

Estimation of genetic parameters for growth and wool traits in South African Merino sheep

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Abstract

The estimation of genetic parameters allows for the accurate prediction of estimated breeding values (EBVs), which play a crucial role in developing selection indices used to generate genetic progress for economically important traits. This study aimed to estimate genetic parameters and EBVs for the South African Merino sheep breed. A population of 864 754 South African Merino sheep were included in this study. Pedigree information included animals born between 1919 and 2022, of which 457 757 (52.94%) were females and 406 996 (47.06%) were males. Variance components were estimated for all sheep born after 2009, consisting of 62 460 sheep. A multi-trait animal model was used to estimate the variance components, using VCE6 statistical software. Heritability values and standard errors were estimated for seven traits: direct weaning weight (0.25 ± 0.01), maternal weaning weight (0.20 ± 0.00), body weight at wool test (0.26 ± 0.01), clean fleece weight (0.33 ± 0.01), staple length (0.33 ± 0.00), fibre diameter (0.63 ± 0.00), and coefficient of variation of fibre diameter (0.43 ± 0.00). Using the same genetic models as used for variance component estimation, EBVs were predicted using PEST2. Genetic trends were determined by averaging the EBVs of the measured animals per year of birth per trait, and these were compared to the national trends provided by SA Stud Book. This study updates the variance components and EBVs of the South African Merino sheep breed, enabling the accurate genetic selection of animals and facilitating faster genetic progress.

Keywords: genetic trends, heritability estimates, multi-trait animal models, wool

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Introduction

The Merino and Merino-derived sheep breeds are widely spread across the globe and represent an economically important genetic resource (Ciani *et al.*, 2015). The initial expansion of the Merino breed began in the 19th century in northern Europe, with later further expansion into other countries and continents, including South Africa, Australia, and North America, through the use of both direct selection and cross-breeding with native sheep breeds (Diez-Tascon *et al.*, 2000). Merino South Africa was established in 1937 to represent all South African Merino sheep breeders, and is still the official organisation for the management and communication of the Merino industry (Merino South Africa, 2023). The modern Merino is a dual-purpose breed, producing wool and mutton, and is able to adapt to

and produce in the varying, harsh climates and weather conditions that are common to South Africa (Granero *et al.*, 2022). It has also been used as the basis for the development of various South African composite breeds, including the Dormer and Dohne Merino (Ciani *et al.*, 2015).

The South African national sheep population peaked in 2013 at 24.5 million sheep (Statista, 2023), but has generally followed a decreasing trend, declining by 500 000 head from 22.09 million in 2019 to 21.6 million in 2020 (Statista, 2023). The number of South African Merino sheep has also decreased, declining from 9.9 million sheep in 2020 to 9.7 million sheep in 2021 (Department of Agriculture, Forestry & Fisheries, 2022). This decrease in the South African sheep population is mainly owing to ongoing pressure from drought, stock theft, and predation (Department of Agriculture, Land Reform and Rural Development, 2021). The small stock industry contributes 8% to 10% of total animal product income, with the bulk of this income derived from meat and then wool (Zenda *et al.*, 2023).

Sheep production in South Africa plays a key role in the livelihoods of rural communities as it provides food security, employment, and a source of income, and is also a cheap source of manure for crop production (Nyam *et al.*, 2020). There are roughly 8000 commercial sheep farms and 5800 communal farmers throughout South Africa (Department of Agriculture, Land Reform and Rural Development, 2021). Sheep farming contributes to sustainable production in extensive pastoral areas, particularly where no alternative production can be practiced – for example, in the vast, climatically extreme Karoo region forming part of central South Africa (Cloete *et al.*, 2014). The majority of Merino sheep farming in South Africa occurs in the dry western and central districts located in mainly the Northern Cape, Free State, and Eastern Cape provinces (Cloete, 2010). The South African Merino breed plays a significant role in both the meat and wool industries because of its ability to thrive in highly diverse and harsh environments (Granero *et al.*, 2022). Historically, emphasis was primarily placed on wool production; however, owing to the increase in the price of lamb and mutton, the Merino was developed into a more balanced, dual-purpose breed with meat production being considered, along with wool traits (Cloete *et al.*, 2004).

Small stock selection practices and improvement services have undergone several changes in response to fluctuations in demand, as well as with the development of advanced statistical and technological procedures (Schoeman *et al.*, 2010). Rapid progress is being made in data capturing, resulting in the genetic evaluation of the South African Merino becoming increasingly efficient and accurate, allowing for fast genetic progress (Cloete *et al.*, 2014). Continuous scientific and statistical developments are providing further advancements in animal breeding, including progress in estimating the true genetic merit of livestock using estimated breeding values (EBVs) (Koopae & Koshkoiyeh, 2014). Accurately estimating breeding values is imperative as it influences the response to selection and the potential genetic gain a breeding programme can achieve, and it reflects the risk of whether or not an EBV will change over time when more information becomes available (Bijma, 2012). In the future, sheep farming is expected to become an increasingly important meat industry because of increased population demand for livestock-derived foods, as well as the ability of sheep to adapt to varying climates (Gowane *et al.*, 2017). Therefore, in order to develop efficient breeding programmes that allow for rapid genetic progress, accurate genetic parameters and EBVs are essential (Safari *et al.*, 2005).

There is limited recent scientific literature available that provides updated variance components for the South African Merino sheep population. No new variance components have been published for the South African Merino sheep breed in the past decade, despite ongoing changes in breeding practices and environmental pressures, and improvements in data recording. Accurate estimation of variance components is essential to ensure the reliability of EBVs, which directly influence selection decisions and the rate of genetic progress. Therefore, this study aimed to update the genetic parameters and EBVs for key wool and growth traits in the South African Merino population.

Materials and methods

Pedigree and performance data for the South African Merino sheep breed were obtained from SA Stud Book with the required consent of the South African Merino Breeders Association. Data included a selection of routinely recorded growth and wool measurements, including weaning weight (WW, kg), body weight at wool test (BWW, kg), clean fleece weight (CFW, kg), fibre diameter (FD, μm), coefficient of variation of fibre diameter (CVFD, %), and staple length (SL, mm). Data were obtained from official wool tests and analysed by the Wool Testing Bureau in Gqeberha. Ethical approval for the use of

secondary data was obtained from the Ethics Committee of the Faculty of Natural and Agricultural Sciences at the University of Pretoria (reference number: NAS144/2023).

The population of South African Merino sheep included in this study consisted of 864 754 sheep, of which 457 757 (52.94%) were females and 406 996 (47.06%) were males. The pedigree information included animals born between 1919/07/20 and 2023/05/29. Dams were known for 658 787 sheep (76.18%), and sires were known for 603 605 (69.80%) sheep. Both parents (sire and dam) were known for 578 839 (66.94%) sheep, while both parents were unknown for 181 201 (20.95%) sheep. The sheep used in this study originated from 298 breeders. Most contemporary groups were connected because breeders consciously used reference sires to link different contemporary groups. Some artificial insemination sires used in the industry over the years were included in this study, which resulted in ample genetic linkages across contemporary groups.

Traits for which variance components were estimated were WW, BWV, SL, CFW, FD, and CVFD. The numbers of records, unique dams and sires, and flocks for weight and wool traits are summarised in Table 1.

Table 1 The numbers of records, unique dams and sires, and flocks for each trait measured for the South African Merino sheep breed

Trait	Number of records	Number of dams	Number of sires	Number of flocks
Weaning weight (kg)	581 242	175 629	6874	175
Body weight at wool test (kg)	457 233	27 171	2818	91
Clean fleece weight (kg)	517 319	27 115	2790	92
Fibre diameter (µm)	471 941	27 264	2837	93
Coefficient of variation of fibre diameter (%)	458 303	25 043	2350	87
Staple length (mm)	459 303	27 181	2739	92

The datasets were imported into the R Studio statistical software program (RStudio Team, 2020) for data editing and manipulation, and statistical analyses. Datasets were filtered to exclude all animals with no WW measurements or incomplete records. Records with unknown dams, animals that were hand-reared, and lambs produced from embryo transfer were removed and excluded from the analysis. The dataset was then cleaned by checking for and removing any duplicated records. Using the accepted production norms for South African Merino sheep that are applied in the Logix National Genetic Evaluation of SA Stud Book (i.e. 10–80 kg for WW, 30–150 days for age at weaning, and 10–96 months for age of dam), the biological limits of these traits were assessed for implementation during the editing of the data. The confidence intervals at a 95% level were determined. Adjusting to two standard deviations from the mean, sheep that had WWs outside the range of 11–44 kg, sheep outside the range of 35–182 days of age at weaning, and records where dams had ages outside the range of 19–71 months were removed.

Accepted production norms for phenotypic indices for the South African Merino sheep breed applied in the Logix National Genetic Evaluation of SA Stud Book (i.e. 50–160 kg for BWV, 45–170 kg for CFW, 60–140 µm for FD, 50–170 mm for SL, 260–900 days for age at shearing, and 150–540 days for length of test) were also applied during the editing of the wool traits.

Environmental effects that significantly influence the traits of interest were identified in order to construct contemporary groups and to allow for the adjustment for differences of these effects in the model when estimating the variance components for the traits. This was done by analysis of variance (ANOVA), using R at a significance level of 0.05.

The following model was implemented:

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

where: y = economic trait of interest,

fixed effects = categorical effects such as sex and breeder, and

covariate functions = continuous functions such as age at weighing.

For WW, the environmental effects tested for in the ANOVA model included the farm where the animal was weaned, the year of weaning, the sex of the animal, the birth status (born as a single, twin, triplet, or quadruplet lamb), the rearing status (reared as a single, twin, triplet, or quadruplet lamb), the age at weaning in days (tested for as linear and quadratic regressions), the age of the dam as a categorical trait (three levels: 1 = <30 months, 2 = 30–60 months, and 3 = >60 months), or the age of the dam in months (tested as a linear or quadratic regression). An environmental code (allocated by the farmer to indicate pasture/feeding differences between lambs weaned in the same contemporary group), management code (allocated by the farmer to indicate differences in management between lambs weaned in the same contemporary group), season (two or three seasons per year), and reference number (number of the weaning test in which the lamb was measured for WW) were also included as environmental effects in the ANOVA model.

For WW, the age of the dam was fitted as a continuous variable as it achieved a higher R^2 value than the dam age code, which was fitted as a class effect. The construction of the contemporary groups was as follows: As the reference number of the weaning test already indicated which lambs were weighed together, it was concatenated with the farm to ensure that the reference number was linked to the relevant farm. Furthermore, the environmental and management codes were also included in the concatenation, so that the contemporary group included all lambs that were reared together in the same environment and subjected to the same management procedures.

For wool traits, the environmental effects tested for significance with ANOVA included farm of measurement, year of measurement, age at wool test, age of the dam as a categorical effect, age of the dam in months as a continuous variable, and rearing status. The environmental and group codes (allocated by the farmer for animals within the same contemporary groups that were subjected to different pasture, feeding, or management regimes), season, and reference number of the wool test were also tested for their significance. As rams and ewes always participate in different wool tests, no adjustment for sex differences within a contemporary group was required for inclusion in the genetic model.

Variance components were estimated using multi-trait animal models that included the environmental effects that significantly influenced the data as fixed or continuous effects, as well as random permanent environmental and sire $\times$ herd effects, depending on the trait. Regarding the genetic effects, both direct and maternal genetic effects were included. A pedigree depth of three generations was used. Variance components were estimated using the VCE6 package (Groeneveld *et al.*, 2010) based on REML methods.

The dataset used for variance component estimation included all traits evaluated in this study, as well as the significant environmental effects and contemporary groups. The dataset only included animals born between 2009 and 2022 to ensure that relevant and reliable estimates were produced based on recent generations. The dataset and pedigree file were initially processed using PEST software (Groeneveld, 2019) for recoding. The recoded dataset and pedigree file were then applied in the VCE6 package (Groeneveld *et al.*, 2010) for variance component estimation. Before conducting the multi-trait evaluation, variance components were estimated for each trait separately, followed by all bi-trait combinations, after which a multi-trait evaluation including all traits was performed. The genetic models used for the multi-trait variance component estimation of the weight and wool traits are provided below:

The final genetic model for WW (Model 1) was:

$$y_{ijklmnopqrs} = \mu + CG_{ij} + sex_{ik} + rstat_{il} + bstat_{im} + age_{in} + dam\ age_{io} + HXS_{ip} + PE_{iq} \\ + maternal_{ir} + animal_{is} + e_{ijklmnopqrs}$$

where: $y_{ijklmnopqrs}$ = the WW of the i th animal;

μ = the population mean;

CG_{ij} = the contemporary group of the i th animal i (where CG is the reference number $\times$ environmental code $\times$ management group);

sex_{ik} = the sex k of animal i ;

$rstat_{il}$ = the rearing status l of animal i (reared as a single, twin, triplet, or quadruplet lamb);

$bstat_{im}$ = the birth status m of animal i ;

age_{in} = the linear regression of age n of animal i on WW;

$dam\ age_{io}$ = the linear regression o of the age of the dam of animal i on WW;

HXS_{ip} = the random herd by sire effect p for animal i ;

PE_{iq} = the random permanent environmental effect q for dam of animal i ;

$maternal_{ir}$ = the random maternal additive genetic effect r of dam for animal i ;

$animal_{is}$ = the random direct additive genetic effect s of animal i ;

$e_{ijklmnopqrs}$ = the random residual effect.

The final genetic model for the wool traits (Model 2) was:

$$y_{ijklmno} = \mu + CG_{ij} + rstat_{ik} + age_{il} + dam\ age_{im} + maternal_{in} + animal_{io} + e_{ijklmno}$$

where: $y_{ijklmno}$ = the wool trait of the i th animal;

μ = the population mean;

CG_{ij} = the contemporary group of the i th animal i (where CG is the reference number $\times$ environmental code $\times$ group code);

$rstat_{ik}$ = the rearing status k of animal i (reared as a single, twin, triplet, or quadruplet lamb);

age_{il} = the linear regression of age l of animal i on the wool trait;

$dam\ age_{im}$ = the linear regression m of the age of the dam of animal i (excluded for SL);

$maternal_{in}$ = the random maternal additive genetic effect n of dam for animal i ;

$animal_{io}$ = the random direct additive genetic effect o of animal i ;

$e_{ijklmno}$ = the random residual effect.

Body weight at wool test, CFW, FD, and CVFD all used the same model. However, the model used for SL differed as the age of the dam was not included because it did not have a significant influence on the trait. Unlike the model used for WW, the models used for the wool traits excluded the random HXS and permanent environmental effects.

Breeding values were estimated using best linear unbiased prediction (BLUP) methodology as implemented in PEST2 (Groeneveld *et al.*, 2019). The same genetic models as used for variance component estimation were used for breeding value estimation. The complete, edited dataset containing all animals across all years was used, with the pedigree built back across all generations. The EBVs obtained from the PEST2 evaluation were then used to calculate genetic trends by averaging the EBVs of measured animals per year of birth, for every trait. For the comparison with national genetic trends, a base year of 2018 was implemented for all traits by determining the average EBV for measured animals born in 2018 and deducting it from all the animals' EBVs for each trait. This ensured that the average for 2018 was set to zero for all traits, similar to the national trends. Genetic trends in the form of line graphs were constructed in R (RStudio Team, 2020) and compared with the national Merino genetic trends obtained from SA Stud Book.

Results and discussions

Descriptive statistics for the edited South African Merino sheep breed data were obtained using R (RStudio team, 2020) (Table 2).

Table 2 Descriptive statistics for weight and wool traits of the South African Merino sheep population

Trait	Min	1st	Med	Mean	3rd	Max	SD
Weaning weight (kg)	10.00	24.40	28.50	28.89	33.00	62.50	6.50
Body weight at wool test (kg)	15.60	39.00	46.60	47.38	55.00	100.00	11.58
Staple length (mm)	50.20	92.29	104.80	105.72	118.10	169.80	19.43
Clean fleece weight (kg)	2.60	3.36	4.36	5.45	6.12	10.50	1.07
Fibre diameter (μ m)	11.10	16.20	17.10	17.15	18.10	24.50	01.45
CV of fibre diameter (%)	10.50	15.50	16.90	17.18	18.50	33.50	3.30

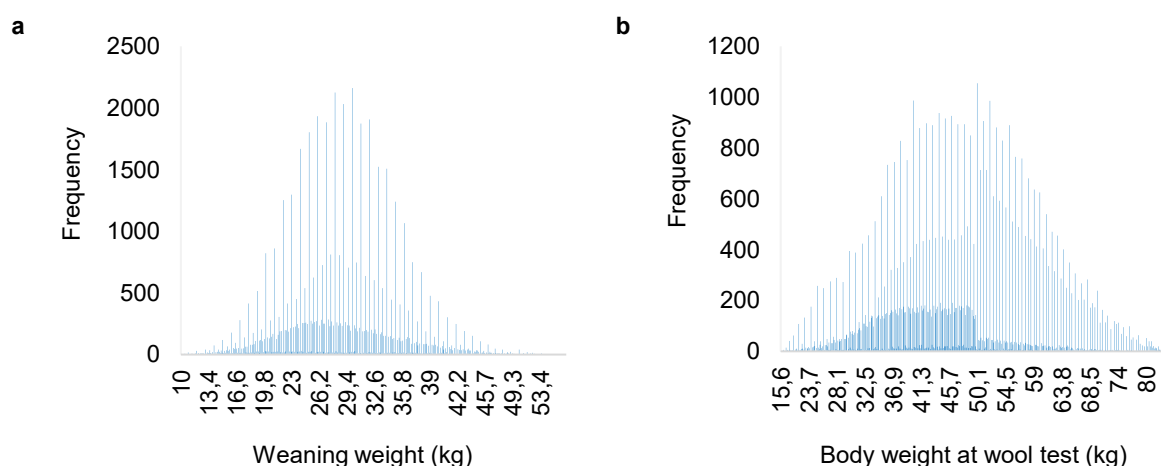
Min: minimum; 1st: first quartile; Med: median; 3rd: third quartile; Max: maximum; SD: standard deviation; CV: coefficient of variation.

To assess the distribution of the edited data for each trait, skewness and kurtosis analyses were performed in R (RStudio team, 2020). The skewness and kurtosis values are shown in Table 3 and their distribution in Figure 1.

Table 3 Skewness and kurtosis values ($\pm$ standard errors) and descriptions of the distributions of weight and wool traits of the South African Merino sheep breed

Trait	Skewness statistic	Kurtosis statistic	Distribution
Weaning weight (kg)	0.31 ± 0.0098	3.27 ± 0.0196	Approximately symmetrical distribution (mesokurtic), but slightly skewed to the right.
Body weight at wool test (kg)	0.34 ± 0.0098	2.94 ± 0.0196	Approximately symmetrical distribution (mesokurtic), but slightly skewed to the right.
Clean fleece weight (kg)	0.55 ± 0.0098	3.57 ± 0.0196	Skewed to the right, with a leptokurtic distribution (heavier tails and a sharper peak).
Staple length (mm)	0.26 ± 0.0098	3.08 ± 0.0196	Right-skewed, indicating that shorter staple lengths are more common.
Fibre diameter (μm)	0.18 ± 0.0098	3.08 ± 0.0196	Approximately symmetrical distribution (mesokurtic), but slightly skewed to the right.
Coefficient of variation of fibre diameter (%)	0.69 ± 0.0098	3.82 ± 0.0196	Skewed to the right with a leptokurtic distribution (heavier tails and a sharper peak).

The skewness and kurtosis statistics indicate that most of the six traits were approximately normally distributed and symmetrical (mesokurtic); however, they exhibited slight right skewness. Notably, CFW and CVFD showed more pronounced right skewness and leptokurtic distributions, as shown in Figure 1 (c, f). This was characterised by heavier tails and sharper peaks. The trends for CFW and CVFD suggest that more extreme values were present and therefore that more variability in the data existed for these two traits. As data are not normalised for the Logix National Genetic Evaluation, no transformation to normalise the data was implemented in this study. Furthermore, SL displayed a multimodal distribution in which multiple peaks were observed, indicating that there were several common values for SL.



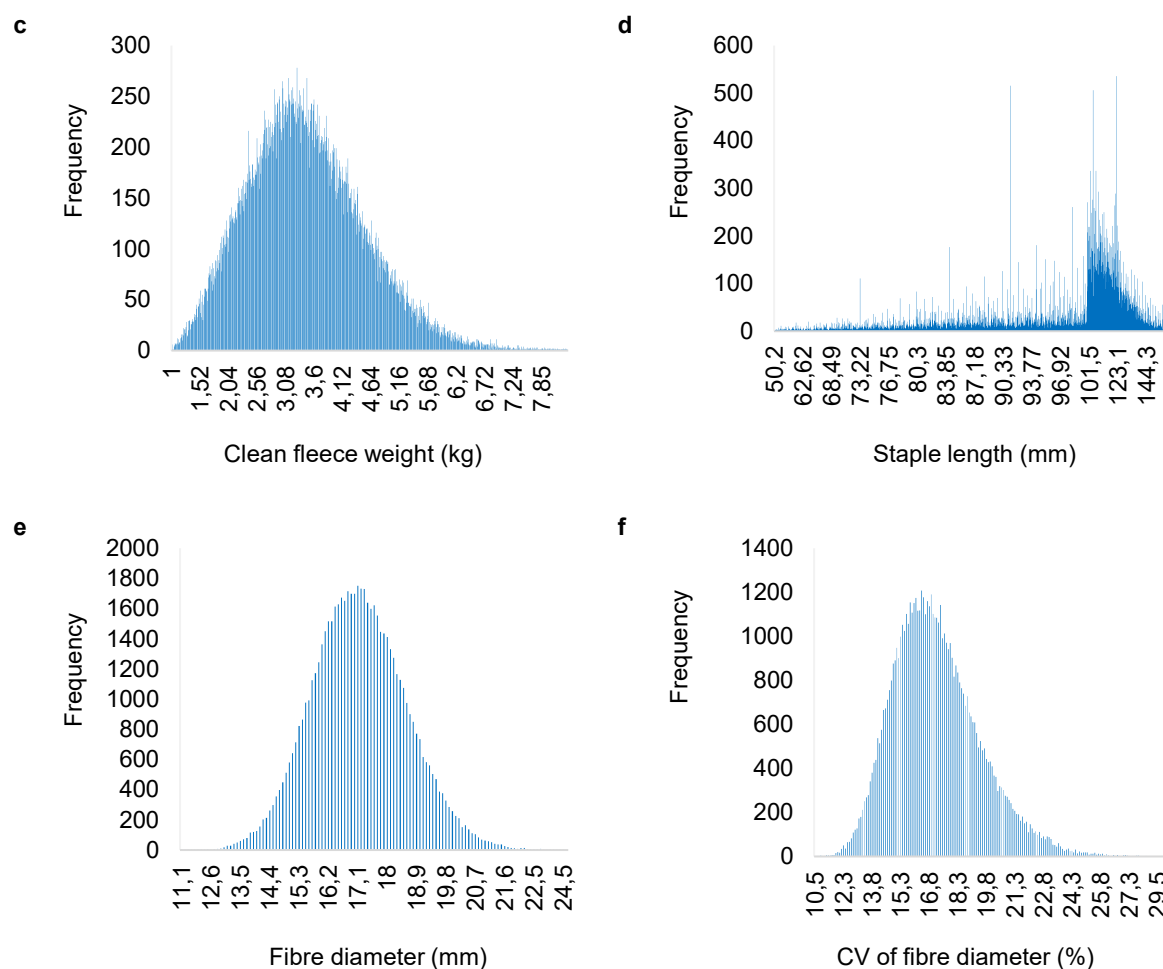


Figure 1 The distributions of (a) weaning weight (kg), (b) body weight at wool test (kg), (c) clean fleece weight (kg), (d) staple length (mm), (e) fibre diameter (μm), and (f) coefficient of variation (CV) of fibre diameter (%) for the South African Merino sheep breed.

The ANOVA for WW indicated that dam age and age at weaning were highly significant as linear and quadratic regressions. The weaning contemporary group (which consisted of the flock, environmental code, and management group), along with the birth status, sex, herd $\times$ sire effect, and rearing status, also had highly significant effects. The final model for WW (Model 1) produced the lowest mean squared error and the highest R^2 value of 0.70, and therefore explained the most variation. Likelihood ratio tests were implemented to assess the inclusion of the random effects (permanent environmental and sire $\times$ herd effects). Convergence was assessed by monitoring the decrease in the residuals and the change in the EBVs between iterations, comparing the means and variances of EBVs across iterations, and by comparing the genetic trends across different convergence criteria to assess their stability, thereby indicating that convergence was reached.

The ANOVA for the wool traits indicated that the age of the sheep, the dam age, the wool contemporary group (consisting of the flock, environmental code, and group number), and the rearing status had highly significant effects. This model produced the lowest mean squared error and the highest R^2 value for the traits BW, FD, and CVFD, and therefore explained the most variation. In contrast, dam age did not have a significant effect on SL and was therefore not included in the final model for this trait. Table 4 shows the fixed and random effects that were found to have significant effects on the measured traits by the ANOVA.

Table 4 Fixed and random effects that significantly affected each trait, as per the analysis of variance

Effects	WW	BWW	FD	CVFD	SL	CFW
Weight contemporary group	X					
Wool contemporary group		X	X	X	X	X
Sex	X					
Birth status	X					
Rearing status	X	X	X	X	X	X
Length of test						
Dam age linear regression	X	X	X	X		X
Sheep age linear regression		X	X	X	X	X
Weaning age linear regression	X					
Dam age quadratic regression	X					
Weaning age quadratic regression	X					
Herd × sire		X	X	X	X	X
R ²	0.70	0.69	0.45	0.25	0.44	0.55

WW: weaning weight; BWW: body weight at wool test; FD: fibre diameter; CVFD: coefficient of variation of fibre diameter; SL: staple length; CFW: clean fleece weight.

Multi-trait variance component estimation

Variance components for wool and weight traits were estimated for the South African Merino sheep breed. Table 5 shows the multi-trait evaluation, including the heritability estimates, the estimates of genetic correlation between the traits, and the respective standard errors of the estimates for the South African Merino sheep breed for all traits evaluated in this study.

The estimates of direct heritability for the traits ranged from 0.25 to 0.63. Notably, WW exhibited the lowest estimate of direct heritability (0.25 ± 0.01), whereas the highest heritability was estimated for FD (0.63 ± 0.00). The estimates of maternal heritability for all six traits were significantly lower, ranging from 0.01 to 0.20. In contrast to the patterns observed for the estimates of direct heritability, WW had the highest estimate of maternal heritability (0.20 ± 0.00), while FD had the lowest (0.01 ± 0.00). These findings highlight the varying degrees of genetic influence on the traits, emphasising the importance of considering both direct and maternal effects in breeding programmes. Furthermore, all the standard errors for both the maternal and direct heritability estimates were low, ranging between 0.00 and 0.04, indicating high precision in the estimation of these values.

In this study, the heritability estimates obtained for WW and BWW were of moderate magnitude (0.25 ± 0.01 and 0.26 ± 0.01 , respectively). The estimate for WW closely aligns with previous studies, including Mortimer & Atkins (1995) and Vaez Torshizi *et al.* (1996), who reported estimates of 0.27 ± 0.03 and 0.27 ± 0.04 , respectively, based on Australian Merino sheep populations. For BWW, slightly lower values were obtained in this study (0.26 ± 0.01) than those reported by Brown *et al.* (2002a), Clarke *et al.* (2003), and Safari *et al.* (2003, 2005) for Australian Merino flocks, where estimates ranged between 0.31 and 0.41. More recent studies continue to support moderate heritability estimates for growth traits in Merino sheep. Nmutandani *et al.* (2018) reported heritability estimates of 0.17 for WW and 0.22 for BWW for South African Merino sheep populations using multivariate models. Similarly, Behrem (2021) reported a heritability of 0.22 ± 0.02 for WW for a Central Anatolian Merino population. These consistent findings across both historical and newer studies, and across various Merino populations, confirm that genetic improvement for WW and BWW is achievable through selective breeding.

Estimates of heritability for the wool traits in the current study ranged from moderate to high, indicating potential for genetic improvement through selection. Clean fleece weight heritability was estimated at 0.33 ± 0.01 , which is slightly higher than the 0.28 ± 0.05 reported by Cloete *et al.* (2005), but lower than the estimates published by Safari *et al.* (2005) and Naidoo & Cloete (2006), who reported values ranging from 0.36 to 0.51. While the heritability estimate for CFW in this study was generally lower than those reported in other studies, it still fell within the range reported in the general literature (0.28 to 0.51; Cloete *et al.*, 2005; Safari *et al.*, 2005; Naidoo & Cloete, 2006). Staple length had a

heritability of 0.39 ± 0.01 , which is consistent with previous studies, including Cloete *et al.* (2006) and Safari *et al.* (2005), who reported estimates of 0.37 and 0.46, respectively. The relatively high heritability for SL indicates that rapid genetic gain can be expected in selection programmes, which is particularly beneficial, as increasing SL is commercially desirable because it increases both wool yield and quality by forming strong and more even yarns (Holman & Malau-Aduli, 2012).

In the current study, FD exhibited the highest heritability (0.63 ± 0.00) of all six traits. This corresponds to values reported in other studies: 0.59 ± 0.02 , 0.57 ± 0.05 , and 0.62 ± 0.03 by Safari *et al.* (2005), Matebesi *et al.* (2009), and Brown *et al.* (2010), respectively. Given that FD is the most economically important wool trait, its high heritability is particularly advantageous, as it indicates that much of the variation present is due to genetics, and that the trait is highly responsive to selective breeding. Since finer wool (i.e. a lower FD) commands higher prices, this allows for substantial improvements in wool quality and profitability (Holman & Malau-Aduli, 2012). The heritability estimate for CVFD was moderate, at 0.43 ± 0.01 . This estimate was slightly lower than those reported in earlier studies by Hill (2001), Wuliji *et al.* (2001), and Matebesi *et al.* (2009), who estimated heritability values for CVFD ranging from 0.60 to 0.61. The heritability for CVFD estimated in this study reflects meaningful potential for genetic progress and reinforces the value of using EBVs to enhance both fleece quantity and quality traits in the South African Merino sheep breed.

A moderate maternal heritability value of 0.20 ± 0.00 for WW was estimated. This maternal heritability estimate was within the range of those reported in previous studies that also used multi-trait animal models, such as Mortimer & Atkins (1995), Vaez Torshizi *et al.* (1996), and Annalla & Serradilla (1998), who reported heritability estimates ranging between 0.11 and 0.38. More recently, Cloete *et al.* (2001) estimated a maternal heritability for WW of 0.10 ± 0.04 for a South African Merino sheep population. The maternal heritability estimate for WW in this study indicates that moderate genetic progress can be achieved by selection in this population, which is especially important as WW significantly influences lamb growth and overall health.

The genetic correlations between traits were also estimated in the multi-trait evaluation and are displayed in Table 5. The genetic correlation between direct WW and maternal WW estimated in this study was -0.48 ± 0.01 , which indicates a moderate, negative relationship. This unfavourable genetic correlation suggests that selecting for an increased direct WW will result in a decreased maternal WW, and vice versa. The direct correlation between WW and BWW was 0.55 ± 0.01 . This correlation estimate indicates a strong, positive relationship between these two traits. Thus, as the WW of the sheep increases, their BWW will also increase, and vice versa. This genetic correlation was slightly higher than the estimate of 0.47 obtained by Safari *et al.* (2005). This correlation is regarded as favourable, as WW and BWW are both economically important traits and improvements in both these traits can lead to improved growth rates, increased productivity, and a better market value, and therefore an increase in the profitability of the sheep farming enterprise (Wang *et al.*, 2024).

The genetic correlation between BWW and CFW was 0.00021 ± 0.01 , indicating a negligible relationship between these two traits and suggesting that changes in BWW will have almost no direct impact on CFW, and vice versa. However, this genetic correlation was much lower than those reported in other studies that also used multi-trait animal models to analyse the South African Merino population. Cloete *et al.* (1998) and Cloete *et al.* (2006) reported correlation estimates of 0.37 ± 0.03 and 0.26 ± 0.11 , respectively. The lower genetic correlation observed in this study is likely caused by variations in the data structure and effects included in the model. Fibre diameter had a positive, unfavourable genetic correlation with CFW (0.18 ± 0.00) and SL (0.20 ± 0.01), indicating that there is a tendency for sheep that have longer SLs and heavier CFW to also have coarser fibres, reducing the wool's overall market value. The genetic correlations obtained in this study were within the range of those reported in other studies. Estimates for the genetic correlation between FD and CFW reported in previous studies ranged between 0.28 and 0.36 (Safari *et al.*, 2005; Cloete *et al.*, 2005; Cloete *et al.*, 2006), and estimates for the genetic correlation between FD and SL reported in previous studies ranged between 0.16 and 0.24 (Naidoo & Cloete, 2006; Olivier & Cloete, 2007; Matebesi *et al.*, 2009).

Table 5 Multi-trait variance component evaluation for direct and maternal effects on wool and weight traits of South African Merino sheep, and their respective heritability values (on the diagonal, $\pm$ standard error) and genetic correlations (above the diagonal, $\pm$ standard error)

		Direct effects						Maternal effects					
		WW	BWW	CFW	FD	SL	CVFD	WW	BWW	CFW	FD	SL	CVFD
Direct effects	WW	0.25 $\pm$ 0.01	0.55 $\pm$ 0.01	0.07 $\pm$ 0.01	0.06 $\pm$ 0.00	-0.0 $\pm$ 0.00	-0.03 $\pm$ 0.00	-0.48 $\pm$ 0.01	-0.33 $\pm$ 0.02	-0.09 $\pm$ 0.02	-0.06 $\pm$ 0.03	0.12 $\pm$ 0.03	0.18 $\pm$ 0.02
	BWW		0.26 $\pm$ 0.01	0.00 $\pm$ 0.01	0.14 $\pm$ 0.00	0.02 $\pm$ 0.01	-0.11 $\pm$ 0.00	0.07 $\pm$ 0.01	-0.04 $\pm$ 0.02	0.02 $\pm$ 0.02	-0.49 $\pm$ 0.04	-0.05 $\pm$ 0.03	0.16 $\pm$ 0.02
	CFW			0.33 $\pm$ 0.01	0.18 $\pm$ 0.00	0.24 $\pm$ 0.01	0.09 $\pm$ 0.00	-0.18 $\pm$ 0.01	-0.35 $\pm$ 0.02	-0.32 $\pm$ 0.02	-0.11 $\pm$ 0.03	-0.02 $\pm$ 0.03	0.16 $\pm$ 0.02
	FD				0.63 $\pm$ 0.00	0.20 $\pm$ 0.01	-0.07 $\pm$ 0.00	0.11 $\pm$ 0.01	0.17 $\pm$ 0.02	0.13 $\pm$ 0.02	-0.12 $\pm$ 0.03	0.08 $\pm$ 0.03	-0.09 $\pm$ 0.10
	SL					0.33 $\pm$ 0.00	-0.12 $\pm$ 0.00	-0.04 $\pm$ 0.01	-0.04 $\pm$ 0.02	-0.08 $\pm$ 0.02	-0.15 $\pm$ 0.03	-0.30 $\pm$ 0.04	-0.06 $\pm$ 0.01
	CVFD						0.43 $\pm$ 0.00	-0.03 $\pm$ 0.01	-0.04 $\pm$ 0.02	0.04 $\pm$ 0.02	0.11 $\pm$ 0.03	0.21 $\pm$ 0.03	-0.30 $\pm$ 0.03
Maternal effects	WW							0.20 $\pm$ 0.00	0.91 $\pm$ 0.01	0.66 $\pm$ 0.02	-0.31 $\pm$ 0.03	0.12 $\pm$ 0.03	-0.13 $\pm$ 0.02
	BWW								0.08 $\pm$ 0.00	0.81 $\pm$ 0.01	-0.19 $\pm$ 0.04	0.17 $\pm$ 0.03	-0.18 $\pm$ 0.02
	CFW									0.06 $\pm$ 0.00	0.10 $\pm$ 0.04	0.47 $\pm$ 0.03	-0.15 $\pm$ 0.02
	FD										0.01 $\pm$ 0.00	0.52 $\pm$ 0.04	-0.27 $\pm$ 0.02
	SL											0.02 $\pm$ 0.00	-0.17 $\pm$ 0.02
	CVFD												0.02 $\pm$ 0.00
	PEE												
	Wean	0.05 $\pm$ 0.01											

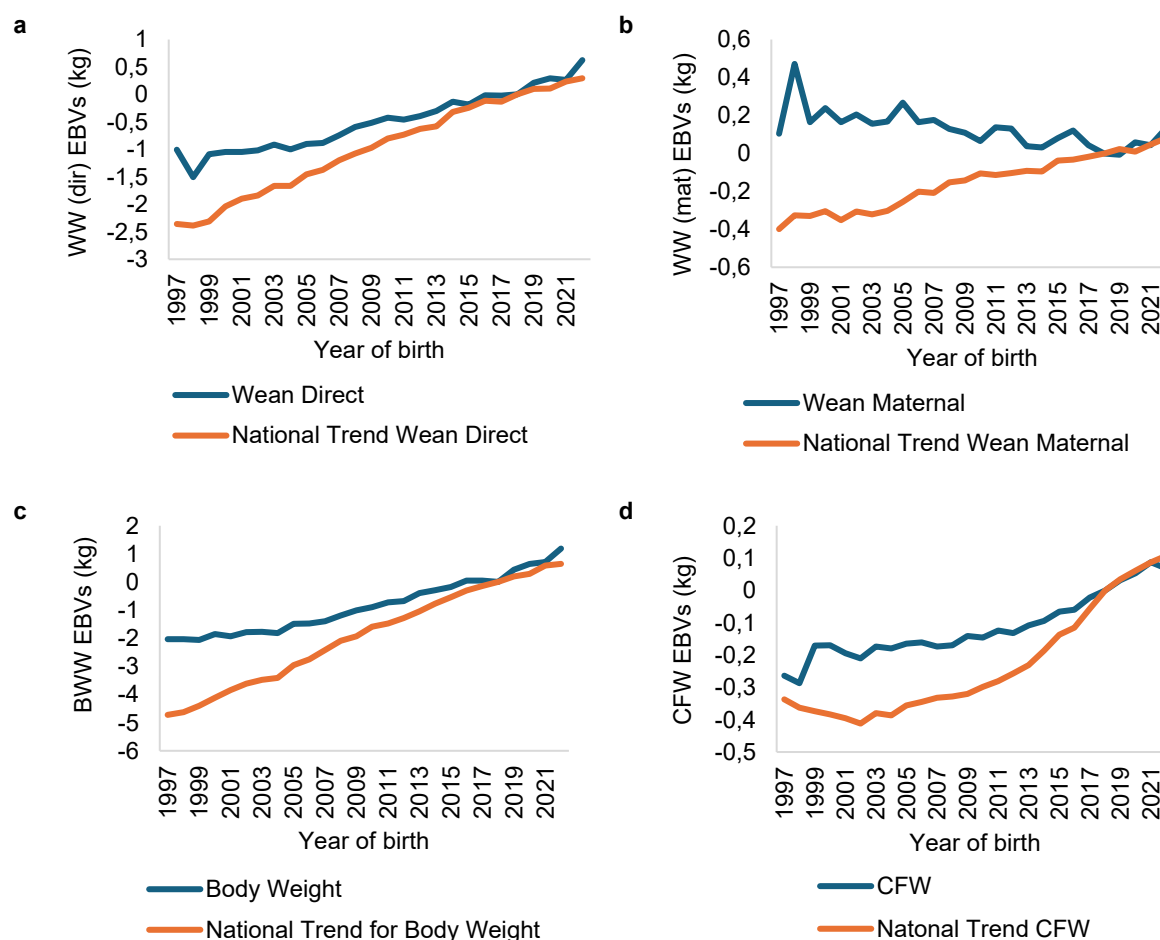
WW: weaning weight; BWW: body weight at wool test; CFW: clean fleece weight; FD: fibre diameter; SL: staple length; CVFD: coefficient of variation of fibre diameter; PEE: permanent environment effect.

The estimated genetic correlation between FD and CVFD was -0.07 ± 0.00 , which indicates a weak, unfavourable relationship between these two traits. This negative correlation suggests that as FD increases, the variability in FD tends to decrease, and vice versa. This genetic correlation is similar to those obtained in previous studies: -0.12 ± 0.07 (Cloete *et al.*, 2006), -0.11 (Naidoo & Cloete, 2006), and -0.08 ± 0.05 (Matebesi *et al.*, 2009). While reducing variation and achieving a more uniform fleece is generally desirable, this outcome is undesirable if it coincides with an increase in FD. Furthermore, SL and CVFD had a correlation estimate of -0.12 ± 0.00 . This negative, favourable correlation is similar to those of other studies, including Notter *et al.* (2007) and Matebesi *et al.* (2009), who reported estimates of -0.06 and -0.11 ± 0.06 , respectively. However, Naidoo & Cloete (2006) reported a higher estimate of -0.38 . The negative correlation between SL and CVFD is generally considered favourable, as breeders can reduce the variability of the wool fibres and increase the SL, further improving wool quality and increasing profitability.

Genetic trends based on average EBVs per year of birth per trait

Based on the same multi-trait animal models used to estimate variance components, breeding values for the South African Merino sheep breed were estimated for growth and wool traits of economic importance. Breeding values were estimated using 2018 as the base year, and genetic trends for each trait were determined by averaging the EBVs per year of birth for the measured animals. These trends were then compared to those obtained from the Logix National Genetic Evaluation, which uses the same base year of 2018. However, it should be noted that genetic groups with unknown parents are incorporated in the pedigree in the National Genetic Evaluation, to ensure that animals with missing parent information enter the genetic evaluation at appropriate genetic levels. This was not, however, done in this study.

Figure 2 shows the genetic trends for each trait, calculated by averaging the EBVs of measured animals per year of birth.



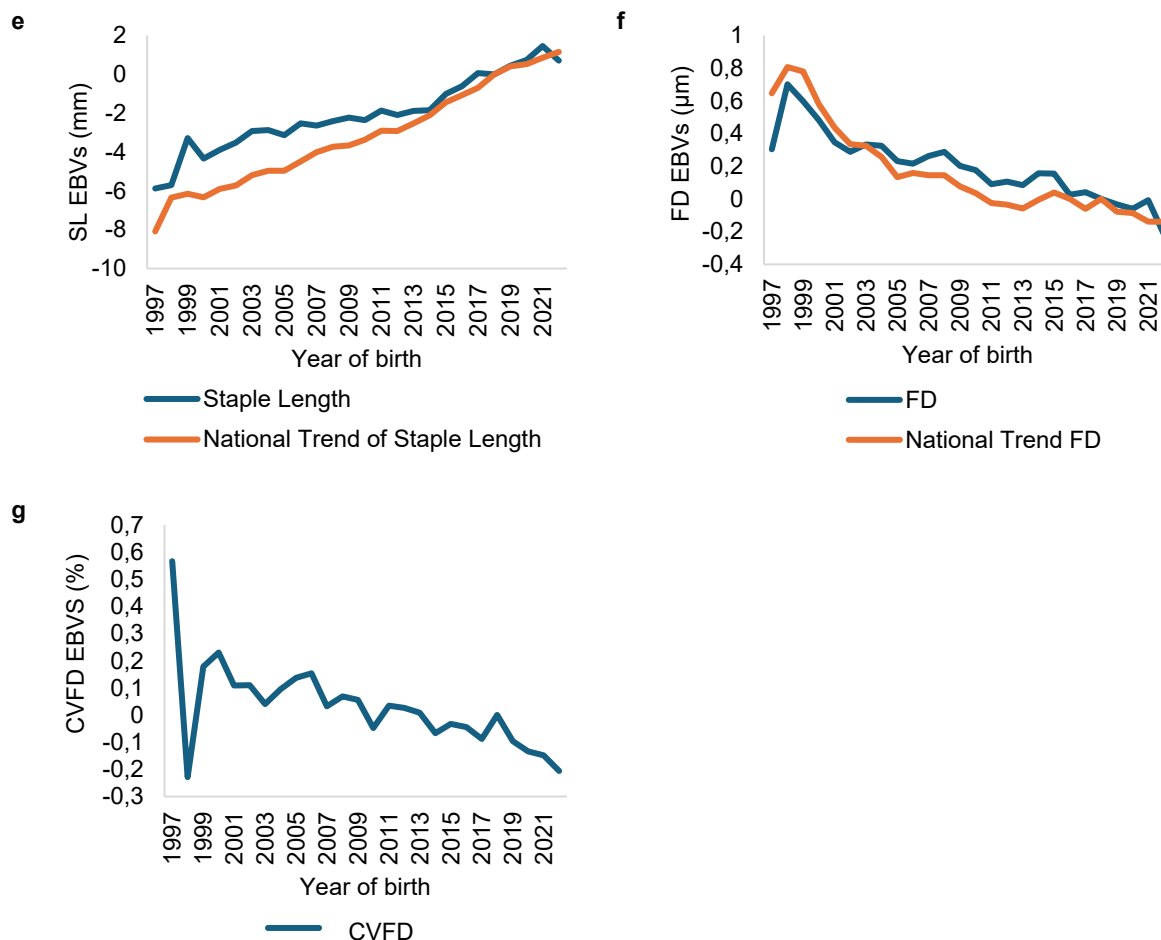


Figure 2 The average estimated breeding values (EBVs) calculated in this study, plotted against the national trends for (a) direct weaning weight (WW (dir), kg), (b) maternal weaning weight (WW (mat), kg), (c) body weight at wool test (BWW, kg), (d) clean fleece weight (CFW, kg), (e) staple length (SL, mm), (f) fibre diameter (FD, μm), and (g) coefficient of variation of fibre diameter (CVFD, %) for the South African Merino sheep breed.

The average EBVs observed in this study closely mirrored the national genetic trends reported for the South African Merino breed. Across all traits, the patterns of genetic progress aligned with those documented at the national level. This consistency suggests that the selection pressures and breeding objectives applied within the study population are broadly representative of industry-wide practices.

The genetic trends for WW and BWW followed a similar, upward trajectory. Direct WW increased genetically from an average of -1.01 kg for animals born in 1997 to 0.26 kg for animals born in 2021. This represented an increase of 2.35 standard deviation units. The general increase in average EBVs over time showed that breeding strategies have been successful in the genetic improvement of direct WW. Maternal WW, however, decreased genetically from an average of 0.10 kg for animals born in 1997 to 0.04 kg for animals born in 2021. This represented a decrease of 0.61 standard deviation units. The observed decreasing trend of EBVs per year of birth for maternal WW indicates a decline in the genetic potential for this trait over time. This is further supported by the negative, unfavourable genetic correlation between direct and maternal WW discussed previously: as direct WW increases, the maternal WW tends to decrease. This decreasing trend for maternal WW can be improved by implementing more balanced breeding objectives in which focus is placed on both growth and maternal traits.

The BWW followed a similar pattern to that of the direct WW, in which a steady increase in the average EBV per year of birth was observed. The genetic potential of the animals increased, on average, from -2.03 kg for animals born in 1997 to 0.71 kg for animals born in 2021. This represented an increase of 2.79 standard deviation units. The national trend for BWW shows a higher rate of genetic gain over

the years than that found in this study. The increases in the average EBVs per year of birth observed for WW and BWW show continuous genetic progress for these traits, which is largely beneficial, as higher weights generally indicate better growth performance in young animals. This may lead to heavier animals that are better prepared for the subsequent stages of development (Fraser & Saville, 2000). Increased WWs also result in an increase in overall profitability as animals that are weaned heavier are sold for higher prices on the market. Furthermore, animals with higher WWs require less time and fewer resources to reach market weight, resulting in reduced input costs (Madikadike & Tyasi, 2024).

Clean fleece weight and SL also followed similar, upward trajectories. The CFW increased genetically from an average of -0.26 kg for animals born in 1997 to 0.08 kg for animals born in 2021. This represented an increase of 3.54 standard deviation units. The average EBVs from the national trends were 0.34 kg in 1997, increasing to 0.08 kg in 2021. This indicated that the average EBVs per year of birth from the national trends followed a similar pattern to the trend obtained in this study, with both reaching 0.08 kg in 2021. For SL, the genetic merit of the animals increased from -5.88 mm in 1997 to 1.46 mm for animals born in 2021, showing an increase of 3.87 standard deviation units. The national trend for staple length increased from -8.09 mm for animals born in 1997 to 0.86 mm for animals born in 2021, indicating a steeper slope and therefore a faster rate of genetic improvement compared to the trend in this study. The increases in the genetic trends observed for both CFW and SL indicate that genetic improvement has been made for these wool traits. Clean fleece weight is an economically important trait as higher prices are offered for heavier fleeces, and this trait is therefore directly related to the commercial value of the wool (Holman & Malau-Aduli, 2012). A longer SL is similarly beneficial as it is commercially desirable because of its tendency to spin more easily, as well as its ability to perform better during wool processing, and fleeces with higher SLs therefore have higher economic value (Holman & Malau-Aduli, 2012).

The FD, as well as the CVFD, both followed a favourable, downward trajectory, with the average EBVs over the birth years decreasing. The genetic potential of animals for FD decreased on average from 0.30 μ m for animals born in 1997 to -0.01 μ m for animals born in 2021. This represented a decline of 1.52 standard deviation units. The average EBV per year of birth from the national trends decreased from 0.65 μ m to -0.14 μ m between 1997 and 2021, which is a steeper slope than that obtained in this study, indicating a faster rate of genetic improvement. A decrease in the average EBV per year of birth for CVFD was also observed. The genetic potential of the animals decreased on average from 0.57% for animals born in 1997 to -0.15% for animals born in 2021. This represented a decline of 4.49 standard deviation units. As CVFD is not included in the Logix National Genetic Evaluation, no comparison to the national trend could be made. The steady decline in average EBVs for both traits over the years indicates that genetic gain has been achieved. Lower EBVs are beneficial for both traits as fine, soft, and more uniform wool is considered more desirable as it can be processed into higher value textiles and thus has a higher economic value (Khan *et al.*, 2012).

The national trends for most traits recorded in this study, including direct WW, maternal WW, CFW, and FD, exhibited a faster rate of genetic progress, as indicated by the steeper slopes in their respective graphs. This was probably because of the inclusion of genetic groups with missing parent information in the pedigree for the National Genetic Evaluation.

Conclusions

The purpose of this study was to estimate the genetic parameters of the South African Merino sheep breed, capturing the most recent information, in order to estimate accurate breeding values based on these representative variance components. The updated variance components and EBVs for economically important wool and weight traits in South African Merino sheep allow for increased accuracy in selection and therefore accelerated genetic progress within the breed. By incorporating updated variance components derived from the most recent generations, this study ensures that EBVs reflect current genetic dynamics, thereby improving the reliability of selection decisions.

The heritability estimates obtained in this study demonstrated variation between traits, indicating substantial genetic potential for improvement across all traits evaluated. Fibre diameter exhibited the highest heritability, suggesting considerable potential for effective selection. In contrast, maternal WW showed the lowest heritability, indicating a greater influence of environmental factors on this trait. The moderate to high heritability estimates observed for traits in this study confirm that genetic improvement through selection remains achievable for both wool and growth traits in the South African Merino breed.

Furthermore, both favourable and unfavourable genetic correlations were identified between the traits evaluated, highlighting the importance of balanced selection to ensure that improvement in one trait does not adversely impact the improvement of other traits. In particular, the moderate negative genetic correlation observed between direct and maternal WW indicates a potentially antagonistic relationship between growth and maternal ability. This relationship should be carefully considered in breeding strategies to prevent unintended declines in maternal performance while selecting for improved growth.

Genetic trend analyses indicated ongoing genetic change within the population and provided insight into the effectiveness of current selection practices. The results showed generally favourable genetic trends, particularly for wool traits, reflecting sustained selection for improved fibre characteristics and fleece production. However, the trends also highlighted the importance of monitoring traits such as maternal performance to ensure that progress in production traits does not occur at the expense of other economically important characteristics. When compared with national evaluations, these trends demonstrate the value of updated genetic evaluations for monitoring and guiding long-term breeding progress within the South African Merino breed.

It is recommended that future studies include the evaluation of fertility traits in the South African Merino sheep breed, alongside the wool and weight traits assessed in this study. Reproductive performance plays a crucial role in the profitability of sheep enterprises, making the estimation of variance components and EBVs especially valuable for breeding programmes. By broadening the scope of the analysis to include fertility traits, a more comprehensive understanding of the genetic potential of the South African Merino sheep breed can be achieved. Furthermore, to strengthen the accuracy and applicability of genetic evaluations, increased participation in performance recording within the small stock industry is recommended. Consistent and comprehensive data recording will enhance the reliability of EBVs and support more effective selection strategies across diverse production environments.

Overall, the results emphasise the importance of regularly re-estimating the genetic parameters of a population to enhance the accuracy and effectiveness of breeding programmes. This will enable breeders to make more informed decisions, ultimately leading to improved livestock performance, profitability, and sustainability.

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Author contributions

C. Visser conceptualised the manuscript. K. Sieber drafted the manuscript and performed the statistical analyses. All authors (K. Sieber, B.E. Mostert, and C. Visser) contributed to interpretation of data, writing, and revising the manuscript.

Conflict of interest

B.E. Mostert is employed by SA Stud Book, an entity that utilises the results in selling the resulting EBVs to breeders. The other authors have no conflicts of interest to declare.

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