates, and increasing population size are fundamental strategies that can effectively limit the rapid rate of inbreeding (Wakchaure & Ganguly, 2015). It is recommended to maintain the effective population size at levels above 50 so that acceptable levels of genetic variability are maintained, and the trend of inbreeding is limited. When the effective population size drops below 50, the inbreeding curve increases quickly (de Oliveira et al., 2023; Oldenbroek & van der Waaij, 2014).

3.5 Conclusion

The pedigree analysis conducted on three Omani breeds, including Jebel Akhdar (JA) goats, Batinah (BA) goats, and Omani sheep (OS), demonstrated that the amount of inbreeding within these breeds is considerably low, being within acceptable levels. Likewise, the proportions of the inbred animals are at a moderate level. This observation suggests that the mating system implemented for these populations is reasonably well-designed. However, it is possible that the inbreeding levels may have been underestimated due to the small number of equivalent complete generations in the pedigree. Thus, to precisely estimate the amount of inbreeding in the future, genomic data may be used in conjunction with pedigree data. Although the levels of inbreeding in this study are at present low, there has been a notable and significant increase in the rate of inbreeding for all three breeds over time. Additionally, there is an observed rise in the frequency of inbred animals, particularly in the latest years. As a result, it will be important to monitor the level of inbreeding in the forthcoming years as well as take measures to keep it at acceptable levels. In this way, inbreeding depression can be avoided, and genetic variability is maintained for a sustainable genetic improvement programme.

CHAPTER FOUR

ESTIMATION OF GENETIC PARAMETERS OF GROWTH TRAITS IN *JEBEL AKHDAR* AND *BATINAH* GOATS, AND *OMANI SHEEP*

4.1 Abstract

Environmental and genetic factors both contribute to the expression of growth traits. Investigating the impact of these factors is crucial for improving breeding schemes. The objective of this study was to estimate the genetic parameters of growth traits, specifically birth weight (BW), weaning weight (WW), six-month weight (W6), and twelve-month weight (W12), for Jebel Akhdar (JA) and Batinah (BA) goats, as well as Omani (OS) sheep in Oman. The data collected from Wadi Qurayyat Livestock Research Station (WQLRS) between 2008 and 2020 was used for the analysis. Records of 2,826 animals for BW, 2,342 for WW, 1,706 for W6, and 1,265 for W12 were used in JA goats. A total of 2,609 records of animals with BW, 2,186 records with WW, 1,689 records with W6, and 1,208 records with W12 were utilised in the study of BA goats. A total of 3,530 records of animals were used in the OS sheep study for BW, 3,120 animals for WW, 2,374 animals for W6, and 1,745 animals for W12.

Sex, birth type, and year were shown to have a high level of statistical significance ($P < 0.001$) for all growth traits in the three breeds. However, the variable of pen was only found to be significant for BW and WW in goat breeds and only for WW in sheep. The age of the dam (mother), which was included as a covariate, was found to have a significant effect on BW and WW in all breeds, as well as on W6 in Batinah goats. Hence, all significant fixed factors were taken into account in the estimation of genetic parameters for the growth traits. The Restricted Maximum Likelihood (REML) method of fitting the animal model in WOMBAT software was used for estimating the (Co) variance components and corresponding genetic parameters and breeding values. The direct heritability estimates for BW, WW, W6, and W12 in JA goats were 0.13 ± 0.04 , 0.11 ± 0.04 , 0.19 ± 0.05 , and 0.21 ± 0.06 , respectively.

Compared to that, the estimates for BW, WW, W6, and W2 were 0.17 ± 0.04 , 0.16 ± 0.04 , 0.16 ± 0.04 , and 0.24 ± 0.04 , respectively. The results for BW, WW, W6, and W12 in Omani sheep were 0.16 ± 0.03 , 0.15 ± 0.03 , 0.28 ± 0.05 , and 0.48 ± 0.05 , respectively. Significant maternal effects were observed in the traits of BW, WW, and W6 in all three breeds. Furthermore, maternal effects were significant in W12 in JA goats. The genetic correlations among the various traits across the three breeds were significantly positive and strong, with the exception of correlations with the BW trait, which exhibited modest correlations. These findings highlight the potential for significant genetic improvement in the growth traits of Omani breeds, given their adequate additive genetic variability and the positive genetic correlations that exist between them, especially with regard to the post-weaning traits.

The genetic trend was estimated by conducting a regression analysis of the average breeding values against the birth year. Similarly, the phenotypic trend was determined by conducting a regression analysis of the adjusted means against the birth year. The genetic trend revealed a significant and positive pattern for all growth traits in the three breeds, although the phenotypic trend was only significant for the W12 phenotype. In JA goats, the yearly increase in genetic gain for BW, WW, W6, and W12 was 0.01 kg, 0.09 kg, 0.13 kg, and 0.20 kg, respectively. In BA goats, the annual increase in genetic gain for BW, WW, W6, and W12 was 0.01 kg, 0.08 kg, 0.10 kg, and 0.18 kg, respectively. In OS sheep, the annual increase in genetic gain for BW, WW, W6, and W12 was 0.01 kg, 0.13 kg, 0.22 kg, and 0.39 kg, respectively. The positive genetic trend observed indicates that there was an effective implementation of a breeding effort aimed at enhancing the growth traits of these breeds.

4.2 Introduction

Small ruminants, including goats and sheep, are significant to farmers, especially small-scale producers, since they have an affordable production cost, can adapt to scarce resources, have good reproductive efficiency, provide meat and milk, and have a short production cycle for marketing (Pond & Pond, 2000). The population size of goats in Oman is estimated to be 2.4 million, while the population size of sheep is estimated to be 642 thousand. Both of them collectively account for around 81% of the country's overall livestock population (NCSI, 2021).

In Oman, there are several recognised and distinguished breeds of sheep and goats, including Jebel Akhdar and Batinah goats and Omani sheep. These breeds are widely used and significant in terms of their productivity and reproductive capacities in comparison to other breeds. They are primarily raised for meat production (Shaat & Al-Habsi, 2016). The Ministry of Agriculture (MAF) of Oman has developed breeding stations with the objective of improving the performance of indigenous livestock. One of these stations is the Wadi Qurayyat Livestock Research Station (WQLRS). It accommodates the aforementioned breeds of goats and sheep.

Genetic improvement can increase the productivity of animals by estimating the genetic parameters of specific populations' underlying traits and subsequently selecting genetically superior animals for breeding (Oyieng et al., 2022). It is of the utmost importance for animal breeders to assess the genetic variability of the desired trait and how it correlates to other traits in order to carry out an effective selective genetic improvement (Singh et al., 2022). One important parameter that must be accurately estimated is the trait's heritability, which indicates the extent of available genetic variability and explains the relative influence of additive genetic effects on a

trait (Getabalew et al., 2019). Another significant parameter is genetic correlation, which estimates the genetic correlation between traits and, as a result, shows the strength and direction of the correlation between them (Rae, 1952).

The growth potential of an animal is indicative of its ability to produce meat (Bangar et al., 2020). Growth traits are influenced by environmental and genetic effects, so their estimation is important for animal improvement (Zhang et al., 2009). In addition to the direct additive genetic influences of the individual, the dam (mother) may also have an impact on the phenotype of its progeny, particularly with early growth traits (Mrode, 2014). Therefore, examining the significance of these effects in the statistical models used to estimate the genetic parameters is important in order to minimise a possible bias.

The primary objective of the current study was to estimate the heritability of growth traits: birth weight (BW), weaning weight (WW), weight at 6 months (W6), and weight at 12 months (W12), and the genetic and phenotypic correlations among these traits in Omani Jebel Akhdar (JA) goats, Omani Batinah (BA) goats, and Omani sheep (OS). Additionally, the study aimed to evaluate the three breeds' genetic and phenotypic trends for the investigated traits between 2008 and 2020.

4.3 Results

4.3.1 Significance of fixed effects

The importance of environmental fixed effects affecting various growth traits for the breeds of Omani Jebel Akhdar goat (JA), Omani Batinah goat (BA), and Omani sheep (OS) is diagrammatically illustrated in **Figures 17, 18, and 19**, respectively. While the importance of these factors in details along with least square means are presented in **Tables 12, 13, and 14** attached in **appendix (D)**. The growth traits at all age stages for the three breeds were significantly influenced by variables of sex, year, and type of birth, with a high level of significance ($P < 0.001$). The variable pen only influenced early growth traits; in JA and BA goats, BW and WW were influenced, but in OS sheep, it was only WW. The age of the dam had a significant impact ($P < 0.01$) on the variability in BW and WW in JA goat and in BW, WW, and W6 in BA goat. While in the OS sheep, it was only significant for the trait of BW. It did not have a significant impact on post-weaning traits ($P > 0.05$) for all breeds except for W6 in BA goats ($P < 0.01$).

Male animals exhibited heavier weight than females at all stages across all three breeds. The difference between the means of the two sexes increased as animals grew. The birth year (2008-2020) displayed a changing growth pattern at different ages, except for W12. Single-born animals exhibited more body weight than twin-born animals across all three breeds. The lowest difference between the two groups was reported in terms of BW, but the most significant difference was observed at WW. The greatest effect of dam's age was observed on WW in JA (0.19) and BA (0.18) goats, but it was 0.07, 0.06, and 0.04 on BW for the corresponding breeds of OS, BA, and JA.

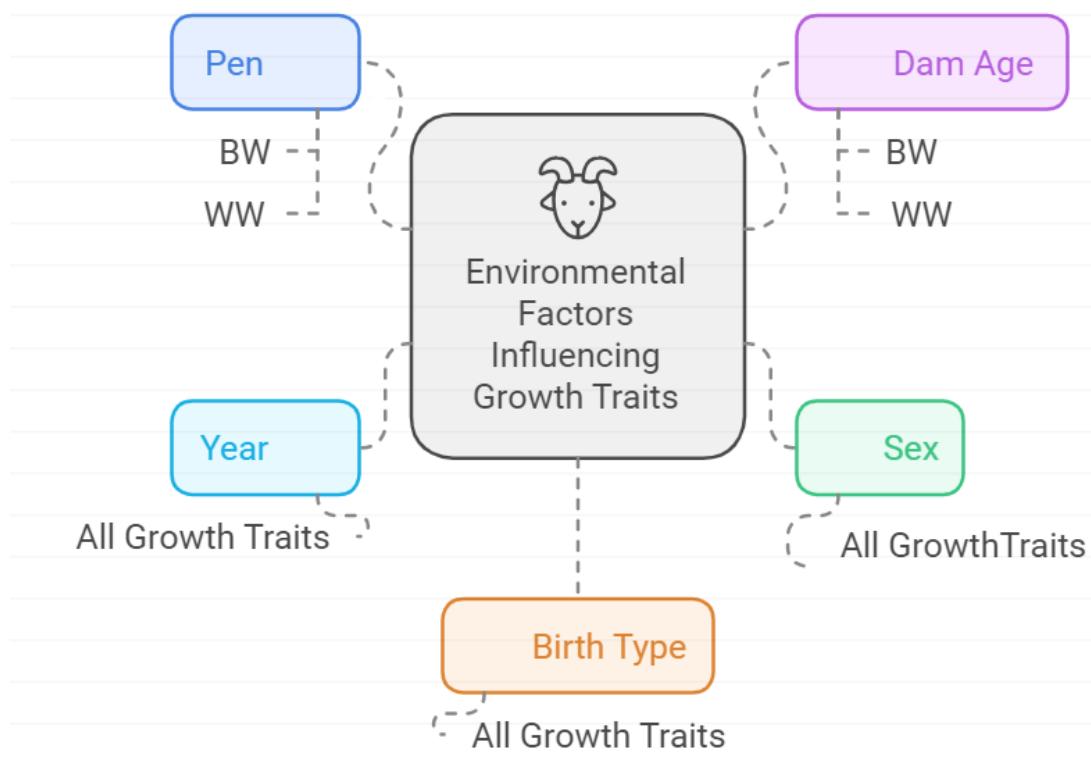


Figure 17. Influencing of non-genetic factors on growth traits of Omani Jebel Akhdar goats.

The diagram presents the significant impact of fixed effects (Pen, Year, Sex, Birth type, and Dam age) on growth variability in Omani Jebel Akhdar goats at BW, WW, W6, and W12. The effect was considered significant at $P < 0.05$.

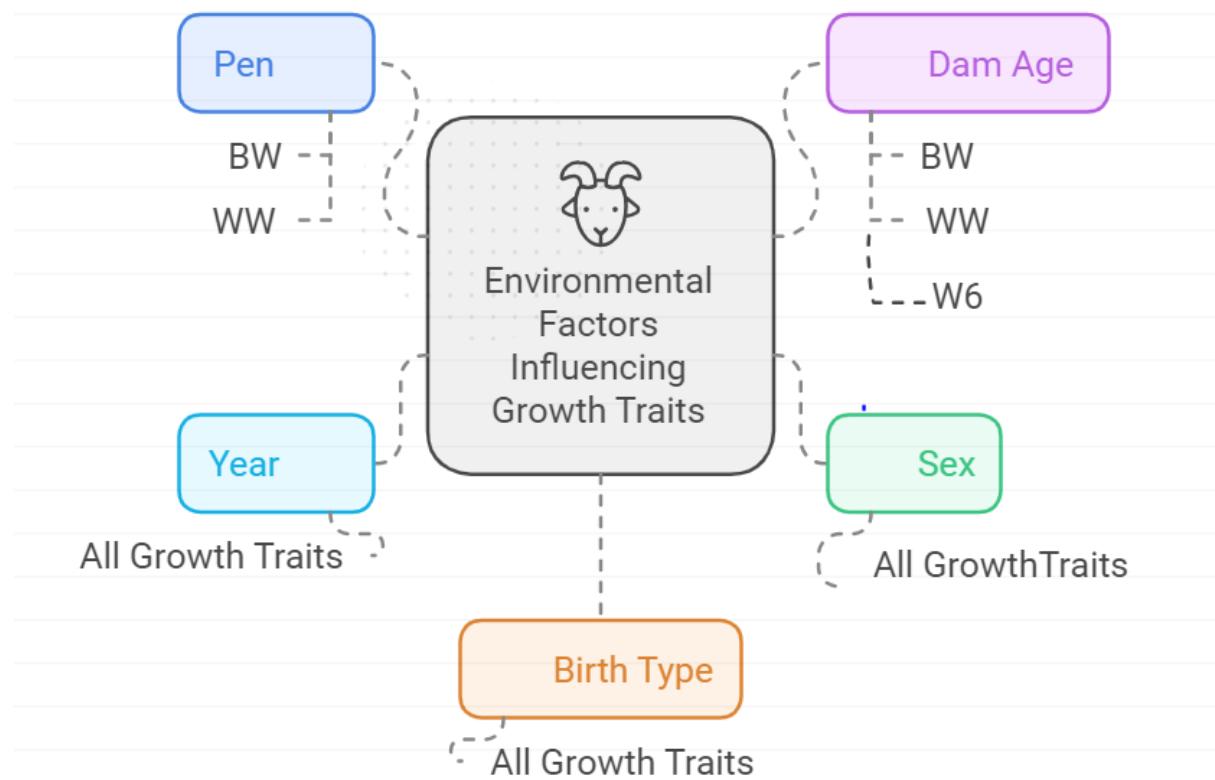


Figure 18. Influencing of non-genetic factors on growth traits of Omani Batinah goats.

The diagram presents the significant impact of fixed effects (Pen, Year, Sex, Birth type, and Dam age) on growth variability in Omani Batinah goats at BW, WW, W6, and W12. The effect was considered significant at $P < 0.05$.

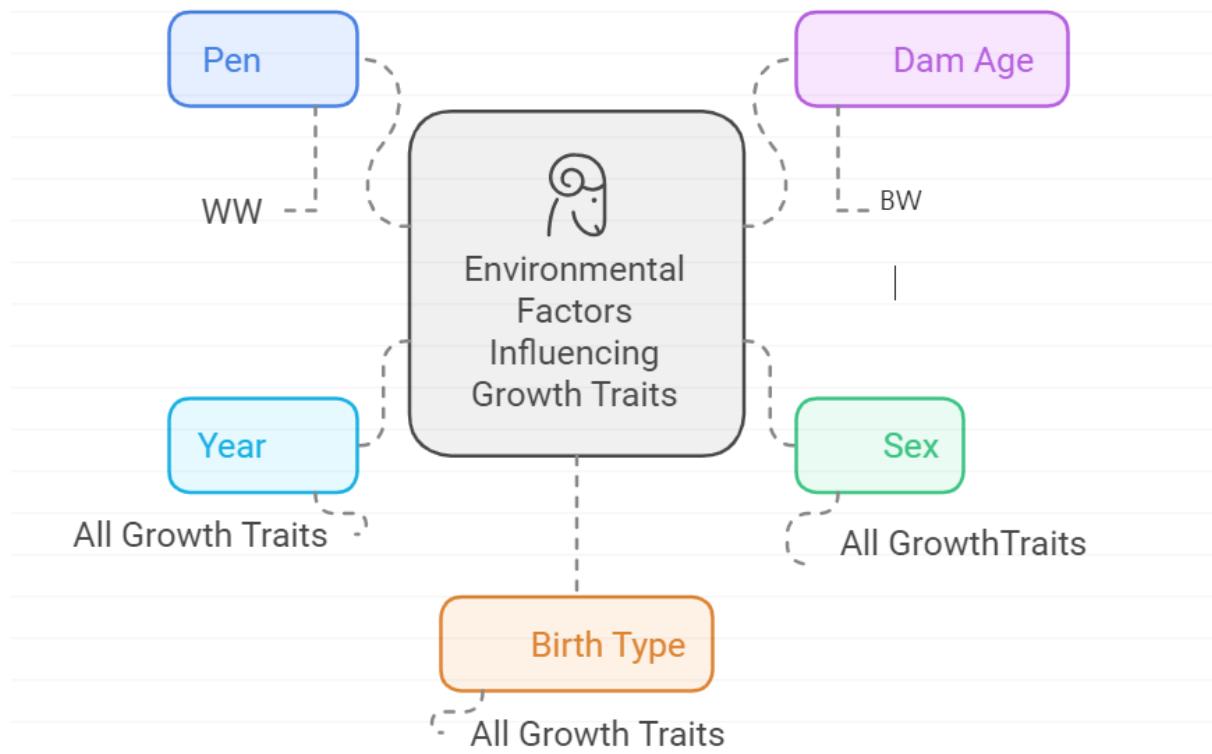


Figure 19. Influencing of non-genetic factors on growth traits of Omani sheep.

The diagram presents the significant impact of fixed effects (Pen, Year, Sex, Birth type, and Dam age) on growth variability in Omani Batinah goats at BW, WW, W6, and W12. The effect was considered significant at $P < 0.05$.

4.3.2 Estimates of (Co)variance components

4.3.2.1 *Models' comparison*

Six various animal mixed models (including or excluding maternal influences) were utilised to fit the data for the traits of BW, WW, W6, and W12 in JA and BA goats, as well as OS sheep. The output of these models with the values of *LRT* and *AIC* is shown in tables **12**, **13**, and **14**, with the most suitable model highlighted in bold.

Model (1), which solely accounted for direct additive genetic effects, adequately explained the variation of the W12 trait in BA goats and OS sheep. The remaining models did not increase the likelihood significantly. However, in JA goats, model (2) was found to be the most appropriate for this trait, as confirmed by the likelihood ratio test and lowest AIC value. Model (2) accounted for both direct and maternal additive genetic effects. It was also suitable for evaluating BW in both goats' breeds. This model significantly enhanced the likelihood of predicting BW weight in both goats' breeds. Nevertheless, the addition of maternal permanent environmental influences together with maternal genetic effects, as in model (5) did not result in significant gains compared to model (2).

Model (4), which considered both direct additive genetic effects and maternal permanent environmental influences, was the most appropriate for assessing the traits of WW and W6 in all studied breeds, as well as the trait of BW in OS sheep. It yielded better results for the WW and W6 traits across all three breeds. This finding was supported by both the increase in log likelihoods and the lowest AIC values.

Table 12. Log Likelihood (Log L) and Akaike information criterion (AIC) of the six animal models for the growth traits in Omani Jebel Akhdar goats.

BW (birth weight), **WW** (weaning weight), **W6** (Six-months weight), **W12** (Yearling weight); the best-fit model is in bold.

(No) Models	BW		WW		W6		W12	
	<u>Log L</u>	<u>AIC</u>	<u>Log L</u>	<u>AIC</u>	<u>Log L</u>	<u>AIC</u>	<u>Log L</u>	<u>AIC</u>
(1) $y = Xb + \beta a + e$	580.404	-1,156.81	-3,476.647	6,957.294	-2,542.829	5,085.658	-2,287.773	4,579.546
(2) $y = Xb + \beta a + Zm + e,$ $Cov(a, m) = 0$	615.355	-1,224.71	-3,464.407	6,934.814	-2,538.572	5,083.144	-2,285.418	4,576.836
(3) $y = Xb + \beta a + Zm + e,$ $Cov(a, m) = A\sigma_{a,m}$	616.887	-1,225.77	-3,463.003	6,934.006	-2,538.572	5,085.144	-2,285.340	4,578.680
(4) $y = Xb + \beta a + Wc + e$	608.342	-1,210.68	-3,461.692	6,929.384	-2,537.187	5,080.374	-2,286.370	4,579.500
(5) $y = Xb + \beta a + Zm + Wc + e,$ $Cov(a, m) = 0$	616.896	-1,225.79	-3,460.914	6,929.828	-2,536.957	5,081.914	-2,285.400	4,578.800
(6) $y = Xb + \beta a + Zm + Wc + e,$ $Cov(a, m) = A\sigma_{a,m}$	618.247	-1,226.49	-3,459.810	6,929.620	-2,536.956	5,083.912	-2,285.321	4,580.642

Table 13. Log Likelihood (Log L) and Akaike information criterion (AIC) of the six animal models for the growth traits in Omani Batinah goats.

BW (birth weight), **WW** (weaning weight), **W6** (Six-months weight), **W12** (Yearling weight); the best-fit model is in bold.

(No)	Models	BW		WW		W6		W12	
		Log L	AIC	Log L	AIC	Log L	AIC	Log L	AIC
(1)	$y = Xb + \beta a + e$	572.307	-1,140.61	-3,300.792	6,605.584	-2,471.265	4,946.530	-2,137.370	4,278.74
(2)	$y = Xb + \beta a + Zm + e,$ $Cov(a, m) = 0$	591.850	-1,177.70	-3,282.573	6,571.146	-2,461.733	4,929.466	-2,137.312	4,280.624
(3)	$y = Xb + \beta a + Zm + e,$ $Cov(a, m) = A\sigma_{a,m}$	592.507	-1,177.01	-3,281.400	6,570.800	-2,461.495	4,930.990	-2,137.295	4,282.590
(4)	$y = Xb + \beta a + Wc + e$	587.562	-1,169.12	-3,272.303	6,550.606	-2,461.609	4,929.218	-2,137.219	4,280.438
(5)	$y = Xb + \beta a + Zm + Wc + e,$ $Cov(a, m) = 0$	592.374	-1,176.75	-3272.303	6,552.606	-2,460.682	4,929.364	-2,137.219	4,282.438
(6)	$y = Xb + \beta a + Zm + Wc + e,$ $Cov(a, m) = A\sigma_{a,m}$	592.963	-1,175.93	-3,271.458	6,552.916	-2,460.259	4,930.518	-2,137.212	4,284.424

Table 14. Log Likelihood (Log L) and Akaike Information Criterion (AIC) of the six animal models for the growth traits in Omani sheep.

BW (birth weight), **WW** (weaning weight), **W6** (Six-months weight), **W12** (Yearling weight); the best-fit model is in bold.

(No)	Models	BW		WW		W6		W12	
		Log L	AIC	Log L	AIC	Log L	AIC	Log L	AIC
(1)	$y = Xb + \beta a + e$	331.124	-658.248	-5,179.624	10,363.25	-4,105.778	8,215.556	-3,476.77	6,957.55
(2)	$y = Xb + \beta a + Zm + e,$ $Cov(a, m) = 0$	383.031	-760.062	-5,140.160	10,286.32	-4,099.191	8,204.382	-3,476.61	6,959.22
(3)	$y = Xb + \beta a + Zm + e,$ $Cov(a, m) = A\sigma_{a,m}$	384.676	-761.352	-5,139.955	10,287.91	-4,098.805	8,205.61	-3,475.14	6,958.27
(4)	$y = Xb + \beta a + Wc + e$	393.583	-781.166	-5,132.203	10,270.41	-4,099.095	8,204.19	-3,474.91	6,955.82
(5)	$y = Xb + \beta a + Zm + Wc + e,$ $Cov(a, m) = 0$	394.759	-781.518	-5,130.302	10,268.6	-4,097.999	8,203.998	-3,474.88	6,957.75
(6)	$y = Xb + \beta a + Zm + Wc + e,$ $Cov(a, m) = A\sigma_{a,m}$	395.867	-781.734	-5,130.285	10,270.57	-4,097.597	8,205.194	-3,474.21	6,958.43

4.3.2.2 Heritability estimates

Tables **15**, **16**, and **17** present the heritability estimates obtained by the six animal models for the studied growth traits in Jebel Akhdar (JA) and Batinah (BA) goats and Omani sheep (OS), respectively. The summary of results and discussion will focus on the results from the best appropriate model (highlighted in bold). Model 1, which just accounted for direct additive genetic effects, gave the highest estimates of direct heritability for all studied traits across the three breeds. The estimates for BW, WW, W6, and W12 were as follows: for JA goats, the estimates were 0.29 ± 0.04 , 0.19 ± 0.04 , 0.24 ± 0.05 , and 0.29 ± 0.06 ; for BA goats, the estimates were 0.29 ± 0.04 , 0.26 ± 0.04 , 0.23 ± 0.05 , and 0.24 ± 0.04 ; and for OS sheep, the estimates were 0.26 ± 0.03 , 0.28 ± 0.04 , 0.35 ± 0.04 , and 0.48 ± 0.05 . Incorporating maternal effects, either genetic, environmental, or both, as in the remaining models resulted in a substantial reduction in the estimates of direct heritability.

The best appropriate model revealed that pre-weaning traits (BW and WW) had lower estimates of direct heritability than post-weaning traits (W6 and W12). In JA goats, the estimates were 0.13 ± 0.04 for BW and 0.11 ± 0.04 for WW. In BA goats, they were relatively higher, with 0.17 ± 0.04 for BW and 0.16 ± 0.04 for WW. In OS sheep, the estimates were 0.16 ± 0.03 for BW and 0.15 ± 0.03 for WW. On the other hand, post-weaning traits showed higher heritability estimates, except for the trait of W6 in BA goats (constant with pre weaning traits). The direct heritability estimates for W6 and W12 were 0.19 ± 0.05 and 0.21 ± 0.06 in JA goats, 0.16 ± 0.04 and 0.24 ± 0.04 in BA goats, and 0.28 ± 0.05 and 0.48 ± 0.05 in OS sheep.

With regards to maternal effects, the expression of body weight at BW in goats was substantially influenced by maternal genetic effects (17% in JA and 13% in BA),

whereas in OS sheep, it was primarily influenced by maternal permanent environmental influences (19%), with no significant contribution from maternal genetic effects ($P > 0.05$). Maternal permanent environmental influences exerted an impact on the traits of both WW and W6 across all breeds (10% and 8% in JA, 16% and 11% in BA, and 19% and 8% in OS). The yearling weight (W12) was primarily controlled by only the direct additive genetic effects, with the exception in JA goats, where maternal genetic influences made some significant contribution ($P < 0.05$) to approximately 6% of the total phenotypic variance.

Table 15. Heritability estimates \pm SE of growth traits in Omani Jebel Akhdar goats estimated from all six animal models, with best model in bold.

σ_a^2 , σ_m^2 , σ_c^2 , σ_p^2 , σ_e^2 , and σ_{am} are animal additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance, phenotypic variance, error variance, and covariance of animal and maternal additive genetic effects, respectively; h^2_d (direct heritability), h^2_m (maternal heritability), pe^2 (Proportion of phenotypic variance explained by maternal permanent environmental effects), r_{am} (genetic correlation between animal and maternal additive genetic effects).

Trait	σ_a^2	σ_m^2	σ_{am}	σ_c^2	σ_e^2	σ_p^2	$h^2_d \pm SE$	$h^2_m \pm SE$	$pe^2 \pm SE$	$e^2 \pm SE$	r_{am}
BW											
1	0.07	-	-	-	0.17	0.24	0.29 \pm 0.04	-	-	0.71 \pm 0.04	-
2	0.03	0.04	-	-	0.17	0.24	0.13 \pm 0.04	0.17 \pm 0.02	-	0.71 \pm 0.04	-
3	0.04	0.05	-0.02	-	0.17	0.26	0.15 \pm 0.05	0.19 \pm 0.04	-	0.65 \pm 0.04	-0.35 \pm 0.16
4	0.04	-	-	0.03	0.17	0.24	0.17 \pm 0.04	-	0.13 \pm 0.02	0.71 \pm 0.04	-
5	0.03	0.03	-	0.01	0.17	0.24	0.13 \pm 0.04	0.13 \pm 0.03	0.04 \pm 0.03	0.71 \pm 0.03	-
6	0.04	0.04	-0.01	0.01	0.17	0.26	0.15 \pm 0.05	0.15 \pm 0.05	0.04 \pm 0.03	0.65 \pm 0.04	-0.36 \pm 0.18
WW											
1	1.35	-	-	-	5.86	7.21	0.19 \pm 0.04	-	-	0.81 \pm 0.04	-
2	0.67	0.71	-	-	5.82	7.2	0.09 \pm 0.04	0.10 \pm 0.02	-	0.81 \pm 0.04	-
3	0.93	1.06	-0.45	-	5.64	7.63	0.12 \pm 0.05	0.14 \pm 0.04	-	0.74 \pm 0.04	-0.46 \pm 0.20
4	0.81	-	-	0.74	5.6	7.15	0.11 \pm 0.04	-	0.10 \pm 0.02	0.78 \pm 0.04	-
5	0.71	0.23	-	0.55	5.65	7.14	0.10 \pm 0.04	0.03 \pm 0.03	0.08 \pm 0.03	0.79 \pm 0.04	-
6	0.97	0.5	-0.36	0.54	5.49	7.5	0.13 \pm 0.05	0.07 \pm 0.04	0.07 \pm 0.03	0.73 \pm 0.04	-0.51 \pm 0.23
W6											
1	1.82	-	-	-	5.67	7.49	0.24 \pm 0.05	-	-	0.76 \pm 0.05	-
2	1.14	0.55	-	-	5.74	7.43	0.15 \pm 0.05	0.07 \pm 0.03	-	0.77 \pm 0.05	-
3	1.13	0.55	0.01	-	5.74	7.42	0.15 \pm 0.06	0.07 \pm 0.04	-	0.77 \pm 0.05	0.01 \pm 0.039
4	1.43	-	-	0.62	5.41	7.46	0.19 \pm 0.05	-	0.08 \pm 0.03	0.73 \pm 0.05	-
5	1.30	0.17	-	0.48	5.50	7.45	0.17 \pm 0.05	0.02 \pm 0.04	0.06 \pm 0.04	0.74 \pm 0.05	-
6	1.28	0.16	0.02	0.48	5.51	7.43	0.17 \pm 0.06	0.02 \pm 0.04	0.06 \pm 0.04	0.74 \pm 0.05	0.03 \pm 0.66

W12

1	4.23	-	-	-	10.18	14.41	0.29 ± 0.06	-	-	0.71 ± 0.06	-
2	2.95	0.91	-	-	10.38	14.24	0.21 ± 0.06	0.06 ± 0.03	-	0.73 ± 0.06	-
3	2.64	0.76	0.28	-	10.56	13.96	0.19 ± 0.07	0.05 ± 0.04	-	0.76 ± 0.06	0.20 ± 0.52
4	3.71	-	-	0.69	9.94	14.34	0.26 ± 0.06	-	0.05 ± 0.03	0.69 ± 0.06	-
5	2.98	0.83	-	0.11	10.33	14.25	0.21 ± 0.06	0.06 ± 0.05	0.01 ± 0.04	0.72 ± 0.06	-
6	2.67	0.67	0.28	0.11	10.51	13.96	0.19 ± 0.08	0.05 ± 0.05	0.01 ± 0.04	0.75 ± 0.06	0.21 ± 0.56

Table 16. Heritability estimates ± SE of growth traits in Omani Batinah goats estimated from all six animal models, with best model in bold.

σ_a^2 , σ_m^2 , σ_c^2 , σ_p^2 , σ_e^2 , and σ_{am} are animal additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance, phenotypic variance, error variance, and covariance of animal and maternal additive genetic effects, respectively; h^2_d (direct heritability), h^2_m (maternal heritability), pe^2 (Proportion of phenotypic variance explained by maternal permanent environmental effects), r_{am} (genetic correlation between animal and maternal additive genetic effects).

Trait	σ_a^2	σ_m^2	σ_{am}	σ_c^2	σ_e^2	σ_p^2	$h^2_d \pm SE$	$h^2_m \pm SE$	$pe^2 \pm SE$	$e^2 \pm SE$	r_{am}
BW											
1	0.07	-	-	-	0.17	0.24	0.29 ± 0.04	-	-	0.71 ± 0.04	-
2	0.04	0.03	-	-	0.17	0.24	0.17 ± 0.04	0.13 ± 0.02	-	0.71 ± 0.04	-
3	0.05	0.04	-0.01	-	0.17	0.26	0.19 ± 0.05	0.15 ± 0.04	-	0.65 ± 0.04	-0.23 ± 0.18
4	0.05	-	-	0.02	0.17	0.24	0.21 ± 0.04	-	0.08 ± 0.02	0.71 ± 0.04	-
5	0.03	0.03	-	0.01	0.18	0.25	0.12 ± 0.04	0.12 ± 0.03	0.04 ± 0.03	0.72 ± 0.03	-
6	0.04	0.04	-0.01	0.01	0.17	0.26	0.15 ± 0.05	0.15 ± 0.05	0.04 ± 0.03	0.65 ± 0.04	-0.36 ± 0.18
WW											
1	2.01	-	-	-	5.82	7.83	0.26 ± 0.04	-	-	0.74 ± 0.04	-
2	1.17	1.16	-	-	5.58	7.91	0.15 ± 0.04	0.15 ± 0.03	-	0.71 ± 0.04	-
3	1.46	1.6	-0.55	-	5.39	8.45	0.17 ± 0.05	0.19 ± 0.05	-	0.64 ± 0.04	-0.36 ± 0.18

4	1.21	-	-	1.26	5.31	7.78	0.16 ± 0.04	-	0.16 ± 0.03	0.68 ± 0.04	-
5	1.21	0.01	-	1.25	5.31	7.78	0.16 ± 0.04	0.00 ± 0.03	0.16 ± 0.04	0.68 ± 0.04	-
6	1.45	0.24	-0.36	1.29	5.17	8.15	0.18 ± 0.05	0.03 ± 0.05	0.16 ± 0.04	0.63 ± 0.04	-0.61 ± 0.37
W6											
1	1.58	-	-	-	5.41	6.99	0.23 ± 0.05	-	-	0.77 ± 0.05	-
2	0.94	0.82	-	-	5.24	7	0.13 ± 0.04	0.12 ± 0.03	-	0.75 ± 0.04	-
3	0.84	0.66	0.2	-	5.31	6.81	0.12 ± 0.05	0.10 ± 0.04	-	0.78 ± 0.04	0.27 ± 0.42
4	1.10	-	-	0.79	5.08	6.97	0.16 ± 0.04	-	0.11 ± 0.03	0.73 ± 0.04	-
5	0.99	0.42	-	0.44	5.13	6.98	0.14 ± 0.05	0.06 ± 0.04	0.06 ± 0.04	0.73 ± 0.04	-
6	0.84	0.18	0.25	0.48	5.22	6.72	0.13 ± 0.05	0.03 ± 0.05	0.07 ± 0.04	0.78 ± 0.04	0.64 ± 0.40
W12											
1	3.16	-	-	-	9.92	13.08	0.24 ± 0.04	-	-	0.76 ± 0.05	-
2	3.04	0.13	-	-	9.9	13.07	0.23 ± 0.06	0.01 ± 0.03	-	0.76 ± 0.05	-
3	2.92	0.05	0.12	0	9.98	12.95	0.23 ± 0.08	0.00 ± 0.04	0	0.77 ± 0.06	0.33 ± 0.40
4	3.06	-	-	0.2	9.81	13.07	0.23 ± 0.06	-	0.02 ± 0.03	0.75 ± 0.06	-
5	3.06	0	-	0.2	9.81	13.07	0.23 ± 0.06	0.00 ± 0.04	0.02 ± 0.04	0.75 ± 0.06	-
6	2.98	0	0.06	0.18	9.85	13.01	0.23 ± 0.08	0.00 ± 0.06	0.01 ± 0.04	0.76 ± 0.06	0.72 ± 0.52

Table 17. Heritability estimates ± SE of growth traits in Omani sheep estimated from all six animal models, with best model in bold.

σ_a^2 , σ_m^2 , σ_c^2 , σ_p^2 , σ_{am}^2 , and σ_{am} are animal additive genetic variance, maternal additive genetic variance, maternal permanent environmental variance, phenotypic variance, error variance, and covariance of animal and maternal additive genetic effects, respectively; h^2_d (direct heritability), h^2_m (maternal heritability), pe^2 (Proportion of phenotypic variance explained by maternal permanent environmental effects), r_{am} (genetic correlation between animal and maternal additive genetic effects).

σ_a^2	σ_m^2	σ_{am}	σ_c^2	σ_e^2	σ_p^2	$h^2_d \pm SE$	$h^2_m \pm SE$	$pe^2 \pm SE$	$e^2 \pm SE$	r_{am}
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BW

1	0.08	-	-	-	0.23	0.31	0.26 ± 0.03	-	-	0.74 ± 0.03	-
2	0.04	0.07	-	-	0.22	0.33	0.12 ± 0.03	0.21 ± 0.02	-	0.67 ± 0.03	-
3	0.05	0.08	-0.02	-	0.21	0.34	0.15 ± 0.04	0.24 ± 0.04	-	0.62 ± 0.03	-0.30 ± 0.14
4	0.05	-	-	0.06	0.21	0.32	0.16 ± 0.03	-	0.19 ± 0.02	0.66 ± 0.03	-
5	0.04	0.01	-	0.05	0.21	0.31	0.13 ± 0.03	0.03 ± 0.03	0.16 ± 0.03	0.68 ± 0.03	-
6	0.05	0.02	-0.01	0.05	0.2	0.32	0.16 ± 0.04	0.06 ± 0.04	0.16 ± 0.03	0.63 ± 0.03	-0.39 ± 0.21

WW

1	3.00	-	-	-	7.73	10.73	0.28 ± 0.04	-	-	0.72 ± 0.04	-
2	1.35	2.13	-	-	7.41	10.89	0.12 ± 0.03	0.20 ± 0.03	-	0.68 ± 0.03	-
3	1.46	2.31	-0.24	-	7.35	11.12	0.13 ± 0.04	0.21 ± 0.04	-	0.66 ± 0.03	-0.13 ± 0.19
4	1.56	-	-	2.00	7.06	10.62	0.15 ± 0.03	-	0.19 ± 0.02	0.66 ± 0.03	-
5	1.42	0.62	-	1.48	7.13	10.65	0.13 ± 0.03	0.06 ± 0.03	0.14 ± 0.03	0.67 ± 0.03	-
6	1.45	0.66	-0.06	1.48	7.11	10.70	0.14 ± 0.04	0.06 ± 0.04	0.14 ± 0.03	0.66 ± 0.03	-0.06 ± 0.30

W6

1	4.39	-	-	-	8.27	12.66	0.35 ± 0.04	-	-	0.65 ± 0.04	-
2	2.97	1.06	-	-	8.46	12.49	0.24 ± 0.05	0.08 ± 0.03	-	0.68 ± 0.04	-
3	2.68	0.83	0.40	-	8.61	12.12	0.22 ± 0.05	0.07 ± 0.03	-	0.71 ± 0.04	0.27 ± 0.32
4	3.44	-	-	0.98	8.07	12.49	0.28 ± 0.05	-	0.08 ± 0.02	0.65 ± 0.04	-
5	3.05	0.57	-	0.58	8.26	12.46	0.24 ± 0.05	0.05 ± 0.03	0.05 ± 0.03	0.66 ± 0.04	-
6	2.73	0.37	0.38	0.57	8.42	12.09	0.23 ± 0.05	0.03 ± 0.04	0.05 ± 0.03	0.70 ± 0.04	0.38 ± 0.53

W12

1	10.80	-	-	-	11.81	22.61	0.48 ± 0.05	-	-	0.52 ± 0.04	-
2	10.76	0.27	-	-	11.74	22.76	0.47 ± 0.05	0.01 ± 0.02	-	0.52 ± 0.07	-
3	12.36	1.18	-1.95	-	10.80	22.39	0.55 ± 0.07	0.05 ± 0.03	-	0.48 ± 0.05	-0.51 ± 0.17
4	10.08	-	-	1.01	11.40	22.49	0.45 ± 0.05	-	0.05 ± 0.02	0.51 ± 0.05	-
5	10.05	0.13	-	0.99	11.38	22.55	0.45 ± 0.05	0.02 ± 0.02	0.04 ± 0.02	0.50 ± 0.05	-
6	11.48	0.86	-1.43	0.75	10.71	22.37	0.51 ± 0.08	0.04 ± 0.03	0.03 ± 0.03	0.48 ± 0.06	-0.46 ± 0.22

4.3.2.3 Genotypic and phenotypic correlations among growth traits

The direct genetic correlations among the four growth traits across the three breeds typically exhibited positive direction and moderate to strong correlations, as illustrated in **Table 18**. The post-weaning trait (W6) demonstrated the highest paired genetic correlations, with values exceeding 0.90 with W12 and at least 0.85 with WW across all breeds.

The coefficients between BW and other traits were 0.77 ± 0.11 (BW-WW), 0.55 ± 0.13 (BW-W6), and 0.54 ± 0.13 (BW-W12) in JA goats, 0.62 ± 0.12 (BW-WW), 0.47 ± 0.14 (BW-W6), and 0.53 ± 0.13 (BW-W12) in BA goats, and 0.56 ± 0.11 (BW-WW), 0.52 ± 0.10 (BW-W6), and 0.47 ± 0.10 (BW-W12) in OS sheep. While it was 0.85 ± 0.06 (WW-W6), 0.80 ± 0.06 (WW-W12), and 0.98 ± 0.03 (W6-W12) in JA goats, 0.91 ± 0.05 (WW-W6), 0.85 ± 0.08 (WW-W12), and 0.98 ± 0.05 (W6-W12) in BA goats, and 0.89 ± 0.03 (WW-W6), 0.76 ± 0.06 (WW-W12), and 0.92 ± 0.02 (W6-W12) in OS sheep.

The phenotypic correlations between traits were predominantly positive and relatively strong, with at least a 0.45 coefficient, except for the correlations with BW, which exhibited smaller magnitudes ranging from 0.15 to 0.25. The remaining correlations ranged from 0.45 to 0.74. The phenotypic correlation between W6 and W12 had the greatest magnitude (≥ 0.70) across all breeds. The coefficients for the several comparisons in JA goats were as follows: 0.24 ± 0.02 (BW-WW), 0.20 ± 0.02 (BW-W6), 0.15 ± 0.03 (BW-W12), 0.66 ± 0.01 (WW-W6), 0.45 ± 0.02 (WW-W12), and 0.71 ± 0.02 (W6-W12). The coefficients in BA goats were as follows: 0.25 ± 0.02 (BW-WW), 0.20 ± 0.20 (BW-W6), 0.19 ± 0.03 (BW-W12), 0.67 ± 0.01 (WW-W6), 0.50 ± 0.02 (WW-W12), and 0.70 ± 0.02 (W6-W12). The coefficients for OS sheep were as follows:

0.21 ± 0.02 (BW-WW), 0.20 ± 0.02 (BW-W6), 0.21 ± 0.02 (BW-W12), 0.70 ± 0.01 (WW-W6), 0.54 ± 0.02 (WW-W12), and 0.74 ± 0.01 (W6-W12).

Table 18. Genetic correlations \pm SE in (bold), and phenotypic correlations \pm SE in (parenthesis) of growth traits in Jebel Akhdar and Batinah goats and Omani sheep.

Trait	BW	WW	W6	W12
Jebel Akhdar goats				
BW		0.77 ± 0.11	0.55 ± 0.13	0.54 ± 0.13 (0.08 ± 0.80)
WW	(0.24 ± 0.02)			0.85 ± 0.06 0.80 ± 0.06
W6	(0.20 ± 0.02)	(0.66 ± 0.01)		0.98 ± 0.03
W12	(0.15 ± 0.03)	(0.45 ± 0.02)	(0.71 ± 0.02)	
Batinah goats				
BW		0.62 ± 0.12	0.47 ± 0.14	0.53 ± 0.13
WW	(0.25 ± 0.02)		0.91 ± 0.05	0.85 ± 0.08
W6	(0.20 ± 0.02)	(0.67 ± 0.01)		0.98 ± 0.05
W12	(0.19 ± 0.03)	(0.50 ± 0.02)	(0.70 ± 0.02)	
Omani sheep				
BW		0.56 ± 0.11	0.52 ± 0.10	0.47 ± 0.10
WW	(0.21 ± 0.02)		0.89 ± 0.03	0.76 ± 0.06
W6	(0.20 ± 0.02)	(0.70 ± 0.01)		0.92 ± 0.02
W12	(0.21 ± 0.02)	(0.54 ± 0.02)	(0.74 ± 0.01)	

4.3.3 Genetic and phenotypic trends of the growth traits

Starting from 2010 to 2020, there was a fluctuating rise in genetic change across the traits of WW, W6, and W12 in the three different breeds of JA goats, BA goats, and OS sheep (Figures **20**, **21**, and **22**, respectively). However, the trait of BW showed almost a constant trend in all three breeds. Table **19** showed that the average estimated breeding values for the traits of BW, WW, W6, and W12 increased annually by 0.01 kg, 0.09 kg, 0.13 kg, and 0.20 kg in JA goats, respectively. In BA goats, the values increased by 0.01 kg, 0.08 kg, 0.10 kg, and 0.18 kg, respectively. In OS sheep, the values increased by 0.01 kg, 0.13 kg, 0.22 kg, and 0.39 kg, respectively.

Although genetic changes occurred across the investigated years in all traits of the three breeds, there were no significant changes in the traits' phenotypes, except for the trait of W12, which displayed an annual phenotypic change of 0.93 kg, 0.69 kg, and 0.66 kg in JA, BA, and OS, respectively (Table **20**). All other traits displayed oscillating patterns of growth and decline throughout the 13-year period (Figures **23**, **24**, and **25**).

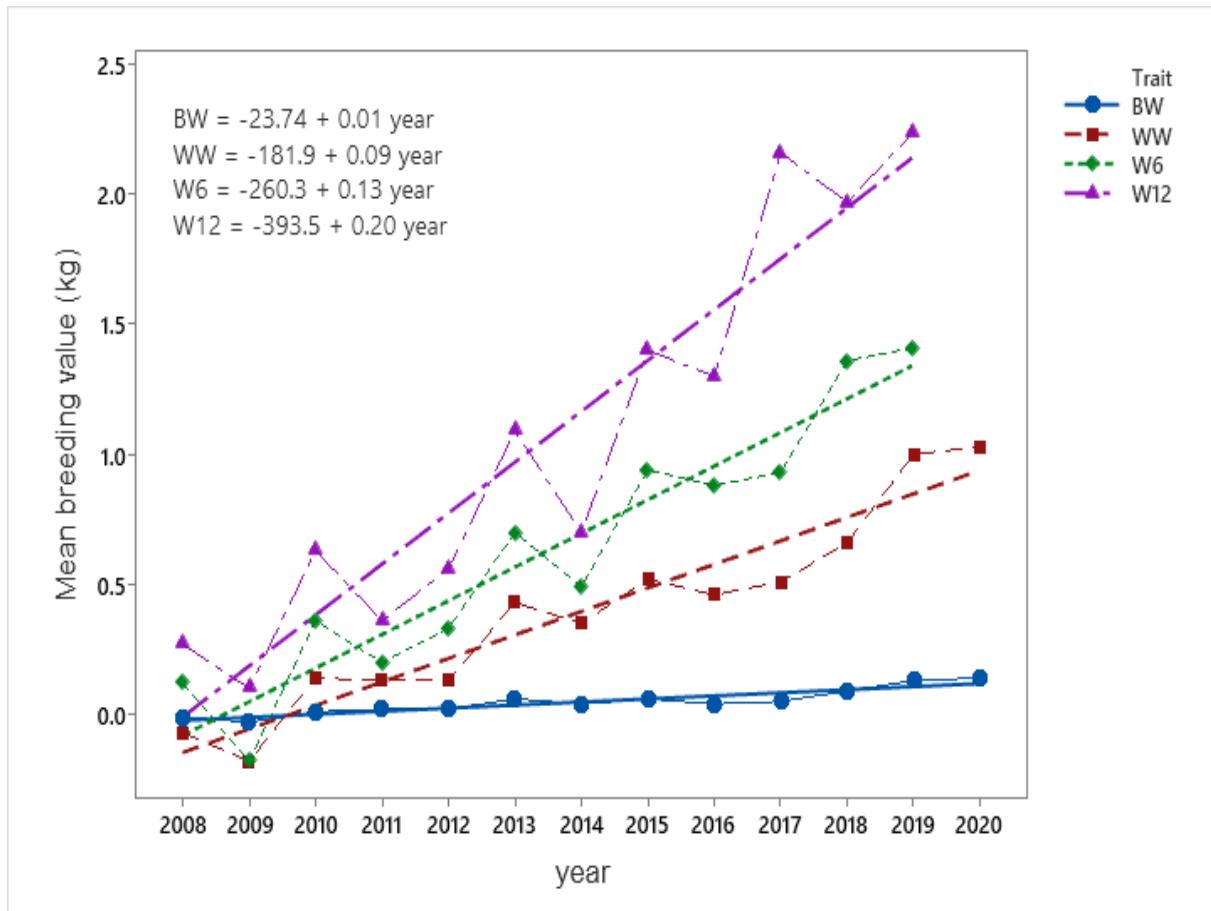


Figure 20. Genetic trend (2008-2020) of various growth traits in Omani JA goats.

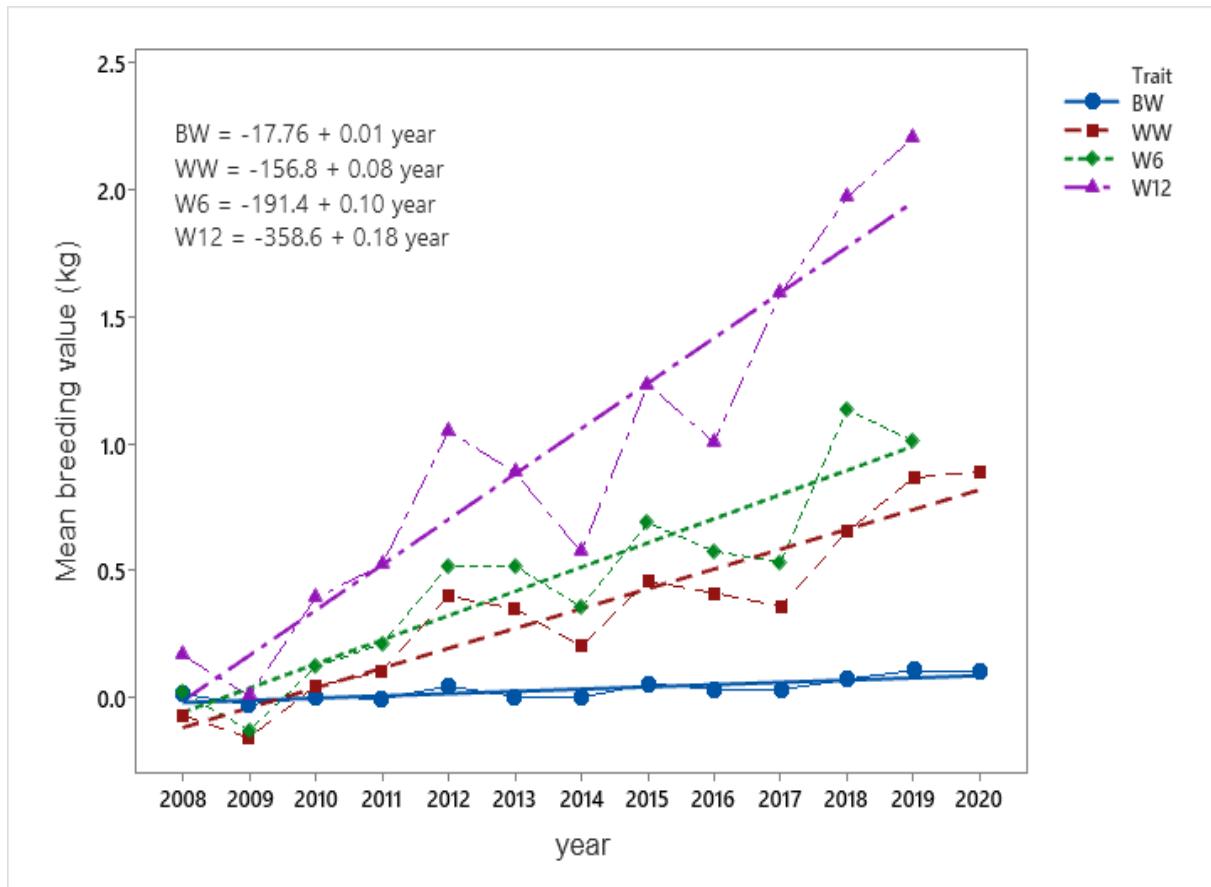


Figure 21. Genetic trend (2008-2020) of various growth traits in Omani BA goats.

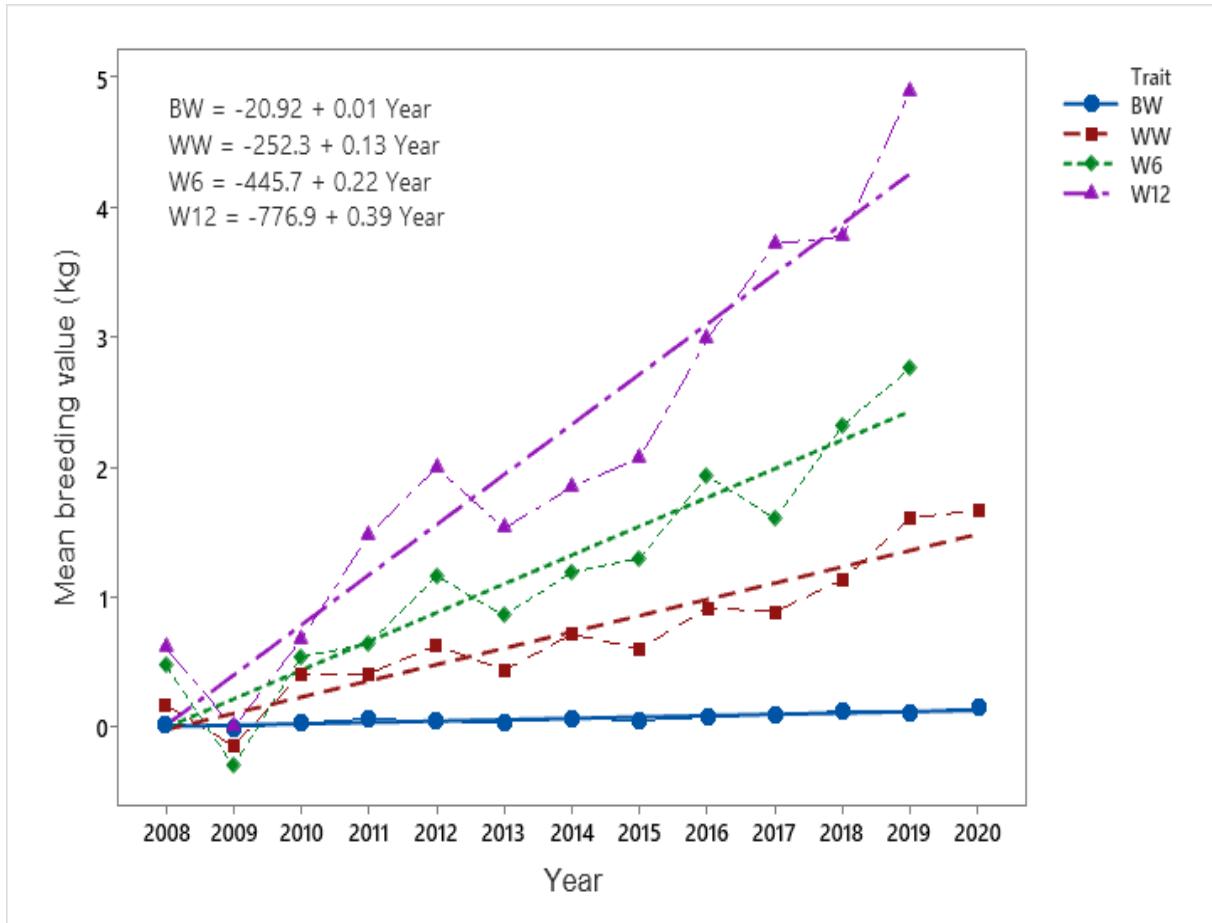


Figure 22. Genetic trend (2008-2020) of various growth traits in Omani OS sheep.

Table 19. Genetic trend of the growth traits in JA and BA goats and OS sheep.

	Regression coefficient	P-Value	R ²
JA goats			
BW	0.01	0.0000	85.14%
WW	0.09	0.0000	91.55%
W6	0.13	0.0000	89.65%
W12	0.20	0.0000	88.49%
BA goats			
BW	0.01	0.0004	69.43%
WW	0.08	0.0000	86.90%
W6	0.10	0.0000	83.42%
W12	0.18	0.0000	86.88%
OS sheep			
BW	0.01	0.0000	86.63%
WW	0.13	0.0000	87.54%
W6	0.22	0.0000	87.33%
W12	0.39	0.0000	90.96%

Table 20. Phenotypic trend of the growth traits in JA and BA goats and OS sheep.

	Regression coefficient	P-Value	R ²
JA goats			
BW	-0.01	0.62	2.36%
WW	-0.01	0.88	0.22%
W6	0.07	0.73	1.29%
W12	0.93	0.007	54.38%
BA goats			
BW	-0.00	0.89	0.19%
WW	0.11	0.22	13.52%
W6	0.03	0.86	0.31%
W12	0.69	0.04	35.81%
OS sheep			
BW	-0.02	0.31	9.46%
WW	-0.02	0.76	0.88%
W6	0.14	0.42	6.54%
W12	0.66	0.01	54.38%

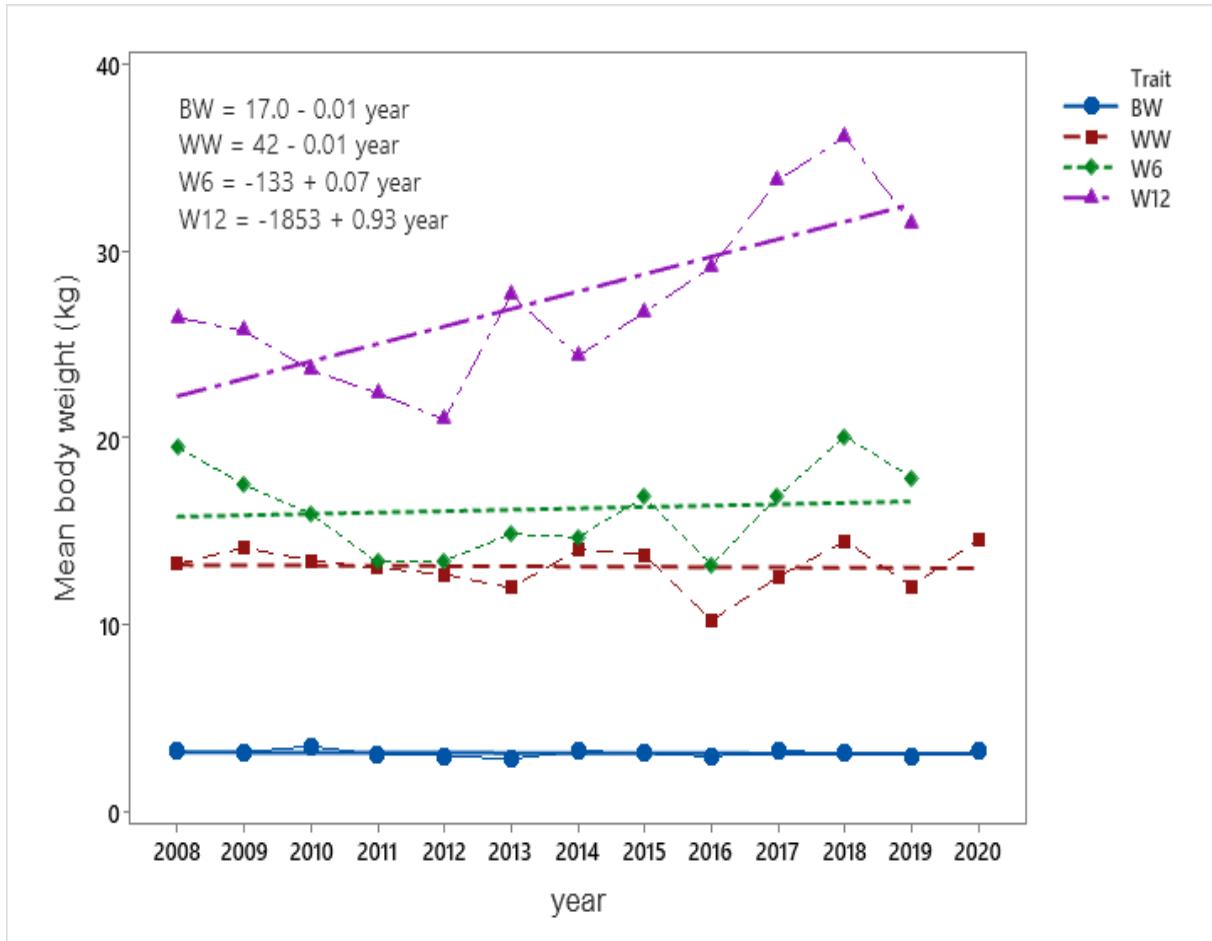


Figure 23. Phenotypic trend (2008-2020) of various growth traits in Omani JA goats.

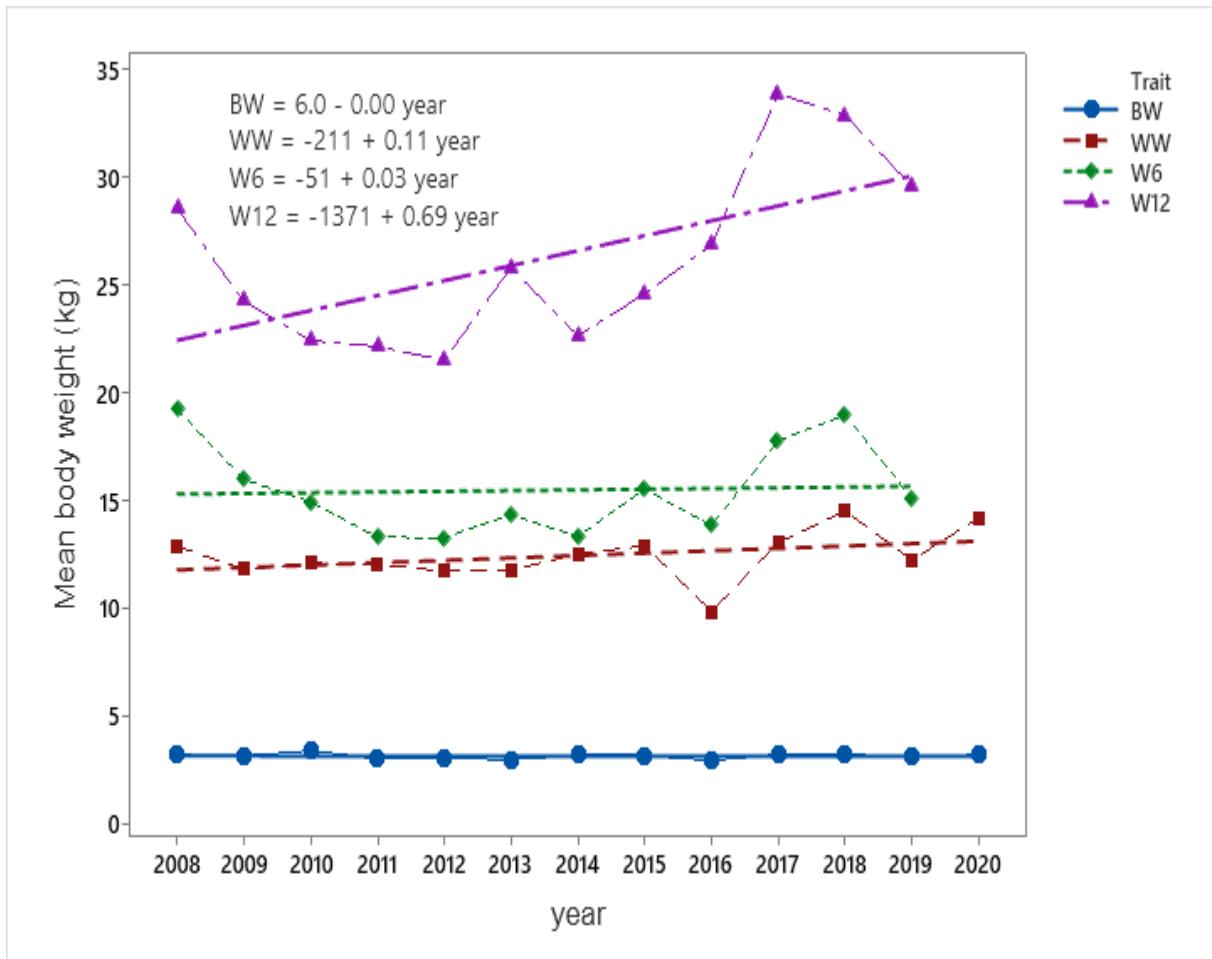


Figure 24. Phenotypic trend (2008-2020) of various growth traits in Omani BA goats.

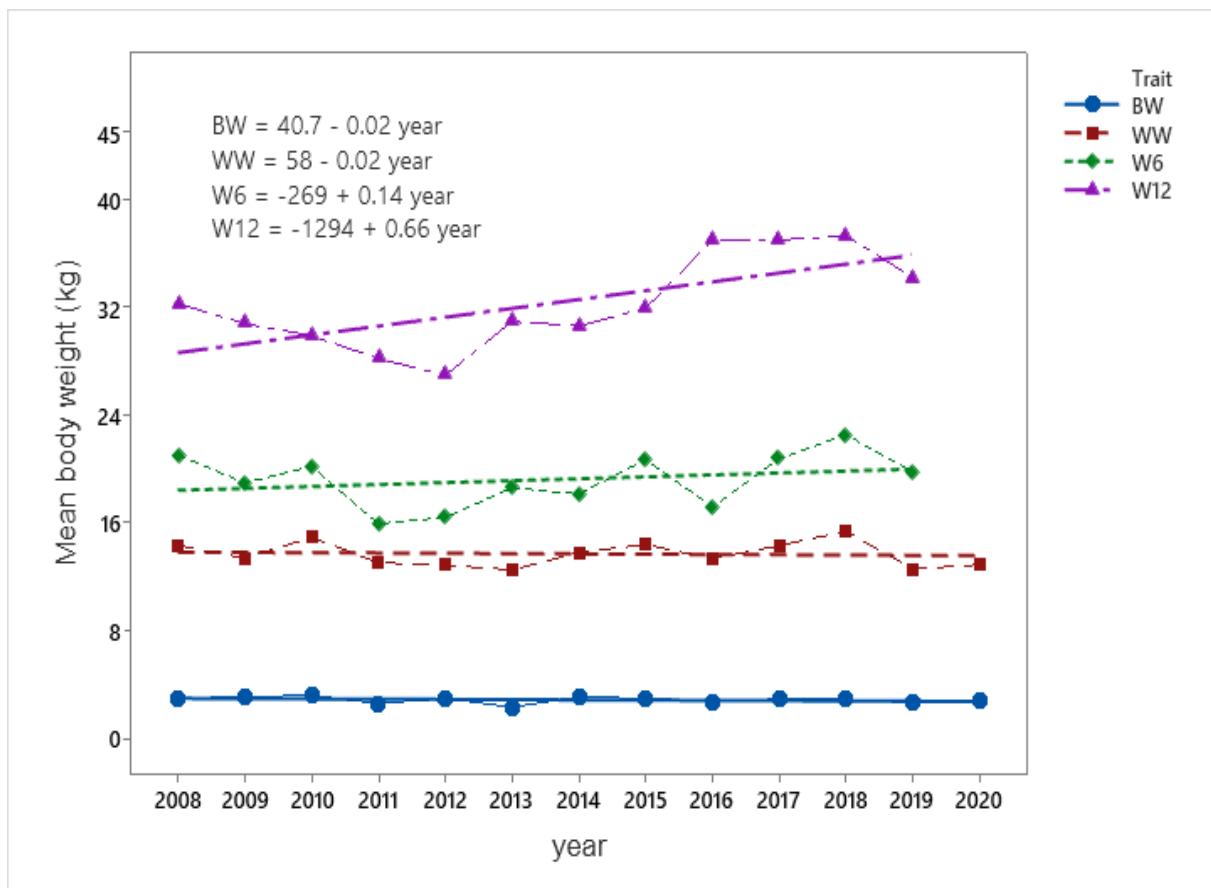


Figure 25. Phenotypic trend (2008-2020) of various growth traits in Omani OS sheep.

4.4 Discussion

4.4.1 Importance of environmental fixed factors on growth traits

Investigating the environmental fixed factors is important in livestock production systems as they can impact the estimation of genetic parameters. The impact of these factors varies depending on the specific traits and breeds being examined. Hence, it is essential to look at the significance of these factors and correct the data for these factors to avoid any bias in the estimation of variances (Chauhan et al., 2021; Singh et al., 2022).

The sex of the animal, type of birth, and year of birth had a highly significant impact ($P < 0.001$) on the variation observed in each stage of growth in the three breeds: Jebel Akhdar (JA) and Batinah (BA) goats, and Omani (OS) sheep. These findings are supported by other studies conducted by several researchers including Al-Shorepy et al. (2002), Baneh et al. (2012), Bedhane et al. (2013), Mahala et al. (2019), Oyieng et al. (2022), Tesema et al. (2022), and Zhang et al. (2009).

Males' animals exhibited heavier weight in comparison to females across the four growth traits in the three breeds. The weight difference between the two sexes continuously increased with age, attaining 0.36 kg, 1.44 kg, 1.68 kg, and 4.31 kg for BW, WW, W6, and W12, respectively, in JA goats, and 0.71 kg, 1.86 kg, 1.66 kg, and 4.6 kg for BW, WW, W6, and W12, respectively, in BA goats. The weight differences for BW, WW, W6, and W12 in OS sheep were 0.44 kg, 1.86 kg, 1.66 kg, and 4.6 kg, respectively. The observed increases suggest that males may exhibit greater efficacy than females in their response to environmental improvements (Al-Shorepy et al., 2002; Zhang et al., 2009). Hormonal and genetic differences between males and

females may be the cause of the variations caused by sex (Bedhane et al., 2013). Androgens, which are sex hormones, have a greater influence on muscle development in males compared to females, whereas estrogen limits skeletal growth in females. Furthermore, it has been reported that dams carrying a male fetus have a greater number of cotyledons and possess placentas with higher weight compared to those carrying a female fetus, perhaps influencing this variability (Tesema et al., 2022).

Type of birth was another important source of variation associated with all studied traits across the three breeds. The primary factor contributing to this difference may be the competition among multiple-born animals for uterine space and milk consumption until weaning (Baneh et al., 2012). Consequently, the amount of nutrition provided during the prenatal stage is lower for twins compared to single births, and the amount of milk consumed by twins is also reduced. The difference typically decreases following the weaning stage, thus indicating the animals' decreased dependence on milk during this period, and the growth potential for twins begins catching up (Bedhane et al., 2013; Zhang et al., 2009).

The significance of the year can be attributed to climate change, food availability, and the spread of potential diseases (Mahala et al., 2019; Tesema et al., 2022). The apparently upward trend observed in weight at W12 compared to other traits over the last four years suggests that this particular trait may possess a higher level of heritability and that animals respond more effectively to selective breeding.

Dam's age has been included as a covariate or as a fixed effect with many levels in linear mixed models according to the literature. It has been considered as a fixed effect in studies like Baneh et al. (2012), Bahreini Behzadi et al. (2007) and Al-Shorepy

et al. (2002). However, other research, including those of Hızlı et al. (2022) and Erdoğan Ataç et al. (2023), included the age of the dam as a covariate. In the current study, it has been fitted as a covariate because the age of dam is a continuous variable with so many levels and that it has a linear relationship with body weights.

4.4.2 Importance of maternal effects on growth traits

The dam can affect the performance of its offspring by passing on its direct additive genetic effects during fertilization and by providing a suitable environment, including nourishment and maternal care. The ability of a dam to create an appropriate environment is determined by both genetic factors, referred to as maternal genetic effects, and environmental factors, referred to as maternal environmental influences. Maternal effects exert a more significant influence on early growth characteristics, such as birth weight (BW) and weaning weight (WW), in comparison to other later traits. (Mrode, 2014). Their impact is expected to diminish from birth to yearling age; as the animal develops, its need for its dam reduces (Bahreini Behzadi et al., 2007). However, they may also have an impact later on traits such as W6 and W12, as noticed by Bahreini Behzadi et al. (2007) in Kermani sheep, Areb et al. (2021) in Bonga sheep, and Singh et al. (2022) in Barbari goats. Due to carryover from the before-weaning stage, certain traits may still exhibit maternal influences in adulthood (Bangar et al., 2020).

The present study found that when maternal effects were excluded, the direct heritability of all traits in the three breeds was overestimated. This conclusion is consistent with the results reported by Meyer (1992). Meyer observed that the

estimation of additive genetic variance is higher when maternal effects are excluded. This study revealed that maternal effects had a noteworthy influence on the traits of BW, WW, and W6 in all breeds. Unexpectedly, maternal influences had a significant effect on the weight of JA goats at 12 months. This was unexpected, as animals at this stage should not depend on their dams for any sort of support. Hence, it is important to consider maternal effects when estimating the genetic parameters of these traits to avoid inflated parameters and ensure that the genetic potential of animals is not masked by maternal effects. This matters because it could have an impact on the selection of superior animals (Oyieng et al., 2022).

The inclusion of maternal genetic effects, as implemented in model 2, was appropriate for analysing the BW trait among goats' breeds as well as the W12 trait in JA goats. This is in agreement with the results reported by Tesema et al. (2020) and Singh et al. (2022). Nevertheless, numerous studies have demonstrated that maternal permanent environmental effects, either alone or together with maternal genetic effects, play a substantial influence on the determination of these traits, surpassing the impact of maternal genetic effects alone (Bangar et al., 2020; Singh et al., 2022; Zhang et al., 2009). The study found that maternal genetic effects were as important as direct additive genetic effects in determining body weight at birth in both breeds of goats. In particular, this factor explained 17% of the total variation in observable traits in the JA breed and 13% in the BA breed. In W12, it made up 6% of the variation in JA goat phenotypes.

Across the three breeds, Model 4 presented the most appropriate representation of WW and W6 traits, plus BW in OS sheep. This model takes into account the influence of maternal permanent environmental effects. A number of

investigations have arrived at the same conclusion (Baneh et al., 2012; I et al., 2017; Tesema et al., 2022). These maternal influences may be reflected by the environment and capacity of the uterus, as well as by the mothering ability and milk production, all of which influence the phenotypic differences in these specific traits. For the breeds of OS sheep, JA goats, and BA goats, they provide an explanation for 10% and 8%, 16% and 11%, and 19% and 8% of the variability of WW and W6. They were responsible for 19% of the variation in BW of OS sheep. The significance of maternal influences in these breeds, in relation to the variability observed in these specific traits, must be taken into account when estimating genetic parameters and breeding values. Consequently, the selection programme becomes more effective.

4.4.3 Heritability estimation of growth traits

The estimation of heritability for the desired trait, which measures the proportionate influence of additive genetic effects on the total variability of observable traits within a population, is the foundation of animal breeding programmes. It explains the extent to which the trait can be improved by genetic selection. Therefore, estimating it is required for predicting how individuals will respond to selection and to calculate their specific EBVs (Getabalew et al., 2019). The heritability estimation should not be affected by feed differences, even though the examined breeds were fed concentrate according to the age and physiological stage of the animals. This is a result of the animals being grouped and fed similar quantities for every trait that was being studied. Furthermore, the factors of pens and dam's age may took account for any variability resulting from the feeding of the dams.

In this study, pre-weaning traits exhibited lower direct heritability in comparison to post-weaning traits. These findings indicate that the way animals are managed before they are weaned significantly affects how their genetic potential is expressed (Bedhane et al., 2013). The study found that the direct heritabilities for BW and WW were 0.13 and 0.11 in JA goats, 0.17 and 0.16 in BA goats, and 0.16 and 0.15 in OS sheep. In contrast, for W6 and W12 in JA goats, the direct heritabilities were 0.19 and 0.21, for BA goats, they were 0.16 and 0.24, and for OS sheep, they were 0.28 and 0.48. The presence of these heritability estimates suggests that genetic selection can be implemented to improve these growth traits in the Omani breeds, and the rate of improvement is determined by their magnitude.

reported low direct heritability values for BW and WW in Nellore sheep (0.08 and 0.03, respectively). Dhakad et al. (2022) found similar results in Malpura sheep, with heritability values of 0.15 for BW and 0.13 for WW. Chauhan et al. (2021) observed a heritability value of 0.10 for WW in Harnali sheep. Bangar et al. (2020) reported a heritability value of 0.09 for BW in Jakhrana goats. However, several studies have reported higher estimates for these traits. For instance, Baneh et al. (2012) found in Naeini goats value of 0.25 for BW, Bosso et al. (2007) reported in West African dwarf goat a value of 0.50 for BW, Areb et al. (2021) observed in Bonga sheep values of 0.56 and 0.36 for BW and WW, respectively, and Singh et al. (2022) recorded in Barbari goats 0.31 and 0.23 for BW and WW, respectively.

According to Olayemi et al. (1997), the low estimates of direct heritability for pre-weaning traits suggest that these traits are mostly impacted by environmental factors

rather than genetics. The inadequate nutrition management of dams may be a contributing factor to the low estimates of the direct heritability for traits before weaning in this study, resulting in a significant variation in the environment. In addition, the inclusion of maternal effects may have contributed to the low estimates of direct heritability. Tesema et al. (2022) reported that animal selection based on performance is ineffective when heritability is less than 0.15. Instead, it is recommended to select animals based on breeding values that are estimated from multiple sources, including sires, offspring, and their own performance records. Selecting animals based on lowly heritable traits is expected to result in a slow improvement in genetic merit (Mandal et al., 2015).

The heritability of the W6 trait was relatively moderate in JA goats (0.19), but a bit lower in BA goats (0.16). The heritability of this trait had a higher magnitude in OS sheep, with a value of 0.28. Sharif et al. (2022) reported a heritability of 0.20 in Lohi sheep; Singh et al. (2016) revealed a heritability of 0.28 in Marwari sheep 0.28, Chauhan et al. (2021) found a heritability of 0.18 in Harnali sheep; Singh et al. (2022) observed a heritability of 0.18 in Barbari goats; and Areb et al. (2021) found a heritability of 0.22 in Bonga sheep. Higher estimates than the current study have been reported by Bangar et al. (2020) in Jakhrana goat (0.53), and Hassan et al. (2013) in exotic goat (0.45).

The W12 trait demonstrated the highest estimates of direct heritability in comparison to other growth traits across all the breeds that were examined. This indicates that animals at one year of age possess more ability to manifest their genetic

potential. The OS sheep exhibited the highest estimations, with a value of 0.48, while the BA and JA goats showed moderate values of 0.24 and 0.21, respectively. The size of the flock, the twinning rate, and the implementation of a proper culling strategy at six months of age may have contributed to the less genetic variability in goat breeds compared to sheep. Estimates of direct heritability, which vary from moderate to high, suggest the existence of considerable additive genetic variance. This enables successful selection for additional genetic improvement. Moderate estimates of heritability for this trait in JA and BA goats were reported by Bedhane et al. (2013) in Arsi-Bale Ethiopian goats (0.23) and Singh et al. (2022) in Barbari goats (0.21). Koçak et al. (2023) have found a high estimate of direct heritability in Daglic sheep (0.47), which is in agreement with the current estimate for OS sheep. Lower estimates were found in Jakhrana goats (0.16) (Bangar et al., 2020), in Harnali sheep (0.11) (Chauhan et al., 2021), in Malpura sheep (0.16) (Dhakad et al., 2022) and in Bonga sheep (0.15) (Areb et al., 2021).

4.4.4 Genetic and phenotypic correlations among growth traits

The growth traits of the Omani goats and sheep breeds showed, in general, positive and strong genetic correlations among them, indicating that they are primarily governed by similar genes or genes that are closely linked (Sharif et al., 2022). The correlations ranged from 0.47 for the correlation between BW and W6 in BA goats and between BW and W12 in OS sheep to 0.98 and 0.92 for the correlation between W6 and W12 in JA and BA goats and OS sheep, respectively. This positive correlation implies that improving any trait would enhance the performance of other correlated traits, according to the high estimates of genetic correlations between the

traits (Bangar et al., 2020; Tesema et al., 2022). Robertson (1959) proposed that in order to mitigate the impact of genotypes and environmental interactions, it is recommended that there be a minimum genetic correlation threshold of 0.80 between phenotypes. This suggests that the ranking of animals would be similar across various traits. The present genetic correlations fell within the range reported in other research, including (Singh et al., 2022) (0.26-0.85), (Dhakad et al., 2022) (0.18-0.80), and (Bangar et al., 2020) (0.14-0.99).

Except for the correlations with BW, which showed lower magnitudes ranging from 0.15 to 0.25, the phenotypic correlations between growth traits across all breeds were positive and relatively high. The phenotypic correlations observed in JA goats ranged from 0.20 to 0.71, in BA goats from 0.19 to 0.70, and in OS sheep from 0.20 to 0.74. The phenotypic correlations between W6 and W12 were the largest in magnitude compared to the other correlations between traits (0.71, 0.70, and 0.74 in JA, BA, and OS, respectively). The second-strongest correlations were seen between W6 and WW (0.66, 0.67, and 0.70 in JA, BA, and OS, respectively). The phenotypic correlations between traits may arise from the common environment exposed to the animals at different stages of life (Sharif et al., 2022).

4.4.5 Genetic and phenotypic trends of growth traits

Between 2008 and 2020, the genetic trend in BW traits across all breeds showed a constant pattern of change, indicating that genetic selection was not effective in achieving the desired results. The yearly genetic increment associated with this trait for all breeds was 0.01 kg. The low genetic change might be because of the low heritability of this trait (0.13, 0.17, and 0.16 in OS sheep, BA goats, and JA goats, respectively), as well as its exclusion from being a targeted trait. The same pattern was observed by Bosso et al. (2007) in their research on sheep and goat breeds. However, Gizaw et al. (2007) reported a greater increase in Menz sheep compared to the present investigation, with a value of 0.04 kg/year. Lower estimates have been reported by Shirzeyli et al. (2023) in Markhoz goats (0.001 kg), Areb et al. (2021) in Bonga sheep (0.002 kg), and Esrafili and Behmaram (2023) in Moghani sheep (0.008 kg). A negative genetic trend of -0.02 kg for this trait was reported in Ettawa-grade goats by Hasan and Gunawan (2014). The differences in the published findings might be ascribed to changes in breeds, data structure, utilised statistical methods, and selection criteria.

The remainder of growth traits (WW, W6, and W12) in all three breeds exhibited a fluctuating and increasing trend in genetic changes starting in 2010. More consistent trend has been noticed since 2015, notably in the later growth trait W12. The first two years of the project (2008-2009) exhibited a declining pattern, possibly due to it being the starting year and the introduction of new strategies and management methods. The average breeding value for the traits WW and W6 increased annually by 0.09 kg and 0.13 kg, 0.08 kg and 0.10 kg, and 0.13 kg and 0.22 kg for JA goats, BA goats, and OS sheep, respectively. This indicates that

these traits demonstrated an effective response in comparison to BW, suggesting that animals at a more mature stage are more responsive to selection. The higher heritability estimates of the trait W6 in OS sheep compared to goats can explain the increased value of genetic change at W6. The heritability estimates for W6 were 0.28 in OS sheep, 0.19 in JA goats, and 0.16 in BA goats.

The breeds under investigation showed a more significant genetic change compared to what has been reported in the literature. This could be attributed to the selection of sires with higher breeding values and a potentially larger selection differential. Lower trends for the WW and W6 have been reported by Shirzeyli et al. (2023) in Markhoz goats (0.03 kg and 0.04 kg, respectively), Areb et al. (2021) in Moghani sheep (0.03 kg and 0.06 kg, respectively) and Hasan and Gunawan (2014) in Ettawa Grade goats (-0.02 kg and 0.003 kg, respectively). Nevertheless, higher estimates have been reported by Esrafil and Behmaram (2023) in Menz sheep (0.27 kg and 0.39 kg for WW and W6, respectively), and Gholizadeh and Ghafouri-Kesbi (2015) in Baluchi sheep (0.19 kg for WW). Later, they observed lower estimates for the W6 traits in the same breed (0.08 kg).

The weight at 12 months (W12) displayed the most substantial genetic change across the three breeds, which corresponds to the highest heritability estimate seen across all breeds. The OS sheep displayed the most significant change in this trait, with a growth rate of 0.39 kg per year, in contrast to rates of 0.20 kg and 0.18 kg in JA and BA goats, respectively. OS sheep exhibited significantly higher heritability estimates (0.48) in comparison to goat breeds, which might be responsible for their substantially greater genetic gain. Present genetic changes of the investigated breeds for this trait were much higher than many other breeds,

including West African dwarf goats (0.08kg) and Djallonk'e sheep (0.09 kg) (Bosso et al., 2007), Markhoz goats (0.08 kg) (Gholizadeh & Ghafouri-Kesbi, 2015), Bonga sheep (0.02 kg) (Areb et al., 2021), and Moghani sheep (0.15 kg) (Esrafil & Behmaram, 2023). High genetic changes have been reported by Gholizadeh and Ghafouri-Kesbi (2015) in Baluchi sheep (0.46 kg).

With the exception of the W12 trait, phenotypic changes in growth traits were not statistically significant across the three breeds. For the trait of W12, the JA goats, BA goats, and OS sheep breeds experienced an important weight rise, with annual increases of 0.93 kg, 0.69 kg, and 0.66 kg, respectively. Baba et al. (2020) did not observe any phenotypic gain in all the studied growth traits in Corriedale sheep. Mohammadi and Abdollahi-Arpanahi (2015) have only observed significant phenotypic change with WW and W6 (0.13 kg/year and 0.24 kg/year) in Zandi sheep. Enhancing phenotypic performance can be achieved by implementing different management strategies and improving nutrition (Hasan & Gunawan, 2014). It appears that environmental changes had a greater effect on these breeds' animals at BW, WW, and W6 than they did at W12. Inadequate nutrition, management problems, adverse weather conditions, and poor health can hinder animals from fully manifesting their genetic potential (Esrafil & Behmaram, 2023).

4.5 Conclusion

The growth traits of the studied breeds were significantly influenced by environmental fixed effects such as sex, year, and birth type. However, the age of the dam only had an effect on early growth traits of all breeds, including W6 in Batinah goats. The present study demonstrates that maternal effects played a significant role in accounting for the phenotypic variability of all growth traits in Jebel Akhdar goats. However, in the case of Batinah goats and Omani sheep, maternal influences were shown to be important for all growth traits except for W12. Considering these effects in the statistical models is crucial for an accurate estimation of genetic parameters and, consequently, breeding values. The moderate heritability of W6 and W12 traits in goat breeds and W6 in Omani sheep and the high heritability of W12 in Omani sheep suggest the possibility of further genetic improvement for these traits by selection. All the examined breeds exhibit strong positive genetic and phenotypic correlations between growth traits, except for the trait of BW. This suggests that selecting for an improvement of any given trait would also result in the improvement of other correlated traits. The strongest genetic correlations were seen between W6 and W12, followed by the correlation between W6 and WW. Therefore, selecting W6 would be desirable due to its substantial correlation with other growth traits, resulting in time and labour savings. The positive genetic trend over the course of 13 years indicates that the breeding programme set up to improve the growth traits of the three breeds was successful. Yet, it is important to emphasise the improvement of the animals' environment in order to improve their overall phenotype.

CHAPTER FIVE

OPPORTUNITIES OF IMPLEMENTING GENOMIC SELECTION IN OMANI SHEEP: A SIMULATION STUDY

5.1 Abstract

Genomic selection (GS) is a promising strategy for enhancing genetic improvement by increasing selection accuracy and decreasing the generation interval. It has been commonly adopted in dairy cattle and, to a lesser extent, in small ruminants. The primary advantage of introducing GS in sheep breeding is its potential to improve the accuracy of candidates' selection. Traditionally, individuals are selected based on predicting their estimated breeding values (EBVs) using the pedigree-best linear unbiased prediction (BLUP) approach. Genomic Best Linear Unbiased Prediction (GBLUP) and Single Step-Genomic Best Linear Unbiased Prediction (ssGBLUP) are two prevalent genomic methods used to predict Genomic Estimated Breeding Values (GEBVs) for implementing GS. These two methods employ molecular information throughout the genome to estimate genomic relationships and marker effects, which are then used to predict the GEBVs of animals.

This study aims to explore the possibility of applying GS to Omani sheep by comparing the predictive accuracy of the BLUP, GBLUP, and ssGBLUP methods. The study simulated the genome structure by using 5000 markers and 50 QTLs (with only additive genetic effects). The simulation employed the estimated genetic parameters of growth traits birth weight (BW), six-months weight (W6), and yearling weight (W12) that were obtained from Chapter 4 to represent three distinct levels of heritability: low, moderate, and high. Three varying sizes of reference animals were examined for every trait to evaluate the impact of the reference size on the prediction.

With an average accuracy of 0.64, ssGBLUP has outperformed BLUP (0.56) and GBLUP (0.47) in terms of prediction accuracy across all three traits. The accuracy of the three approaches improved as the heritability level increased. Increasing the reference size improved the genomic prediction accuracy of GBLUP and ssGBLUP by an average of 0.43, 0.48, and 0.50, and 0.61, 0.64, and 0.67 for the two methods, respectively, at reference sizes of 500, 1000, and 2000 animals, respectively. The largest increase in accuracy achieved by ssGBLUP was observed in the low heritable trait (BW), averaging 20% across the three reference sizes. However, the gain difference was minimal (<2%) while transitioning from 1000 to 2000 animals. Thereby, ssGBLUP could be a valuable technique for improving prediction accuracy in comparison to BLUP and GBLUP, especially for traits with low heritability. The results can be used as a theoretical framework for promoting the adoption of genomic selection in Omani sheep.

5.2 Introduction

Recent advancements in DNA sequencing and molecular information enabled the development of high-density SNP chips for livestock and consequently utilised them in genomic selection (GS) (Bertolini et al., 2017a; Rupp et al., 2016). Genomic selection is the process by which genomic estimated breeding values (GEBV) of genotyped candidates are predicted without the use of their phenotypic data, using a reference group of individuals that are both genotyped and phenotyped (Dekkers et al., 2021; Meuwissen et al., 2016). It entails evaluating the effects of SNP-markers in a reference population where individuals have been genotyped and phenotyped for a certain trait. Following that, selected candidates are only required to be genotyped in order to estimate their GEBVs (Meuwissen et al., 2016; Mrode, 2014).

Genomic selection offers potential for maximising genetic improvement by reducing the length of the generation interval (Karimi et al., 2019) and by accurately estimating breeding values at an early stage of an animal's life (Dekkers et al., 2021). It proved its effectiveness in dairy cattle by accurately estimating breeding values early in life and by reducing the generation interval. One key aspect contributing to this success was the high number of offspring produced by every male due to artificial insemination techniques, which results in a small effective population size in the reference group, leading to more accurate estimations of markers' effects. However, in sheep breeds, the issue may be more challenging due to the larger variability that exists among and within sheep breeds, requiring a large number of reference animals (Van der Werf et al., 2014).

Implementing GS in small ruminants, including sheep and goats, can be advantageous for improving prediction accuracy more than reducing the generation

interval. This is especially true for growth traits, as the generation interval is typically shorter in these animals, and most growth traits can be measured early in life. Accurate prediction is essential for the successful implementation of GS. The accuracy is influenced by several factors, such as the size of the reference population, the effective size of the reference set (Lee et al., 2017), the heritability of the trait, the number of QTLs affecting the trait (Dekkers et al., 2021), marker density, and the statistical method of prediction (Karimi et al., 2019). The level of trait's heritability and number of animals in the reference population can improve the accurate estimation of markers' genetic effects. Several studies have demonstrated that the accuracy of genomic prediction improves as heritability level and reference size rise (Karimi et al., 2019; Shumbusho et al., 2013; Song et al., 2019). While the markers' density and the effective population size have a role in increasing accuracy by capturing more additive genetic variation that is caused by QTLs (Pszczola et al., 2012).

The accuracy is determined by the amount of QTL-caused additive genetic variance that markers can explain, as well as the accurate estimation of markers' effects (Lee et al., 2017). As the number of QTLs rises, the genetic variance proportion at each QTL decreases, making it difficult to accurately estimate the effect of markers surrounding that QTL (Yan et al., 2022). The extent of additive genetic variance at a QTL that markers capture corresponds with the degree of linkage disequilibrium between the markers and the QTL; therefore, the number of molecular markers is critical for accuracy (Dekkers et al., 2021; Lee et al., 2017).

This study aimed to investigate the possibility of adopting GS in Omani sheep, along with offering an initial theoretical basis for this endeavour. The study evaluated the accuracy of BLUP, GBLUP, and ssGBLUP in predicting the breeding values of

animals for the growth traits of birth weight (BW), six-month weight (W6), and yearling weight (W12). These specific traits were chosen to represent the level of heritability as low, moderate, and high, respectively. The investigation was conducted using a simulation technique that properly mimics the real pedigree and genetic parameters of the target population.

5.3 Results

5.3.1 Population's structure of reference and validation animals

Basic statistics of the populations of the reference animals (phenotyped and genotyped) and validation animals (only genotyped) are summarized in **Table 21**. Across the three various sizes of the reference group, the average relationship among the reference animals was 0.04, literally unrelated individuals. The direct relatives, i.e., sires and dams, that existed in the reference group for the animals in the validation group increased as the reference size increased because more parents were found in subsequent years. The number of sires and dams in the reference groups was 4 and 60 for a reference size of 500, 9 and 117 for a reference size of 1000, and 13 and 179 for a reference size of 2000.

Table 21. Statistics of populations utilised as reference animals and validating animals of the Omani sheep.

Item	Reference size		
	500 animals	1000 animals	2000 animals
Year of birth	2019-2018	2019-2016	2019-2013
Average relationships among animals	0.04	0.04	0.03
Total animals in the validation group	293	293	293
Year of birth	2020	2020	2020
No. of validating animals with known sires	89	200	292
No. of sires of validating animals	4	9	13
No. of offspring/sire in the validation group	22.25	22.22	22.46
No. of validating animals with known dams	85	181	284
No. of dams of validating animals	60	117	179
No. of offspring/dam in the validation group	1.41	1.54	1.60

5.3.2 Accuracy of prediction

The prediction accuracy was determined by calculating the correlation coefficient between the estimated breeding values and the simulated true breeding values of the validation animals. Overall, the ssGBLUP approach outperformed the BLUP and GBLUP methods in predicting animals' breeding values across the three studied growth traits. The accuracies were on average 0.64, 0.56, and 0.47, for ssGBLUP, BLUP, and GBLUP, respectively. Accuracy improved as the number of animals in the reference population increased, regardless of growth traits. GBLUP achieved accuracies of 0.43, 0.48, and 0.50, whereas ssGBLUP achieved accuracies of 0.61, 0.64, and 0.67 for sample sizes of 500, 1000, and 2000 animals.

5.3.2.1 Accuracy at trait of birth weight (BW)

At the BW trait, the mean accuracy of BLUP, GBLUP, and ssGBLUP were 0.44, 0.40, and 0.53 respectively. The accuracy of genomic prediction using ssGBLUP and GBLUP continuously improves as the number of genotyped animals in the reference population increases (**Figure 26**). GBLUP achieved accuracy values of 0.35, 0.41, and 0.45, whereas ssGBLUP achieved higher accuracies with 0.49, 0.54, and 0.55 at sample sizes of 500, 1000, and 2000 animals, respectively.

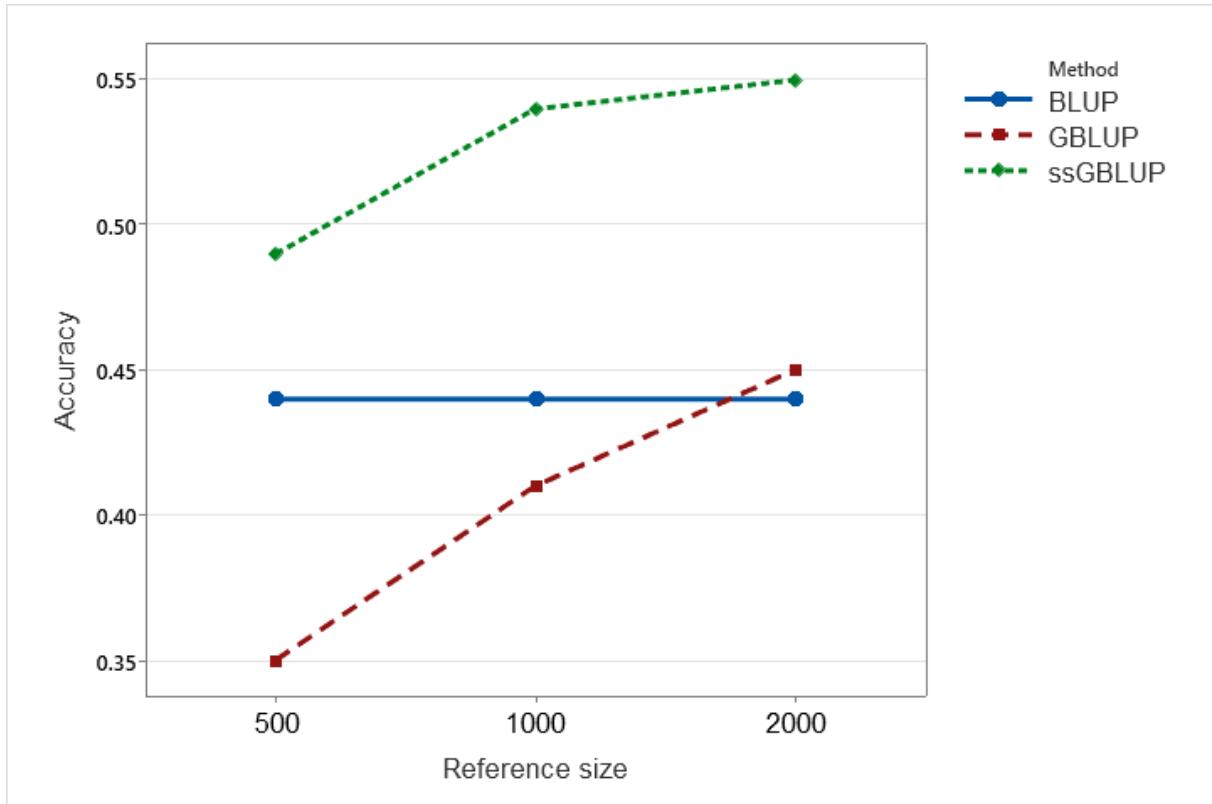


Figure 26. Prediction's accuracy of estimated breeding values of Omani sheep animals for the trait of birth weight (BW) with heritability ($h^2 = 0.16$) by three methods of BLUP, GBLUP, and ssGBLUP under three different reference sizes (500, 100, and 2000 animals).

5.3.2.2 Accuracy at trait of six-month weight (W6)

ssGBLUP demonstrated the highest prediction accuracy across the three sizes of reference population, averaging 0.65 accuracy. Then it was followed by BLUP, with an average accuracy of 0.59, and GBLUP had an average accuracy of 0.50 (**Figure 27**). As the reference size increases, the accuracy of prediction by genomic approaches also increases in a linear way. At sample sizes of 500, 1000, and 2000, the accuracy of ssGBLUP was 0.63, 0.65, and 0.68, respectively, compared to 0.46, 0.50, and 0.53 for GBLUP.

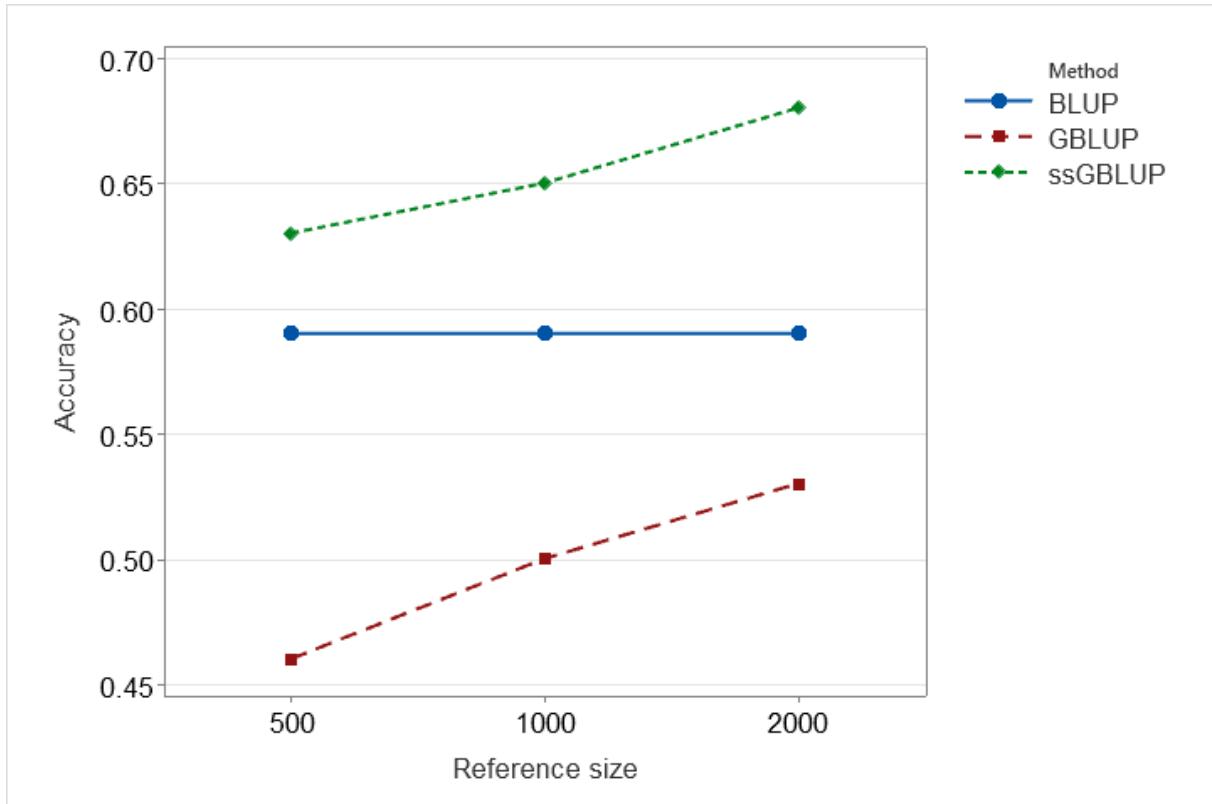


Figure 27. Prediction's accuracy of estimated breeding values of Omani sheep animals for the trait of six-month weight (W6) with heritability ($h^2 = 0.28$) by three methods of BLUP, GBLUP, and ssGBLUP under three different reference sizes (500, 100, and 2000 animals).

5.3.2.3 Accuracy at trait of yearling weight (W12)

Figure 28 shows the trend of prediction's accuracy for the three investigated methods for the trait of W12 across the three sizes of reference populations. ssGBLUP showed the highest prediction accuracy, averaging 0.74 across the three reference population sizes. BLUP achieved an average accuracy of 0.64, whereas GBLUP had an average accuracy of 0.51. The predictive performance of ssGBLUP improved with sample sizes of 500 (0.71), 1000 (0.74), and 2000 (0.77), whereas GBLUP achieved accuracies of 0.49, 0.52, and 0.52 for the same sample size.

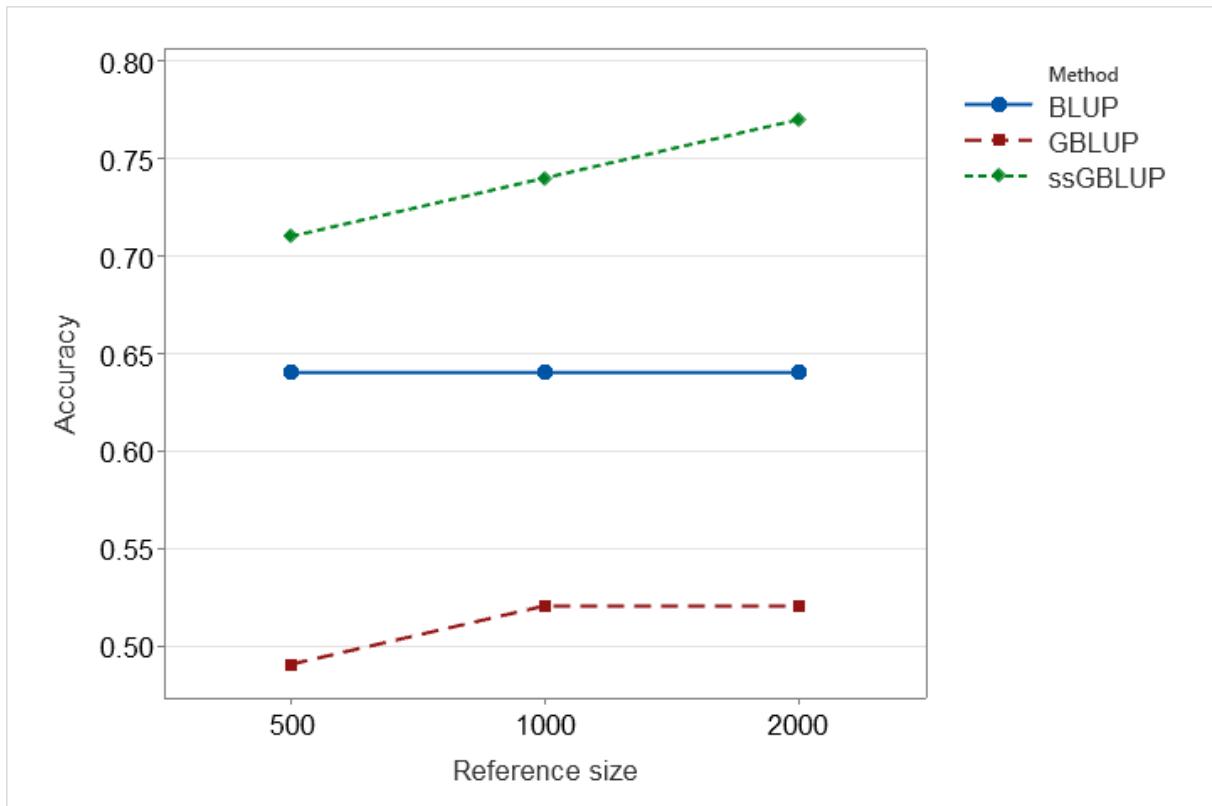


Figure 28. Prediction accuracy of estimated breeding values of Omani sheep animals for the trait of yearling weight (W12) with heritability ($h^2 = 0.48$) by three methods of BLUP, GBLUP, and ssGBLUP under three different reference sizes (500, 100, and 2000 animals).

5.4 Discussion

Rather than utilising a specialised simulation software, the study's simulation was suggested to be based on self-written Fortran code. This suggestion was taken to improve my knowledge of simulation methodologies and how they are implemented by specialised software. The Fortran-based simulation used for this study had some limitations that might be a potential pitfalls. For example, the array size was limited to 6,000, the thing that prevented simulating larger number of markers, the actual number of chromosomes, and distribution of markers and QTL effects. Furthermore, some parameters like linkage disequilibrium, mutation rate and crossover interference were not simulated. Some specialized simulators such as GPOPSIM (Zhang et al., 2015) and QMSim (Sargolzaei & Schenkel, 2009) have much flexibility in terms of QTL numbers, sampling distribution of QTL effects, chromosome numbers and length, and mutation rate. For this reason, it would be suggested to validate this simulation using specialised tools to make it more realistic.

The accuracy of genomic prediction of individuals' breeding values relies on key factors such as the fraction of additive genetic variance at a QTL that can be captured by the markers. The extent of the explained variance is affected by the level of linkage disequilibrium between the QTL and the markers. The accuracy also relies on the precise estimation of the markers' genetic effects (Lee et al., 2017). So, increasing the marker density may enhance genomic prediction's accuracy by increasing the degree of linkage disequilibrium between QTLs and markers (Karimi et al., 2019), and by capturing more of the genomic relationships among animals (Mrode, 2014). Habier et al. (2007) showed that the number of genetic relationships captured by the genetic markers is associated with the accuracy of genomic predictions.

5.4.1 Overall accuracy of predictions

The current simulation study used the real pedigree of the Omani sheep population and the genetic parameters for the growth traits (BW, W6, and W12) that were estimated in Chapter 4. The study showed that the ssGBLUP method performed better than classical BLUP and genomic GBLUP methods in accurately predicting the breeding values of selection candidates for the three growth traits and across the different sizes of reference populations. It yielded an average 14% increase in prediction accuracy compared to BLUP (0.64 vs. 0.56) and a 36% increase compared to GBLUP (0.47). These results aligned with the findings reported by Karimi et al. (2019) who found that ssGBLUP outperformed alternative methods, especially in cases of low heritability traits and low marker density. Also, Song et al. (2019) have reported that ssGBLUP outperformed GBLUP and BLUP in predicting breeding values for seven body measurements in a pig population. Yet, the same study reported that accuracy improvement over the BLUP method was low, averaging only 1%, possibly due to the limited number of genotyped individuals (400 animals).

ssGBLUP's superiority over other methods may be due to its combined use of pedigree and genomic relationships. Additionally, ssGBLUP utilises both genotyped and non-genotyped animal phenotypes, while GBLUP only uses genotyped animal phenotypes (Valerio-Hernández et al., 2023). In addition, the effective population size of the reference population might be small. A smaller effective population size will be expected to result in fewer independent chromosomal segments, leading to a lower number of markers and phenotypes that are involved in tracking genetic variability and estimating SNP effects properly (Pszczola et al., 2012).

Despite having a reference size of 2,000 genotyped animals, GBLUP predicted less accurately than traditional BLUP. This could be because the size of the genotyped animals used for GBLUP estimate differs much from that of the ungenotyped animals used for BLUP estimation. The reference size should be greater than 2,000 animals for GBLUP to outperform BLUP, according to Karimi et al. (2019) research. Further, the animals in the reference set and the validation set may not have close enough genetic relationships, which may have contributed to GBLUP's inability to correctly predict breeding values (Fraslin et al., 2022; Lee et al., 2017). Some studies have also shown that GBLUP was less effective than BLUP in terms of prediction accuracy (Song et al., 2019; Valerio-Hernández et al., 2023).

5.4.2 Influence of heritability and reference size on prediction

The accuracy of the prediction improved steadily as the heritability of the trait increased across all three methods. The accuracy of ssGBLUP was 0.53 for BW, 0.65 for W6, and 0.74 for W12. BLUP obtained values of 0.44, 0.59, and 0.64 for the respective traits. GBLUP accuracies for the three traits, respectively, were lower with values of 0.40, 0.50, and 0.51. Further, the accuracy of the genomic prediction by the ssGBLUP and GBLUP methods improved as the reference size increased. Across the three traits, the gain in accuracy for ssGBLUP and GBLUP was ~16% and ~12% (from 500 to 1000), and ~5% and ~4% (from 1000 to 2000). The accuracy of genomic prediction is expected to decrease with smaller reference sizes and lower heritability and to improve with higher heritability and larger reference populations (Prince & Gowane, 2017; Pszczola et al., 2012). The reason for this might be that for low heritable traits, the proportion of the additive genetic variance caused by QTLs would

be very small compared to high heritable traits. This means that more markers and individuals' phenotypes are needed in order to capture a greater proportion of the additive genetic variance and, consequently, effectively estimate the additive genetic effects of the markers surrounding the QTLs. Additionally, in our study, we found that when the size of the reference population increased, there was a higher probability of identifying closer relatives for the selection candidates, potentially leading to improved accuracy. A number of studies revealed that the accuracy of predicting genomic breeding values is highest when the target animals are closely related to the reference animals (Fraslin et al., 2022; Gowane et al., 2018; Pszczola et al., 2012) , and the relationships among reference animals are minimised (Pszczola et al., 2012), as it is the case in our study that the average relationships among reference animals were 0.04 (unrelated animals).

By considering the low heritable trait (BW), when comparing ssGBLUP to BLUP, the increase in accuracy was 11% for a reference size of 500, 23% for a reference size of 1000, and 25% for a reference size of 2000. The accuracy improvement for the moderately heritable trait (W6) was 7% with a reference size of 500, 10% with a reference size of 1000, and 15% with a reference size of 2000. The gain for the high heritable trait (W12) was 11% (reference size = 500), 16% (reference size = 1000), and 20% (reference size = 2000). Across every case of reference size and heritability level, there was an increase in accuracy observed among comparable methods. However, the comparable gain in accuracy among the genomic methods is higher for the traits with low heritability, especially when sample sizes are 1000 and 2000. ssGBLUP appears to be an effective approach for improving prediction accuracy and enhancing genetic gain, particularly for traits with low heritability, when both BLUP and

GBLUP had accuracies below 0.50. Using a sample size of 1000 animals may be sufficient to substantially enhance accuracy, as the increase in accuracy from 1000 to 2000 animals was not large. Practically applying genomic selection to Omani sheep can be supported theoretically by adopting an appropriate reference population design that maximises the number of sires, unrelated individuals, and population size.

5.5 Conclusion

Genomic selection is a promising tool for breeding projects in livestock, including small ruminants. Genomic selection is expected to improve the accuracy of predicting breeding values, hence improving genetic progress. Simulation can be used to theoretically test and assess methodologies, providing practical guidance for choosing a specific method. The current simulation study has shown that the ssGBLUP approach outperforms BLUP and GBLUP methods in reliably estimating breeding values by exploiting both pedigree and genomic relationships across individuals. The ssGBLUP approach exceeded accuracy across reference populations of varying sizes and different levels of heritability. Its greatest improvement was seen with the low heritability trait (BW), attaining a 20% increase over BLUP and around 33% over GBLUP. Genomic predictions using the ssGBLUP and GBLUP methods improved in accuracy as the reference size and heritability increased. This could be attributed to the fact that low heritable traits involve more phenotypes and genotypes to capture a larger genetic variance. The greater number of direct relatives available for animals in the validation group might enable the genetic markers to capture more genomic relationships and consequently improve their accuracy. We can conclude that ssGBLUP can provide an efficient method for accurately estimating the breeding values of Omani sheep population animals, especially those with low heritable traits. A reference size of 1000 animals can also be considered appropriate, as the difference between 1000 and 2000 animals was not substantial.

CHAPTER SIX

GENERAL DISCUSSION AND CONCLUSION

6.1 Genetic improvement of growth traits in goats and sheep in Oman

The economic value of an animal is largely determined by its growth traits, which can be improved to develop more efficient production systems (Mahala et al., 2019). The animal's growth potential is indicative of its ability to produce meat (Bangar et al., 2020). Thus, the production of meat can be increased by improving growth traits.

Sheep and goats make up almost 81% of the overall livestock population in Oman, with populations of 642,000 and 2,443,000, respectively (NCSI, 2021). They are known for their capacity to thrive in arid and hilly regions, where they can efficiently convert scarce vegetation into nutrients (Mahgoub et al., 2010) and have a short production cycle for red meat production (Pond & Pond, 2000). Sheep and goats in Oman are mostly bred for meat (Shaat & Al-Habsi, 2016). They could therefore be used to contribute significantly to the production of meat in the country and to food security.

Improving growth traits implies understanding and analysing the factors that impact them. These traits are quantitative in nature and are impacted by a combination of environmental and genetic factors, as well as their interactions (Bahreini Behzadi et al., 2007; Falconer, 1996). Genetic improvement is a viable and sustainable approach that can be employed to enhance these traits by selecting animals with superior genetic merit for a certain trait. In order to effectively implement genetic improvement programmes, it is essential to accurately estimate some important genetic parameters that characterise the population, such as the heritability of the desired traits and the genetic correlations between those traits. The heritability of a characteristic indicates its

susceptibility to respond to selection, while genetic correlations reflect the extent and direction of the influence that the selected trait has on other traits under investigation (Singh et al., 2022; Zishiri et al., 2014). Therefore, the primary objective of this thesis was to estimate the heritability and genetic correlations of growth traits, as well as to look into the genetic trend for each trait from 2008 to 2020, targeting the most popular breeds of goats and sheep in Oman: Jebel Akhdar (JA) and Batinah (BA) goats, and Omani sheep (OS). The growth traits comprised birth weight (BW), weaning weight (WW), six-month weight (W6), and yearling weight (W12).

Genetic improvement projects are commonly associated with a rise in inbreeding levels, especially in closed-population schemes that focus on selecting within the breed. Inbreeding has adverse effects on genetic variability (Ceyhan et al., 2011; Mandal et al., 2020) and can lead to inbreeding depression (Falconer, 1996), both of which can impact the success of a breeding programme. The second objective of this thesis was to assess the level of inbreeding in the three populations and monitor its trend from 2008 to 2020.

Genetic improvement efforts in animal breeding rely on the selection of individuals with higher estimated breeding values (EBVs) for specific traits, which can be passed on to their offspring. The Best Linear Unbiased Prediction (BLUP) is the classical method that is frequently used to predict EBVs by utilising the pedigree-based relationships between animals, their phenotypes, and the ratio of environmental variance to the additive genetic variance, denoted as alpha (α) (Mrode, 2014). Since 2001, research has started to look into the possibility of using genomic selection (GS) to enhance genetic improvement through

improving the prediction accuracy of breeding values and reducing generation intervals, benefiting from the advancements in molecular genomics and the development of single nucleotide polymorphism (SNPs) chips for the majority of livestock (Meuwissen et al., 2001). The final chapter of results in the present study has conducted a comparison between the conventional BLUP approach and the genomic techniques of Genomic Best Linear Unbiased Prediction (GBLUP) and Single Step Genomic Best Linear Unbiased Prediction (ssGBLUP) in terms of their ability to reliably predict breeding values. It was based on a simulation of five chromosomes of the sheep's genome, which had 5000 markers and 50 QTLs (with solely additive genetic effects). The simulation used the actual pedigree and heritability level of growth traits that were obtained in Chapter 4. Consequently, theoretical guidelines were developed for implementing genomic selection in sheep and goat populations in Oman.

6.2 Estimation of genetic parameters of growth traits

Animals' predicted response to selection and the eventual genetic improvement of a trait can be inferred from the heritability level of that trait in that population (Getabalew et al., 2019). As a result, the progress of improving that trait genetically would be determined by the extent of its heritability within the specific population.

6.2.1 Heritability of pre-weaning growth traits

In general, the heritability of pre-weaning growth traits in the three breeds studied was relatively low, measuring less than 0.20. The values for the trait of BW were 0.13 ± 0.04 , 0.17 ± 0.04 , and 0.16 ± 0.03 in JA goats, BA goats, and OS sheep, respectively. Similarly, the values for the trait of WW were 0.11 ± 0.04 , 0.16 ± 0.04 , and 0.15 ± 0.03 in JA goats, BA goats, and OS sheep, respectively. The heritability estimates suggest that there is a level of genetic variability in pre-weaning growth traits that can be used for genetic improvement. However, the rate of improvement is expected to be minimal. Tesema et al. (2022) have suggested that when the heritability is below 0.15, it is essential to use animals' EBVs rather than phenotypic selection for the purpose of selection.

The low heritability levels are indicative of the animals' additive genetic effects contributing less to the variance compared to the increased variance caused by environmental variables. Pre-weaning improper management such as dam's nutrition (Olayemi et al., 1997) and including maternal effects in the models used to estimate the heritability (Meyer, 1992) may have contributed to the low levels of heritability for these traits. The importance of maternal effects on these

particular traits must be taken into account when estimating genetic parameters and breeding values in order to avoid any bias or inaccurate estimation (Meyer, 1992; Oyieng et al., 2022).

6.2.2 Heritability of post-weaning growth traits

The growth traits W6 and W12 had higher heritability levels than the earlier growth traits, with values for the corresponding breeds of JA goats, BA goats, and OS sheep reaching 0.19 ± 0.05 and 0.21 ± 0.06 , 0.16 ± 0.04 and 0.24 ± 0.04 , and 0.28 ± 0.05 and 0.48 ± 0.05 , respectively. These values could indicate the ability of animals in later stages of life to express their genetic potential and be more adaptable to environmental changes. Thus, the selection of these traits, especially the W12 trait, is expected to enhance genetic improvement effectively. It has been observed that OS sheep have higher heritability than JA and BA goats. This may be due to a number of factors, including a higher twinning rate and a larger flock size than in goat breeds. In addition, sheep breeds may exhibit greater genetic diversity compared to goats (Van der Werf et al., 2014).

Usually, the impact of the dam on the animal's phenotype diminishes as it grows older, as its dependence on the dam decreases (Bahreini Behzadi et al., 2007). Nevertheless, our research revealed that maternal influences were significant for W6 in goats and sheep and W12 in JA goats, but to a lesser extent compared to early growth traits. The contribution of maternal additive genetic effects to the phenotypic variance in JA goats was around 6% for W12, whereas maternal permanent environmental influences accounted for 8% for W6. Maternal permanent environmental influences accounted for 11% and 8% of the overall

phenotypic variance of the W6 trait in BA goats and OS sheep, respectively. The presence of maternal influences in later stages may be attributed to carryover maternal effects from the pre-weaning stage (Bangar et al., 2020). The absence of maternal effects on W12 in OS sheep and BA goats may have contributed to the higher estimates of heritability (0.24 and 0.48, respectively) compared to JA goats (0.21).

6.2.3 Genetic and phenotypic correlations between growth traits

Strong and positive genetic correlations ranged from 0.47 to 0.98 between the various growth traits. Among the three breeds, the strongest correlations were found between W6 and W12 and between W6 and WW. The genetic correlation between W6 and W12 was 0.98 ± 0.03 , 0.98 ± 0.05 , and 0.92 ± 0.02 for the JA goat, BA goat, and OS sheep breeds, respectively. The genetic correlation between W6 and WW for the corresponding breeds was 0.85 ± 0.06 , 0.91 ± 0.05 , and 0.89 ± 0.03 . The findings suggest that these traits may be regulated by the same genes or by genes that are linked closely (Sharif et al., 2022). Consequently, improving any of these traits would result in the enhancement of the other growth traits in the same way (Bangar et al., 2020; Tesema et al., 2022).

The phenotypic correlations between the growth traits were also strong and positive, except for the correlations with BW (≤ 0.25) in all breeds. Other correlations ranged from 0.45 to 0.74. Again, the trait of W6 was common, with the strongest phenotypic correlations across the three breeds. The correlations between W6 and W12 were 0.71 ± 0.02 , 0.70 ± 0.02 , and 0.74 ± 0.01 for JA

goats, BA goats, and OS sheep. The values for the comparable breeds between W6 and WW were 0.66 ± 0.01 , 0.67 ± 0.01 , and 0.70 ± 0.01 .

Robertson (1959) recommends a minimum threshold of 0.80 for genetic correlations between traits in order to minimise the influence of genotype-environment interactions on these traits. This ensures that the ranking of animals remains consistent across the correlated traits. Given that the trait of W6 has the strongest genetic and phenotypic correlations with WW and W12, it may therefore be the best selection criterion for enhancing the growth traits in the examined breeds. Additionally, because it is recorded earlier than the W12 trait, management costs can be reduced in terms of manpower, nutrition, and time. Yet, we suggest that the selection of animals should be based on animals' EBVs rather than phenotypic selection, especially when it comes to goat breeds. This is because the heritability of W6 in goat breeds is lower (0.19 for JA goats and 0.16 for BA goats) compared to OS sheep (0.28).

6.2.4 Genetic and phenotypic trends of growth traits

All three breeds' growth traits exhibited a positive genetic trend, though to varying extents; W12 exhibited the greatest change and BW the least. In general, the BW trait exhibited an almost constant pattern of genetic change, with an increase of 0.01 kg per year observed across the three breeds. The slow progress of this trait was expected given its lower correlations with other traits in comparison to the correlations among the remaining various traits, as well as a low level of heritability for this trait. Despite having a low heritability similar to that of BW, WW's trait had stronger genetic correlations than BW's, especially with

W6, which could explain why this trait responded better to selection. The annual genetic gain for this trait was 0.09 kg, 0.08 kg, and 0.13 kg in the JA goat, BA goat, and OS sheep breeds, respectively.

Compared to pre-weaning traits, post-weaning traits displayed a stronger tendency for genetic change across the three breeds, indicating greater responsiveness to improvement. The highly strong genetic correlations, above 0.90, between post-weaning traits may have played a crucial role in the large increase, especially considering the higher heritability estimates seen for the W12 trait. The OS sheep breed exhibited the most significant increase in genetic merit, with a rate of 0.22 kg/year for the W6 trait and 0.39 kg/year for the W12 trait. This could be due to the traits' higher heritability values when compared to goats. The annual genetic change for the JA and BA goat breeds was 0.13 kg and 0.10 kg, respectively, for W6, and 0.20 kg and 0.18 kg, respectively, for W12.

Phenotypically, the growth traits showed a significant performance trend ($P < 0.05$) only for the W12 trait. The yearly weight gain for JA goats, BA goats, and OS sheep was 0.93 kg, 0.69 kg, and 0.66 kg, respectively. No significant changes were observed in the other traits during the course of the 13-year period. Even though the genetic merit of animals for these traits changed significantly, phenotypic improvement was not achievable. It appears that these traits were more affected by environmental variations, which might be generated by factors such as nutrition, weather, diseases, and management, compared to the trait of W12. These effects can restrict the manifestation of animals' genetic capacity (Esrafil & Behmaram, 2023; Hasan & Gunawan, 2014). In light of this, phenotypic improvement in tandem with genetic improvement may be achieved by

enhancing management practices and offering sufficient and consistent nutrition throughout time.

6.3 Considerations for improving growth traits

In small ruminants' production, the live bodyweights, growth rate, and reproductive efficiency are all economically significant traits (Baneh et al., 2012). For example, the fast growth rate before weaning may result in heavier animals at weaning, which would enhance the farmer's daily revenues by producing more meat (Al-Shorepy et al., 2002). A higher average daily gain (ADG) causes market weight to be reached more quickly (Mahala et al., 2019). Therefore, ADG can be added as a target trait in addition to the other traits that have been examined in this study in order to determine whether it can be used as a selection criterion to improve growth performance.

When animals are selected based on their live body weights and growth rates, they may end up having a higher rate of fat deposition, which can cause problems with lambing and fertility. Additionally, feed intake would go up, which would be challenging for farmers, especially in dry or semi-arid areas (Mohammadi et al., 2014). As an alternative to bodyweights, feed conversion efficiency might be a better selection criteria to enhance animals' growth and meat production (Arthur et al., 2001). However, the absence of feed intake data may make it challenging to select animals based on feed conversion efficiency. Yet, the Kleiber ratio has been utilised as an indicator of feed conversion efficiency (Arthur et al., 2001; Tesema et al., 2022). The Kleiber ratio enables for the classification of animals with high growth efficiency relative to body size, and is defined as growth rate divided by body mass 0.75 (Kleiber, 1947).

Because growth traits and reproductive traits are often correlated, it is also important to take into account the genetic and phenotypic correlations between

them. This is because enhancing traits of growth may affect an animal's reproductive traits, and ultimately would influence the farm productivity and profitability (Mohammadi et al., 2014; Safari et al., 2007). Accordingly, breeding programs should aim for a comprehensive selection approach that considers growth traits and reproductive traits to minimise any possibility for adverse impacts. Sheep and goat farming may remain sustainable and productive by using a balanced strategy that makes gains in one area don't come at the expense of another.

6.4 Inbreeding level in Jebel Akhdar and Batinah goats, and Omani sheep

Genetic variability has been observed to be in sufficient amount according to the heritability estimates, especially in post-weaning growth traits, among the investigated breeds of goats and sheep in Oman. Moreover, the assessments of inbreeding level were found to be very low across the three examined breeds, which may suggest the presence of adequate genetic variability among the animals. The degree of inbreeding can decrease the level of genetic variability by increasing the occurrence of homozygous genotypes and diminishing the occurrence of heterozygous genotypes (Hartl, 2020). Excessive inbreeding is known to have detrimental effects on an animal's productivity, health, and reproductive capacity via what is termed inbreeding depression (Ceyhan et al., 2011; Falconer & Mackay, 1996; Weigel, 2001).

6.4.1 Estimation of inbreeding level

The study measured the level of inbreeding by calculating the average inbreeding coefficients (F) of all individuals over a 13-year period (2008-2020). Inbreeding levels were found to be 0.67%, 0.65%, and 1.52% in JA goats, BA goats, and OS sheep, respectively. According to DS Falconer and Mackay (1996), inbreeding levels below 10% are regarded as acceptable and are not likely to have harmful impacts. Factors such as the ratio of sires to dams, population size, and the limitation of males to only two mating seasons may have contributed to the observed low levels of inbreeding in these breeds (Wakchaure & Ganguly, 2015).

The proportions of inbred individuals within the respective breeds of JA goats, BA goats, and OS sheep were 17.34%, 19.31%, and 23.48% of the entire population of animals. The level of inbreeding within the inbred groups for the respective breeds was 3.88%, 3.39%, and 6.49%. The majority of these animals had an F value below 6.25%. The findings about the inbred animals assist in clarifying the lower levels that have been estimated for the average inbreeding level.

6.4.2 Trend of inbreeding level

Across the three populations studied, the levels of inbreeding generally exhibited an upward trend from 2008 to 2020. The annual increases were 0.12%, 0.13%, and 0.27% for the JA goat, BA goat, and OS sheep breeds, respectively. According to Nicholas et al. (1989), animal breeding may accept an annual inbreeding rate of up to 0.5%. The increment in inbreeding level was associated with the increased proportions of inbred animals across the years. The number of inbred animals began to slowly increase in 2010, but in the last three years, the rate of increase has become more rapid. Yet, the majority of the increases occurred in animals with a frequency of $F < 6.25\%$, which could contribute to maintaining a low overall level of inbreeding.

Despite the low levels of inbreeding in these populations, there has been a noticeable increase, particularly in recent years. This highlights the need to monitor inbreeding levels and implement efforts to prevent them from reaching unacceptable levels. Introducing new sires, preventing mating between closely related individuals, and increasing the population size are key methods that can

efficiently reduce the accelerated rate of inbreeding (Wakchaure & Ganguly, 2015). Further, it is important to maintain an effective population size of 50 or more in order to minimise the rate of inbreeding and ensure an adequate level of genetic variability (de Oliveira et al., 2023; Oldenbroek & van der Waaij, 2014).

6.5 Potential of implementing genomic selection in Omani sheep

6.5.1 Challenges to implement genomic selection in small ruminants

Practicing genomic selection (GS) in small ruminants is encountered with several factors, such as genotypic cost, size of the reference population, and accuracy of prediction. The implementation of GS in small ruminants may be constrained by the financial aspect, as the expense of single nucleotide polymorphism (SNP) chips can exceed the cost of the animals themselves. Utilizing low-density marker chips could serve as a viable option for GS in small ruminants, as it offers a more cost-effective solution (Habier et al., 2009). However, they may not be efficient enough to accurately estimate markers' effects.

Several factors can contribute to determining the accuracy of genomic prediction, such as the heritability of the trait, the size of the reference population in terms of the number of genotyped animals, the genomic relationships among these animals, as well as their relationships with the validating animals, and the specific statistical method employed. Multiple studies have demonstrated that the accuracy of predictions improves as the trait's heritability level and reference size increase. (Daetwyler et al., 2012; Prince & Gowane, 2017; Pszczola et al., 2012). According to this, more genotyped animals and phenotypic data are required for accurate estimations when heritability is low. The accuracy of prediction is expected to improve when the genetic relationships among the reference animals are minimized and their relationships with the validation population are maximised (Pszczola et al., 2012).

The density of markers plays a crucial role in enhancing genomic prediction by efficiently explaining a greater proportion of the additive genetic variance caused by QTLs. Increasing the number of markers increases the degree of linkage disequilibrium between markers and QTLs, resulting in a greater capture of variance by these markers (Karimi et al., 2019; Lee et al., 2017). Consequently, precise estimations would be obtained for the additive genetic effects. In addition, the higher the number of markers, the greater the level of captured genomic relationships (Mrode, 2014).

6.5.2 Comparison of prediction accuracy between BLUP, GBLUP, and ssGBLUP

One of the goals of this thesis was to explore the possibility of using GS on Omani sheep. This was done by simulating five chromosomes of the ovine genome, employing the real pedigree of the targeted sheep population, and using the estimated heritability levels for the growth traits mentioned in Chapter 4. The study conducted a comparison of the accuracy of predictions for breeding values of animals using three different approaches: BLUP, GBLUP, and ssGBLUP. This comparison was done across three levels of heritability (low, moderate, and high) and three different sizes of reference population (500, 1000, and 2000 animals).

In this investigation, ssGBLUP demonstrated a 14% improvement in prediction accuracy compared to BLUP, and a 36% improvement compared to GBLUP. The superiority of ssGBLUP may be attributed to its utilisation of both pedigree and genomic relationships, as well as being able to take into account all available phenotypic data from both genotyped and non-genotyped animals (Valerio-Hernández et al., 2023). The average accuracies for ssGBLUP, BLUP,

and GBLUP were 0.64, 0.56, and 0.47, respectively. Yet it is important to note that the marker density was rather high, around 12.5 per 1 cM (5000 *markers/400 cM*). This high marker density may have also had an impact on the accuracies (Karimi et al., 2019; Mrode, 2014; Sadan & Valsalan).

The accuracy of prediction increased as the heritability level increased across the three methods. One possible explanation is that for traits with low heritability, the contribution of each QTL to the total additive genetic variance is very minimal compared to traits with high heritability. Therefore, in order to accurately assess the additive genetic effects of the markers surrounding the QTLs, it is necessary to have a larger number of markers and individuals' phenotypes to capture a higher proportion of the additive genetic variance.

The accuracy values for the traits BW (low heritability), W6 (moderate heritability), and W12 (Yearling weight) in the ssGBLUP method were 0.53, 0.65, and 0.74, respectively. The accuracy values for the traits BW (low heritability), W6 (moderate heritability), and W12 (Yearling weight) in the BLUP method were 0.44, 0.59, and 0.64, respectively. The accuracy values for the traits BW (low heritability), W6 (moderate heritability), and W12 (Yearling weight) in the GBLUP method were 0.40, 0.50, and 0.51, respectively. The increase in accuracy achieved by ssGBLUP compared to BLUP is greater for traits with low heritability (20%). This suggests that ssGBLUP, when compared to classic BLUP, has potential as a method for enhancing prediction accuracy. As a result, it can lead to greater improvement gains, particularly for traits with low heritability.

It was observed that as the number of animals in the reference population increased, so did the accuracy of the genomic predictions made by ssGBLUP and GBLUP. However, the increase in accuracy achieved by ssGBLUP, especially for traits with low heritability, was negligible (1%) when the number of animals changed from 1000 to 2000. A reference population consisting of 1000 animals may be adequate for genome prediction when using a high marker density. Our analysis revealed that when the size of the reference population increased, the probability of identifying closer relatives for the selection candidates increased, which might potentially result in enhanced accuracy. Several studies have demonstrated that the precision of predicting genomic breeding values is greatest when the target animals share close genetic relationships with the reference animals (Fraslin et al., 2022; Gowane et al., 2018; Pszczola et al., 2012).

6.5.3 Logistical and economic feasibility of introducing genomic selection in the local breeding programme

There are economic and logistical challenges when implementing genomic selection (GS) in the local sheep breeding program, particularly for smaller populations like Omani sheep. Size of reference population is a major challenging, because it is essential to have a large size of reference animals for attaining accurate genomic prediction, and capturing more genetic relationships. According to the simulation study, the reference size needs to be at minimum 1,000 animals. The study indicated that ssGBLUP yielded considerable accuracy increases over standard BLUP method, particularly with low heritable traits.

However, when the heritability of the trait is low, it needs a large number of genotyped animals and recorded phenotypes to obtain acceptable accuracy (Daetwyler et al., 2012).

A major obstacle in GS for small ruminants is the cost of genotyping, particularly SNP chips, which can be more expensive than the animals themselves. Although it is more cost-effective, using lower-density SNP chips may result in less accurate predictions (Habier et al., 2009). Low-density marker chips might offer a more affordable option, but doing so would necessitate establishing a balance between price and prediction accuracy.

In conclusion, although GS may increase breeding efficiency through increasing the prediction's accuracy, its feasibility depends on controlling the high costs associated with genotyping, and providing a sizable and accurately defined reference population. Whether GS is a viable long-term investment will depend on the scale of the breeding program and the traits being targeted (high vs. low heritability).

6.6 Implementation of the main findings from the thesis

The findings of the thesis can be exploited for a better breeding strategy and genetic improvement of growth traits in Omani Jebel Akhdar (JA) and Batinah (BA) goats, as well as Omani sheep (OS) populations at Wadi Qurayyat Livestock Research Station (WQLRS) in Oman. This can be achieved using the following:

1. The three breeds' growth traits—BW, WW, W6, and W12—exhibited different levels of heritability that can be exploited for an effective genetic improvement programme.
2. Post-weaning growth traits should be given priority as selection criteria for enhancing growth traits, since they have higher heritability levels compared to pre-weaning traits.
3. The trait of W12 across the three breeds is expected to show a higher improvement due to its higher level of heritability compared to other traits.
4. Improving one growth trait would simultaneously improve other growth traits, due to the strong and positive genetic correlations among the traits.
5. The trait of W6 can be used as a selection criterion due to the very strong genetic correlations observed between W6 and both W12 and WW. As a result, both time and management costs are reduced since this trait is measured before the W12 by about six months.
6. Selecting animals based on the trait of W6 is recommended to be based on estimated breeding values (EBVs) instead of phenotypic selection, particularly with goats' breeds.

7. When estimating the breeding values of animals for all growth traits except W12, it is important to take into account the influence of maternal effects. This is necessary to prevent any overestimation of estimates or biased EBVs.
8. The breeding strategy at WQLRS has successfully achieved genetic improvement in growth traits, as evidenced by the positive trend in the average breeding values of the animals from 2008 to 2020, particularly in post-weaning growth traits.
9. Efforts must be undertaken to improve animals' environments, such as feeding and management practices, as there has been no significant change in phenotypes across the growth traits, with the exception of W12.
10. The inbreeding level among the three breeds appeared to be at its lowest level, suggesting effective control measures. However, there has been a persistent increase in the inbreeding level over the past few years, necessitating ongoing monitoring.
11. Introducing new male animals for breeding, limiting mating between closely related individuals, and expanding the size of the population are key factors that can limit the rate of inbreeding.
12. The simulation study in Chapter 5 has provided a theoretical basis for the potential implementation of genomic selection in the examined breeds in the near future.
13. When exploring the actual implementation of genomic selection (GS), it is important to take into account marker density, a reference size of 1000

animals, the use of the ssGBLUP approach, the focus on low heritable traits, and the consideration of relationships between animals in the reference and with selection candidates.

1.7 Possible future work

1. ADG and feed conversion efficiency for the investigated breeds should be examined too for its possibility to be a better selection criterion for enhancing growth.
2. Investigating the correlations between growth traits and reproductive traits is key to look at the influence of improving growth on reproductive performance.
3. Estimating the genetic parameters and genetic trend of reproductive traits.
4. Employing molecular markers to evaluate genomic inbreeding level may offer a more accurate measure compared to pedigree-based inbreeding level.
5. Utilising specialised software like QMSim for simulation purposes to validate the current simulation in this study.
6. Working on a second simulation study to evaluate GS in multibreed goats (JA and BA goats) at varying marker density levels.
7. Conducting genetic parameter estimation and assessing the genetic trend and the extent of inbreeding levels for different breeds housed at several breeding stations in Oman.

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APPENDIX

Appendix (A)

Fortran source code for simulating sheep genome, and individuals' genotypes and phenotypes

implicit double precision (a-h,o-z) ! Accuracy up to 16 digits.

parameter (mxind=5000,mxloci=6000,mxQTL=5000) ! Constant values for maximum individuals, maximum loci, and maximum QTLs, respectively.

! dimensions of arrays : recombination frequency, loci genotypes, QTL locations, individuals' markers alleles, individuals' phenotypes, error terms, true breeding values of individuals, and markers genotypes, respectively.

```
dimension freq(mxloci), npgt(mxind,2,mxloci), iqtl(mxQTL)
dimension mkind(mxind,2,mxloci),ptind(mxind),err(mxind),tbv(mxind)
dimension izygoute(mxind,mxloci)
```

common /seed/ idum

common /simmodel/ iped(mxind,2),mkqtl(mxind,2,mxloci)

! Opening the parameter and output files

open(3,file='par.txt',status='old') !The genetic parameters file.

open(4,file='out.txt',status='old') !The output file of individuals markers alleles.

open(7,file='ped.txt', status='old') ! The pedigree file.

open(12,file='npgt_f.txt', status='old') ! The loci alleles of founder animals.

open(13,file='zygout.txt', status='old') !The marker genotypes and phenotypes.

open(9,file='error.txt',status='old') ! Error terms

open(10,file='t_breeding.txt',status='old') ! True breeding values

open(14,file='mkqtl.txt',status='old') ! Markers and QTLs

open (20,file='qtl_v.txt', status='old') ! variance caused by each QTL.

```
open (21,file='additive.txt', status='old') ! additive genetic effects of QTLs.
```

! Reading the requested parameters for the simulation process

```
read(3,*) n,nchr,nqtl,nloci ! animals, chromosomes, QTLs, and loci,  
respectively.  
read(3,*) (iqtl(i),i=1,nqtl) ! QTLs loci.  
read(3,*) (freq(i),i=1,nloci-1) ! recombination frequency between loci.  
read(7,*)n  
do i=1,n  
read(7,*) (iped(i,j),j=1,2) ! Reading the pedigree file  
end do
```

! Calling the subroutines for the output results in the form of genotypes of markers and phenotypes.

```
call iseed() ! random seed.  
call popgen(n,nloci,nqtl,iqtl,freq,mkind,err,tbv,ptind) ! population generation.  
call zygoute(n,nloci,mkind,izygoute) ! Marker genotypes.  
do i=1,n-359  
write(4,'(5000i2)') (mkind(i,1,j),j=1,5000)  
write(4,'(5000i2)') (mkind(i,2,j),j=1,5000)  
write(13,'(5000i2,2x,f8.4)') (izygoute(i,j),j=1,5000),ptind(i)  
write(9,'(f8.4)') err(i)  
write(10,'(f8.4)') tbv(i)  
end do  
call iexit()  
pause  
stop  
end
```

! Writing subroutine for generating alleles for the founders' genetic loci.

```
subroutine founder_gntp(nloci,freq,npgt) !To create the genotypes of all loci in  
the founders' animals.
```

```
implicit double precision (a-h,o-z)  
parameter (mxind=5000,mxloci=6000)
```

```

dimension npgt(mxind,2,mxloci),freq(mxloci) !All founder animals, diploid, all
genetic loci.

common /seed/ idum

common /simmodel/ iped(mxind,2),mkqtl(mxind,2,mxloci)

npgt=0

do i=1,359

do k=1,nloci

  x=unif()

  if (x.le.0.5d0) then

    npgt(i,1,k)=1

  else

    npgt(i,1,k)=0

  end if

  end do

do k=1,nloci

  x=unif()

  if (x.le.0.5d0) then

    npgt(i,2,k)=1

  else

    npgt(i,2,k)=0

  end if

  end do

end do

!!!!!!!!


```

! Writing a subroutine for generating the formed zygoute from the two alleles of each marker.

Subroutine zygoute(n,nloci,mkind,izygoute) !To create the zygoute (genotype) of the two alleles.

```

implicit double precision (a-h,o-z)

parameter (mxind=5000,mxloci=6000)

```

```

dimension mkind(mxind,2,mxloci), izygoute(mxind,mxloci)
common /simmodel/ iped(mxind,2), mkqtl(mxind,2,mxloci)
do i=1,n
  do j=1,nloci
    if(mkind(i,1,j).eq.mkind(i,2,j).and.mkind(i,1,j).eq.0)then
      izygoute(i,j)=0                                !homozygote for the recessive.
    elseif(mkind(i,1,j).eq.mkind(i,2,j).and.mkind(i,1,j).ne.0)then
      izygoute(i,j)=2                                !Homozygote is dominant.
    else
      izygoute(i,j)=1                                !Heterozygote.
    end if
  end do
end do
return
end
!!!!!!!

```

writing a subroutine for forming the individuals' gametes.

```

subroutine gametogenesis(nloci,ngt,freq,gamete)
! to generate simulated offspring population from two diploid parental genotypes
! at a defined number of linked loci with recombination frequencies freq(i) on
! a defined number of chromosomes.

```

```

implicit double precision (a-h,o-z)
parameter (mxind=5000,mxloci=6000,mxQTL=5000)
integer gamete(mxloci)
dimension freq(mxloci), ngt(2,mxloci)
common /seed/ idum
common /simmodel/ iped(mxind,2),mkqtl(mxind,2,mxloci)
gamete=0
x=unif()
if (x.le.0.5d0) then

```

```

ic=1
gamete(1)=ngt(1,1)
else
  ic=2
  gamete(1)=ngt(2,1)
end if

do i=2,nloci
  x=unif()
  if (x.le.freq(i-1)) then
    ic=2**2-ic
    gamete(i)=ngt(ic,i)
  else
    gamete(i)=ngt(ic,i)
  end if
end do

return
end
!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!

```

! A subroutine to calculate the additive and dominance genetic effects of QTLs

subroutine effects(nqtl,v_qtl,h,a,d,se) !nqtl=no.QTLs, v_qtl=contribution of each QTL to the total additive genetic variance, d_ratio=dminance degree, a=additive effect, d=dominance effect, h=d/2, se=environmental standard deviation.

```

implicit double precision (a-h,o-z)
parameter (mxind=5000,mxloci=6000,mxQTL=5000)
dimension v_qtl(mxQTL),h(mxQTL),a(mxQTL),d(mxQTL),vg(mxQTL)
read(20,*)(v_qtl(i),i=1,nqtl) !reading the contributions of each QTL to the total additive variance.
read(20,*)(h(i),i=1,nqtl) !reading the degree of dominance at each QTL.
h2=0.480d0 ! heritability estimate.

```

```

vg_total=0.0d0          ! Set the total genetic variance to zero to initiate the
summation of variances by all QTLs.

do i=1,nqtl

  a(i)=dsqrt(v_qtl(i)*h2/ ((1-(h(i)/2))**2/4+((h(i)/2)**2/2+(1+(h(i)/2))**2/4)))! to
calculate the additive effect.

  d(i)= a(i)*h(i)      ! to calculate the dominance effect.

  vg(i)=a(i)**2* ((1-(h(i)/2))**2/4+((h(i)/2)**2/2+(1+(h(i)/2))**2/4)) ! for linear
contrast.

  vg(i)=(((a(i)-h(i))**2)/4)+((h(i)**2)/2) +(((a(i)+h(i))**2)/4)! to calculate the
genetic variance for each QTL.

  vg_total= vg_total+vg(i) ! To sum up all the genetic variances of all the
QTLs.,

end do

ve=(1-h2)*vg_total/h2      !Environmental variance considering phenotypic
variance = 1.

se=dsqrt(ve)               ! The standard deviation of the environmental variance.

return

end

!!!!!!!!!!!!!!!!!!!!!!!!!!!!!!

```

! A subroutine for generating the population's animals.

```

subroutine popgen(n,nloci,nqtl,iqtl,freq,mkind,err,tbv,ptind)
implicit double precision (a-h,o-z)
parameter (mxind=5000,mxloci=6000,mxQTL=5000)
integer gamete(mxloci),offqtl(2,mxQTL)
dimension freq(mxloci),npgt(mxind,2,mxloci),iqtl(mxQTL)
dimension ngt1(2,mxloci),ngt2(2,mxloci)
dimension mkind(mxind,2,mxloci),ptind(mxind),err(mxind),tbv(mxind)
dimension(mxQTL),v_qtl(mxQTL),d_ratio(mxQTL),a(mxQTL),d(mxQTL)
,h(mxQTL)

!a = the additive effect of all QTLs; vg = the genetic variance contributed by each
QTL

common /simmodel/ iped(mxind,2),mkqtl(mxind,2,mxloci)
call founder_gntp(nloci,freq,npgt)      ! calling the alleles of each locus in the
founder animals

U = 32.45d0 Population's mean

```

```

call effects(nqtl,v_qtl,h,a,d,se) ! calling the genetic effects of QTLs.

mkqtl=0

mkqtl(:,:,:)=npgt(:,:, :)

DO i= 360,n ! Start generating phenotypes from animal 360, because from
1 to 359 are founder animals without phenotypes.

  isir=iped(i,1) ! Determine the animal's sire.

  idam=iped(i,2) ! Determine the animal's dam.

  if(isir.ne.0.and.idam.ne.0)then

    ngt1(:,:,:)=mkqtl(isir,:,:)
    ! Pick first allele from sire.

    ngt2(:,:,:)=mkqtl(idam,:,:)
    ! Pick second allele from dam

    else if(isir.eq.0 .and.idam.ne.0)then

      ngt1(:,:,:)=npgt(1,:,:)
      ngt2(:,:,:)=mkqtl(idam,:,:)
      ! Pick second allele from dam.

    else if(isir.ne.0 .and.idam.eq.0)then

      ngt1(:,:,:)=mkqtl(isir,:,:)
      ! Pick the first allele from sire

      ngt2(:,:,:)=npgt(1,:,:)

    else

      ngt1(:,:,:)=npgt(1,:,:)
      ngt2(:,:,:)=npgt(2,:,:)>

    end if

call gametogenesis(nloci,ngt1,freq,gamete) ! calling the gametes of the sire to
generate the zygote of offspring.

mkqtl(i,1,:)=gamete(:)

ic=0

it=1

do j=1,nloci

  if (j.ne.iqtl(it)) then

    ic=ic+1

    mkind(i-359,1,ic)=gamete(j)

  else

    offqtl(1,it)=gamete(j)

  end if

end do

```

```
it=it+1
```

```
end if
```

```
end do
```

```
call gametogenesis(nloci,ngt2,freq,gamete) ! calling the gametes of the dam to generate the zygote of offspring.
```

```
mkqtl(i,2,:)=gamete(:)
```

```
ic=0
```

```
it=1
```

```
do j=1,nloci
```

```
if (j.ne.iqtl(it)) then
```

```
    ic=ic+1
```

```
    mkind(i-359,2,ic)=gamete(j)
```

```
else
```

```
    offqtl(2,it)=gamete(j)
```

```
    it=it+1
```

```
end if
```

```
end do
```

! Calculation of QTL effects and breeding values.

```
eqtl=0.0d0 ! Set the initial value of QTL effects to zero for the summation process of all QTLs.
```

```
bv=0.0d0 ! Set the initial breeding value to zero for the summation process of all QTLs.
```

```
do j=1,nqtl ! Summation the effects of all 50 QTLs for all individuals
```

```
if(offqtl(1,j).eq.offqtl(2,j).and.offqtl(1,j).gt.0) then !AA Homozygote
```

```
    eqtl=eqtl+a(j)-d(j)/2 ! QTL effect
```

```
    bv=bv+a(j) ! Breeding value
```

```
else if(offqtl(1,j).eq.offqtl(2,j).and.offqtl(1,j).eq.0) then!aa Homozygote.
```

```
    eqtl=eqtl-a(j)-d(j)/2 ! QTL effect
```

```
    bv=bv-a(j) ! Breeding value
```

```
else
```

```
    eqtl=eqtl ! QTL effect ! Heterozygote.
```

```

bv = bv           ! Breeding value
end if
end do
e=gauss(0.0d0,se) !Error terms follow normal distribution with mean = 0 and
variance.
ptind(i-359)=u+eqtl+e !Phenotype = population mean deviated by genetic merit
(qtl) and environment.

write(14,'(5050i2,2x,f8.4)')(mkqtl(i,2,j),j=1,nloci),ptind(i-359)
END DO
return
end

```

Appendix (B)

Verification of marker alleles and their corresponding genotypes

A screen shot of the simulation output for the marker alleles (0 for recessive and 1 for dominant) for the first 5 animals (each with two rows for the marker alleles, and 10 columns for the last 10 markers of total 5,000 markers), for the trait of W12 in Omani sheep.

1	0	1	1	1	0	1	0	1	1
1	1	0	1	1	1	0	1	1	0
1	0	1	1	1	0	1	0	1	1
1	0	0	0	1	1	0	0	1	0
0	1	0	0	0	1	1	1	0	0
0	0	1	1	1	1	1	1	0	1
0	0	0	1	0	1	1	0	1	0
0	1	0	0	1	0	0	0	1	0
0	0	0	0	1	0	0	1	1	0
1	0	1	1	0	1	1	1	1	0

A screen shot of the simulation output for the marker genotypes for the first 5 animals, along with their simulated phenotypes (Last column) for the trait of W12 in Omani sheep. It contains the last 10 marker genotypes of the total 5,000 markers. Codes 0, 1, and 2 are for recessive homozygous, heterozygous, and dominant homozygous.

2	1	1	2	2	1	1	1	2	1	31.8626
2	0	1	1	2	1	1	0	2	1	32.2876
0	1	1	1	1	2	2	2	0	1	32.8302
0	1	0	1	1	1	1	0	2	0	32.5796
1	0	1	1	1	1	1	2	2	0	32.5813

For example: for the first animal, the marker alleles from (1) are as follows:

1	0	1	1	1	0	1	0	1	1
1	1	0	1	1	1	0	1	1	0

And the resulted markers genotypes would be as the first two of (2)

2	1	1	2	2	1	1	1	2	1
---	---	---	---	---	---	---	---	---	---

The output file shows the proportionate variance contributed by each QTL of the simulated 50 QTLs to the total genetic variance.

0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.20	0.01	0.01	0.01
0.01	0.01	0.01	0.01	0.01	0.10	0.01	0.01	0.01	0.01	0.01
0.01	0.01	0.01	0.10	0.02	0.02	0.02	0.02	0.02	0.02	0.02
0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
!proportional variance explained by the QTL of total genetic variance										

For example, for the trait of W12 ($h^2 = 0.48$), the additive genetic effects (a) caused by the highlighted QTLs would be as follows:

$$1. a_{QTL_{0.01}} = \sqrt{2(V_{QTL_{0.01}})} = \sqrt{2(0.01 \times 0.48)} = 0.0980$$

$$2. a_{QTL_{0.20}} = \sqrt{2(V_{QTL_{0.20}})} = \sqrt{2(0.20 \times 0.48)} = 0.4382$$

$$3. a_{QTL_{0.10}} = \sqrt{2(V_{QTL_{0.10}})} = \sqrt{2(0.10 \times 0.48)} = 0.3098$$

These effects match the output of the simulation, as shown in the following:

0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.4382	
0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.3098	0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.0980	0.3098	0.1386
0.1386	0.1386	0.1386	0.1386	0.1386	0.1386	0.1386	0.1386	0.1386	0.1386	0.1386	0.1386	0.1386	0.1386	0.1386	0.1386	

Appendix (C)

Checking simulated heritability of W12 trait by WOMBAT analysis

WOMBAT analysis, which illustrates that it got estimates almost as similar as those simulated for the trait of W12 by analysing the simulated phenotypes. It was simulated that heritability equals 0.48, and the WOMBAT estimate was 0.49.

```
***** Estimates of residual covariances *****  
Order of fit = 1  
Covariance matrix  
1 0.51683  
Matrix of correlations and variance ratios  
1 0.5060  
Covariances & correlations with approximate sampling errors  
1 COVS Z 1 1 0.516827 0.300562E-01 vrat 0.506 0.036  
  
***** Estimates for RE 1 "ANIMAL" *****  
No. of levels = 3541  
Covariance structure = NRM  
Order of fit = 1  
Covariance matrix  
1 0.50450  
Matrix of correlations and variance ratios  
1 0.4940  
Covariances & correlations with approximate sampling errors  
2 COVS A 1 1 0.504498 0.479744E-01 vrat 0.494 0.036  
  
***** Estimates of phenotypic covariances *****  
Covariance matrix  
1 1.0213  
Covariances & correlations with approximate sampling errors  
3 COVS T 1 1 1.02133 0.316496E-01  
  
===== end of file ======17-03-2024=====13:33=====
```

Appendix (D)

Importance of non-genetic factors along with least square means that influencing growth traits of Omani goats and sheep breeds.

Table D. 1. Significance of non-genetic factors and least squares means (LSM) in kg of growth traits in Omani Jebel Akhdar goats.

BW (birth weight), **WW** (weaning weight), **W6** (Six-months weight), **W12** (Yearling weight). **R²** (Coefficient of model), **CV** (Coefficient of variation), Factors that its levels do not share a letter in Group column are significantly different.

Trait	BW			WW			W6			W12		
	N	LSM ± SE	Group	N	LSM ± SE	Group	N	LSM ± SE	Group	N	LSM ± SE	Group
Overall	2,826	3.16 ± 0.01		2,342	13.27 ± 0.07		1,706	16.30 ± 0.09		1,265	26.85 ± 0.17	
R ²	34.77%			39.94%			44.29%			63.83%		
CV	18.93%			25.65%			21.59%			21.99%		
Pen	P-value = 0.000			P-value = 0.04			P-value = 0.09			P-value = 0.07		
1	208	3.06 ± 0.03	B	180	13.08 ± 0.20	AB	138	16.43 ± 0.23	A	98	27.05 ± 0.37	AB
2	212	3.12 ± 0.03	AB	177	13.47 ± 0.20	AB	131	16.49 ± 0.24	A	100	27.56 ± 0.37	AB
3	225	3.19 ± 0.03	AB	182	13.24 ± 0.20	AB	123	15.81 ± 0.25	A	89	27.76 ± 0.40	AB
4	204	3.19 ± 0.03	AB	149	12.94 ± 0.22	AB	107	15.5 ± 0.26	A	62	27.35 ± 0.48	AB
5	216	3.21 ± 0.03	AB	183	13.29 ± 0.20	AB	132	16.23 ± 0.24	A	99	27.17 ± 0.38	AB
6	182	3.12 ± 0.04	AB	155	13.20 ± 0.22	AB	112	16.32 ± 0.26	A	89	27.47 ± 0.40	AB
7	215	3.22 ± 0.03	AB	170	12.49 ± 0.21	B	116	16.36 ± 0.25	A	90	28.37 ± 0.40	A
8	198	3.29 ± 0.04	A	154	13.63 ± 0.22	A	106	16.54 ± 0.27	A	71	27.63 ± 0.45	AB
9	201	3.12 ± 0.03	B	173	13.33 ± 0.21	AB	135	15.64 ± 0.23	A	101	26.27 ± 0.37	B
10	214	3.14 ± 0.03	AB	181	13.05 ± 0.20	AB	140	16.03 ± 0.23	A	106	27.21 ± 0.36	AB
11	212	3.11 ± 0.03	B	180	13.05 ± 0.20	AB	119	16.15 ± 0.25	A	87	27.66 ± 0.40	AB
12	198	3.22 ± 0.04	AB	173	13.01 ± 0.21	AB	126	16.31 ± 0.24	A	96	27.62 ± 0.38	AB
13	115	3.13 ± 0.05	AB	97	13.40 ± 0.28	AB	76	16.42 ± 0.32	A	55	27.22 ± 0.51	AB
14	92	3.01 ± 0.06	B	78	12.56 ± 0.31	AB	61	16.05 ± 0.35	A	52	26.35 ± 0.52	AB
15	99	3.21 ± 0.05	AB	80	12.90 ± 0.31	AB	65	16.58 ± 0.34	A	56	27.43 ± 0.51	AB
16	35	3.24 ± 0.09	AB	30	13.16 ± 0.51	AB	19	16.15 ± 0.65	A	14	27.79 ± 1.04	AB

Sex	P-value = 0.000			P-value = 0.000			P-value = 0.000			P-value = 0.000		
Male	1,390	3.34 ± 0.01	A	1,142	13.83 ± 0.09	A	819	17.03 ± 0.11	A	578	29.52 ± 0.19	A
Female	1,436	2.98 ± 0.01	B	1,200	12.39 ± 0.09	B	887	15.35 ± 0.11	B	687	25.21 ± 0.17	B
Year	P-value = 0.000			P-value = 0.000			P-value = 0.000			P-value = 0.000		
2008	270	3.24 ± 0.03	B	226	13.27 ± 0.20	BCD	129	19.53 ± 0.25	A	79	26.44 ± 0.56	EFG
2009	183	3.21 ± 0.04	BC	177	14.13 ± 0.22	AB	173	17.51 ± 0.22	B	106	25.72 ± 0.41	FG
2010	185	3.53 ± 0.04	A	180	13.46 ± 0.21	BCD	172	15.96 ± 0.21	C	105	23.62 ± 0.38	HI
2011	216	3.08 ± 0.03	CDE	193	13.05 ± 0.20	CDE	170	13.35 ± 0.21	F	102	22.41 ± 0.38	IJ
2012	188	3.02 ± 0.04	DE	163	12.72 ± 0.23	DEF	146	13.44 ± 0.25	F	107	20.99 ± 0.40	J
2013	229	2.84 ± 0.04	F	181	11.99 ± 0.22	F	166	14.87 ± 0.24	D	165	27.66 ± 0.33	DE
2014	244	3.28 ± 0.03	B	201	14.04 ± 0.20	AB	131	14.69 ± 0.26	DE	129	24.37 ± 0.35	GH
2015	251	3.16 ± 0.03	BCD	219	13.76 ± 0.19	ABC	162	16.84 ± 0.22	BC	158	26.74 ± 0.31	EF
2016	225	2.98 ± 0.03	EF	119	10.26 ± 0.26	G	54	13.21 ± 0.41	EF	52	29.14 ± 0.57	D
2017	250	3.24 ± 0.03	B	190	12.59 ± 0.20	DEF	185	16.91 ± 0.21	BC	68	33.78 ± 0.58	B
2018	189	3.23 ± 0.04	BC	179	14.50 ± 0.22	A	90	20.10 ± 0.29	A	89	36.10 ± 0.41	A
2019	184	3.02 ± 0.04	DE	144	12.07 ± 0.23	EF	128	17.88 ± 0.24	B	105	31.44 ± 0.37	C
2020	212	3.27 ± 0.04	B	170	14.61 ± 0.25	A						
Birth type	P-value = 0.000			P-value = 0.000			P-value = 0.000			P-value = 0.000		
Single	1,446	3.38 ± 0.02	A	1,226	14.8 ± 0.09	A	985	17.17 ± 0.10	A	752	28.01 ± 0.18	A
Twin	1,380	2.94 ± 0.02	B	1,116	11.43 ± 0.09	B	721	15.21 ± 0.12	B	513	26.73 ± 0.19	B
Dam age	P-value = 0.000			P-value = 0.000			P-value = 0.45			P-value = 0.16		
Regression coefficient	0.07 ± 0.02			0.19 ± 0.03			0.03 ± 0.04			-0.09 ± 0.06		

Table D. 2. Significance of non-genetic factors and least squares means (LSM) in kg of growth traits in Omani Batinah goats.

BW (birth weight), **WW** (weaning weight), **W6** (Six-months weight), **W12** (Yearling weight). **R²** (Coefficient of model), **CV** (Coefficient of variation), Factors that its levels do not share a letter in Group column are significantly different.

Trait	BW			WW			W6			W12		
	N	LSM ± SE	Group	N	LSM ± SE	Group	N	LSM ± SE	Group	N	LSM ± SE	Group
Overall	2,609	3.20 ± 0.01		2,186	12.81 ± 0.07		1,689	15.88 ± 0.08		1,208	25.71 ± 0.15	
R ²	33.47%			37.79%			44.12%			59.05%		
CV	18.65%			27.12%			21.56%			20.80%		
Pen	P-value = 0.04			P-value = 0.000			P-value = 0.19			P-value = 0.35		
1	186	3.09 ± 0.04	A	151	12.09 ± 0.23	AB	117	15.43 ± 0.26	A	81	25.71 ± 0.40	A
2	202	3.12 ± 0.04	A	176	12.08 ± 0.22	AB	132	15.15 ± 0.24	A	79	26.19 ± 0.41	A
3	188	3.12 ± 0.04	A	156	11.95 ± 0.24	AB	114	14.90 ± 0.28	A	73	26.76 ± 0.43	A
4	190	3.07 ± 0.04	A	157	11.49 ± 0.24	B	111	15.20 ± 0.28	A	79	26.06 ± 0.41	A
5	186	3.22 ± 0.04	A	163	12.81 ± 0.23	A	130	15.17 ± 0.25	A	89	25.98 ± 0.39	A
6	191	3.18 ± 0.04	A	157	12.73 ± 0.23	A	120	15.71 ± 0.25	A	87	26.75 ± 0.40	A
7	186	3.15 ± 0.04	A	150	12.01 ± 0.24	AB	112	15.46 ± 0.27	A	77	25.91 ± 0.41	A
8	190	3.17 ± 0.04	A	145	12.33 ± 0.24	AB	114	15.04 ± 0.26	A	79	25.77 ± 0.41	A
9	211	3.12 ± 0.03	A	172	12.18 ± 0.22	AB	121	15.58 ± 0.25	A	83	26.37 ± 0.40	A
10	209	3.12 ± 0.03	A	184	12.60 ± 0.21	A	145	15.56 ± 0.23	A	112	25.68 ± 0.34	A
11	189	3.14 ± 0.04	A	162	12.37 ± 0.24	AB	126	15.84 ± 0.26	A	99	26.11 ± 0.37	A
12	192	3.19 ± 0.04	A	160	12.76 ± 0.23	A	133	15.68 ± 0.24	A	91	26.79 ± 0.38	A
13	105	3.09 ± 0.05	A	93	12.69 ± 0.35	AB	81	15.58 ± 0.36	A	71	26.07 ± 0.44	A
14	106	3.04 ± 0.05	A	96	12.75 ± 0.33	AB	83	15.33 ± 0.33	A	71	26.24 ± 0.43	A
15	78	3.25 ± 0.06	A	64	13.48 ± 0.40	A	50	16.26 ± 0.45	A	37	27.16 ± 0.60	A
Sex	P-value = 0.000			P-value = 0.000			P-value = 0.000			P-value = 0.000		
Male	1,302	3.36 ± 0.02	A	1,092	13.35 ± 0.10	A	852	16.29 ± 0.11	A	559	28.54 ± 0.19	A
Female	1,307	2.92 ± 0.02	B	1,094	11.49 ± 0.09	B	837	14.63 ± 0.11	B	649	23.94 ± 0.16	B
Year	P-value = 0.000			P-value = 0.000			P-value = 0.000			P-value = 0.000		
2008	270	3.19 ± 0.03	B	231	12.87 ± 0.19	B	133	19.23 ± 0.24	A	75	28.53 ± 0.45	BC
2009	183	3.14 ± 0.04	BCD	204	11.80 ± 0.22	C	195	15.98 ± 0.22	C	114	24.23 ± 0.36	EF

2010	185	3.40 ± 0.04	A	180	12.08 ± 0.26	BC	174	14.93 ± 0.25	CDE	114	22.40 ± 0.58	FG
2011	216	3.01 ± 0.04	CDE	172	12.04 ± 0.24	BC	151	13.29 ± 0.25	F	90	22.13 ± 0.45	G
2012	188	3.04 ± 0.06	BCDE	69	11.71 ± 0.38	BC	59	13.26 ± 0.39	F	47	21.49 ± 0.58	G
2013	229	2.97 ± 0.06	DE	175	11.75 ± 0.35	BC	149	14.34 ± 0.34	DEF	149	25.79 ± 0.46	DE
2014	244	3.20 ± 0.03	B	177	12.52 ± 0.23	BC	146	13.31 ± 0.23	F	137	22.62 ± 0.32	G
2015	251	3.18 ± 0.03	B	224	12.89 ± 0.19	B	175	15.52 ± 0.21	CD	174	24.57 ± 0.27	E
2016	225	2.93 ± 0.04	E	112	9.84 ± 0.29	D	64	13.83 ± 0.46	EF	64	26.84 ± 0.61	CD
2017	250	3.23 ± 0.03	AB	205	13.04 ± 0.20	B	205	17.77 ± 0.19	B	75	33.84 ± 0.54	A
2018	189	3.22 ± 0.04	AB	158	14.50 ± 0.23	A	89	18.95 ± 0.30	A	88	32.85 ± 0.40	A
2019	184	3.09 ± 0.04	BCDE	159	12.23 ± 0.23	BC	149	15.08 ± 0.23	CDE	81	29.55 ± 0.40	B
2020	212	3.20 ± 0.04	ABC	120	14.20 ± 0.27	A						
Birth type	P-value = 0.000			P-value = 0.000			P-value = 0.000			P-value = 0.000		
Single	1,543	3.37 ± 0.01	A	1,314	14.10 ± 0.09	A	1,084	16.58 ± 0.09	A	798	26.96 ± 0.16	A
Twin	1,066	2.91 ± 0.02	B	872	10.75 ± 0.12	B	605	14.34 ± 0.14	B	410	25.51 ± 0.22	B
Dam age	P-value = 0.000			P-value = 0.000			P-value = 0.001			P-value = 0.63		
Regression coefficient	0.06 ± 0.01			0.18 ± 0.03			0.11 ± 0.03			0.03 ± 0.06		

Table D. 3. Significance of non-genetic factors and least squares means (LSM) in kg of growth traits in Omani sheep.

BW (birth weight), **WW** (weaning weight), **W6** (Six-months weight), **W12** (Yearling weight). **R²** (Coefficient of model), **CV** (Coefficient of variation), Factors that its levels do not share a letter in Group column are significantly different.

Trait	BW			WW			W6			W12		
	N	LSM ± SE	Group	N	LSM ± SE	Group	N	LSM ± SE	Group	N	LSM ± SE	Group
Overall	3,530	3.04 ± 0.01		3,120	14.38 ± 0.07		2,374	20.03 ± 0.09		1,745	32.45 ± 0.14	
R ²	35.40%			33.91%			34.92%			45.56%		
CV	22.10%			27.22%			21.12%			18.46%		
Pen	P-value = 0.13			P-value = 0.04			P-value = 0.46			P-value = 0.35		
1	240	2.84 ± 0.05	A	210	13.61 ± 0.24	A	145	20.02 ± 0.30	A	101	32.99 ± 0.49	A
2	229	2.86 ± 0.05	A	203	13.71 ± 0.24	A	159	19.58 ± 0.29	A	104	33.14 ± 0.48	A
3	235	2.94 ± 0.05	A	208	13.40 ± 0.24	A	143	19.21 ± 0.30	A	99	32.18 ± 0.49	A
4	219	2.89 ± 0.06	A	199	13.26 ± 0.25	A	139	19.38 ± 0.31	A	98	32.88 ± 0.50	A
5	220	2.81 ± 0.07	A	197	13.51 ± 0.25	A	136	19.70 ± 0.31	A	94	33.16 ± 0.51	A
6	225	2.97 ± 0.06	A	200	13.47 ± 0.25	A	150	19.35 ± 0.30	A	116	32.85 ± 0.47	A
7	229	2.86 ± 0.05	A	199	13.49 ± 0.25	A	153	19.27 ± 0.29	A	120	32.21 ± 0.46	A
8	232	2.81 ± 0.06	A	206	13.04 ± 0.24	A	154	19.20 ± 0.29	A	109	33.13 ± 0.47	A
9	231	2.89 ± 0.06	A	205	13.57 ± 0.24	A	149	19.40 ± 0.30	A	112	32.96 ± 0.46	A
10	244	2.78 ± 0.06	A	222	13.69 ± 0.24	A	180	19.31 ± 0.27	A	139	32.68 ± 0.43	A
11	234	2.88 ± 0.05	A	206	13.66 ± 0.24	A	164	18.96 ± 0.28	A	119	31.40 ± 0.46	A
12	240	2.81 ± 0.06	A	208	13.61 ± 0.24	A	163	19.05 ± 0.28	A	118	32.06 ± 0.46	A
13	245	2.88 ± 0.09	A	220	13.37 ± 0.24	A	164	19.09 ± 0.29	A	119	32.91 ± 0.46	A
14	138	3.08 ± 0.07	A	122	13.32 ± 0.31	A	107	18.79 ± 0.35	A	79	31.62 ± 0.55	A
15	154	3.02 ± 0.10	A	130	14.01 ± 0.31	A	116	19.15 ± 0.34	A	81	31.48 ± 0.55	A
16	95	2.84 ± 0.12	A	86	14.29 ± 0.36	A	64	19.07 ± 0.44	A	52	31.43 ± 0.67	A
17	67	2.87 ± 0.09	A	59	14.58 ± 0.44	A	52	18.87 ± 0.49	A	49	30.48 ± 0.70	A
18	53	2.88 ± 0.10	A	40	14.98 ± 0.53	A	36	18.51 ± 0.60	A	36	31.69 ± 0.81	A

Sex	P-value = 0.000			P-value = 0.000			P-value = 0.000			P-value = 0.000		
Male	1,845	2.99 ± 0.02	A	1,636	14.36 ± 0.14	A	1,232	20.25 ± 0.15	A	843	34.95 ± 0.28	A
Female	1,685	2.78 ± 0.02	B	1,484	13.04 ± 0.14	B	1,142	18.19 ± 0.15	B	902	29.63 ± 0.27	B
Year	P-value = 0.000			P-value = 0.000			P-value = 0.000			P-value = 0.000		
2008	294	2.98 ± 0.06	ABCD	268	14.35 ± 0.33	ABCD	173	21.07 ± 0.28	B	120	32.30 ± 0.58	CD
2009	261	3.11 ± 0.07	AB	253	13.40 ± 0.41	BCDE	242	19.00 ± 0.24	DE	121	30.82 ± 0.65	DE
2010	219	3.23 ± 0.06	A	219	14.95 ± 0.32	AB	210	20.21 ± 0.26	BC	157	29.93 ± 0.54	DEF
2011	152	2.62 ± 0.10	DEF	137	13.07 ± 0.38	CDE	133	15.96 ± 0.33	G	81	28.23 ± 0.79	EF
2012	269	3.00 ± 0.07	ABCD	237	12.89 ± 0.35	DE	216	16.43 ± 0.25	G	161	26.98 ± 0.73	F
2013	233	2.35 ± 0.09	F	184	12.54 ± 0.56	CDE	154	18.63 ± 0.31	DEF	152	30.98 ± 1.13	CDEF
2014	327	3.11 ± 0.06	AB	301	13.83 ± 0.32	BCDE	267	18.17 ± 0.23	EF	261	30.65 ± 0.50	DE
2015	351	3.00 ± 0.05	ABC	335	14.42 ± 0.26	ABC	223	20.73 ± 0.24	BC	219	31.96 ± 0.46	CD
2016	259	2.75 ± 0.06	DE	149	13.37 ± 0.65	ABCDE	70	17.21 ± 0.42	FG	70	37.04 ± 1.16	AB
2017	316	2.94 ± 0.04	BCD	292	14.34 ± 0.22	ABC	288	20.81 ± 0.22	B	86	37.04 ± 0.66	A
2018	270	2.91 ± 0.05	BCD	253	15.41 ± 0.28	A	173	22.58 ± 0.28	A	171	37.34 ± 0.55	A
2019	286	2.70 ± 0.05	E	244	12.61 ± 0.28	E	225	19.78 ± 0.25	CD	146	34.23 ± 0.57	BC
2020	293	2.78 ± 0.05	CDE	248	12.92 ± 0.29	DE						
Birth type	P-value = 0.000			P-value = 0.000			P-value = 0.000			P-value = 0.000		
Single	1,396	3.39 ± 0.02	A	1,245	16.57 ± 0.10	A	982	21.37 ± 0.12	A	732	34.27 ± 0.22	A
Twin	1,867	2.87 ± 0.01	B	1,656	13.05 ± 0.09	B	1,224	18.76 ± 0.11	B	904	31.99 ± 0.17	B
Multiple	267	2.40 ± 0.04	C	219	11.48 ± 0.28	C	168	17.52 ± 0.27	C	104	30.62 ± 0.55	C
Dame age	P-value = 0.000			P-value = 0.81			P-value = 0.34			P-value = 0.06		
Regression coefficient	0.04 ± 0.01			-0.01 ± 0.03			-0.04 ± 0.04			-0.12 ± 0.06		