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Including genomic information in the genetic evaluation of production and reproduction traits in South African Merino sheep

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Abstract

Genomic selection (GS) has become common in sheep breeding programmes in Australia, New Zealand, France and Ireland but requires validation in South Africa (SA). This study aimed to compare the predictive ability, bias and dispersion of pedigree BLUP (ABLUP) and single-step genomic BLUP (ssGBLUP) for production and reproduction traits in South African Merinos. Animals in this study originated from five research and five commercial Merino flocks and included between 54,072 and 79,100 production records for weaning weight (WW), yearling weight (YW), fibre diameter (FD), clean fleece weight (CFW) and staple length (SL). For reproduction traits, the dataset included 58,744 repeated records from 17,268 ewes for the number of lambs born (NLB), number of lambs weaned (NLW) and the total weight weaned (TWW). The single-step relationship matrix, *H*, was calculated using PreGS90 software combining 2811 animals with medium density (~50 K) genotypes and the pedigree of 88,600 animals. Assessment was based on single-trait analysis using ASREML V4.2 software. The accuracy of prediction was evaluated according to the 'LR-method' by a cross-validation design. Validation candidates were assigned according to Scenario I: born after a certain time point; and Scenario II: born in a particular flock. In Scenario I, the genotyping rate for the reference population between 2006 and the 2013 cut-off point approached 7% of animals with phenotypes and 20% of their sires. For reproduction traits, about 20% of ewes born between 2006 and 2011 cut-off were genotyped, along with 15% of their sires. Genotyping rates in the validation set of Scenario I were 3.7% (production) and 11.4% (reproduction) for candidates and 35% of their sires. Sires were allowed to have progeny in both the reference and validation set. In Scenario I, ssGBLUP increased the accuracy of prediction for all traits except NLB, ranging between +8% (0.62–0.67) for FD and +44% (0.36–0.52) for WW. This showed a promising gain in

accuracy despite a modestly sized reference population. In the 'across flock validation' (Scenario II), overall accuracy was lower, but with greater differences between ABLUP and ssGBLUP ranging between +17% (0.12–0.14) for TWW and +117% (0.18–0.39) for WW. There was little indication of severe bias, but some traits were prone to over dispersion and the use of genomic information did not improve this. These results were the first to validate the benefit of genomic information in South African Merinos. However, because production traits are moderately heritable and easy to measure at an early age, future research should be aimed at best exploiting GS methods towards genetic prediction of sex-limited and/or lowly heritable traits such as NLW. GS methods should be combined with dedicated efforts to increase genetic links between sectors and improved phenotyping by commercial flocks.

KEYWORDS

genetic prediction, genomic selection, small stock genetics, ssGBLUP, wool sheep

1 | INTRODUCTION

Genomic selection (GS) offers new opportunities to enhance the prediction of breeding values in cases where traditional best linear unbiased prediction (BLUP) methods based on pedigree prove to be limited. GS capitalizes on the ability to capture genetic variation according to genome-wide single nucleotide polymorphism (SNP) markers as an estimate of total genetic merit (Meuwissen et al., 2001). Following the commercialization of affordable genotyping platforms, including for sheep (Kijas et al., 2009), the application of genomic data to enhance the accuracy of genetic prediction has become commonplace across a variety of livestock species (Boichard et al., 2016; Van Eenennaam et al., 2014). In Australia (Brown et al., 2018), New Zealand (Auvray et al., 2011; Dodds et al., 2014), France (Astruc et al., 2022) and Ireland (www.sheep.ie), the use of genome-wide SNP data has already been well incorporated into the genetic evaluation of the major sheep breeds. Advanced stages of development has also been reported for Spain (Marina et al., 2022), and the United Kingdom (Kaseja et al., 2023). Similar strategies have been proposed for South Africa (SA; Cloete et al., 2014), but are yet to be appropriately investigated.

In SA Merino sheep, there has been consistent interest in improving traits such as live weight, fibre diameter or fleece weight in commercial breeding schemes, driven by their perceived monetary value at marketing (Olivier, 1999). Optimizing genetic gain for economically important traits is desirable, but traditional BLUP methods already delivers an effective tool for genetic selection in cases where traits can be recorded at an early age, at a relatively low cost and have a moderate to high heritability (h^2; Safari et al., 2005). Subsequently, benefits of GS to sheep breeding programmes are expected in the increased capacity for predicting 'difficult to measure' traits (van der Werf, 2009; van der Werf et al., 2014), or reproductive output (Shumbusho et al., 2013), which is lowly heritable, recorded late in life and sex-limited.

In order to develop more sophisticated breeding programmes in SA, the use of GS methods requires validation on a local basis. A large effective population size is common for sheep (Kijas et al., 2009, 2012), and particularly so for the Merino breed (Al-Mamun et al., 2015; Ciani et al., 2015; Kijas et al., 2012; Prieur et al., 2017) including SA Merinos (Nel, Gurman, et al., 2022). The high genetic diversity means that relatively lower expectations apply to the realized accuracy from GS, or that a large reference population would be needed (Goddard, 2009). Following the objectives outlined by Cloete et al. (2014), the research sector has been solely responsible for a dedicated genotyping strategy in SA, and animals originating from various research flocks (Schoeman et al., 2010) currently make up the largest majority of the reference population.

Similar to the developments seen for Australian Merinos (Swan et al., 2012, 2014), the research sector could directly contribute to the development of GS methods for SA, but this objective could face various challenges. Generally managed as selection experiments (Schoeman et al., 2010), some resource flocks risk being genetically isolated from the general population of SA Merinos (Nel, Gurman, et al., 2022). Quantitative studies of South African Merinos have been largely limited to within flock analyses of resource flock data, and a combined dataset containing information from both the research and commercial sector has not been tested. The success of genomic prediction will thus depend on how

well information can be usefully translated across boundaries that could exist between flocks and sectors that currently make up the bulk of genotype resources in SA.

To address these issues, this study aimed to validate the use of genomic information in the genetic prediction of SA Merino sheep. This included multiple resource flocks combined with selected commercial Merino breeding studs currently contributing data to the national evaluation system, the National Small Stock Improvement Scheme (NSIS). The study made use of selected economically important live weight and wool traits as well as composite reproduction traits. The results provided here should serve as an indication of the benefit of genomic information for SA and may assist to roadmap further development of more sophisticated breeding programmes for SA Merinos.

2 | MATERIALS AND METHODS

2.1 | Sample populations

Animals in this study can be partitioned by sector of origin as five 'resource' flocks maintained by various research initiatives in SA and five commercial flocks (out of about 231 registered at the SA Merino breeding society) currently contributing records to the NSIS. The general history of the flocks are outlined by Schoeman et al. (2010) with some updates presented by Nel, Gurman, et al. (2022). The flocks are known as the Elsenburg Merino selection experiment (Cloete et al., 2004, 2009; Nel, 2022); the Grootfontein Merino stud (Olivier et al., 1995; Snyman et al., 1998); the Cradock fine wool Merino stud (Olivier, 2014; Schoeman et al., 2010); the Tygerhoek fine wool experimental flock (Cloete et al., 2013) and the Langgewens resource population (Cloete & Cloete, 2015). The level of linkage across resource flocks is variable. The most isolated flock is likely the Elsenburg flock, which only introduced external sires since 2008, and the best connected likely the Grootfontein stud, managed as a 'traditional' Merino breeding flock. The five commercial flocks included in this study are an across flock representation of commercial breeding stock of South African Merinos. However, it is important to note that the particular flocks were selected by criteria of at least some known sire links to various resource flocks. Flocks from the commercial sector are referred to as 'Industry -1, -2, -3, -4 or -5'.

2.2 | Phenotypic data

Phenotypes included two live weight traits: weaning weight (WW) and yearling weight (YW); three wool traits measured also at yearling age: fibre diameter (FD), clean fleece weight (CFW) and staple length (SL); and three reproduction traits as repeated records of the ewe: number of lambs born (NLB), number of lambs weaned (NLW) and the total weight of lambs weaned (TWW). Quality control of phenotypes was performed on a per-flock basis. All production records were screened for being within three standard deviations of the mean. Phenotypes of hand-reared or cross-fostered lambs were removed from the analysis. Records for CFW and SL were pre-corrected for the wool growth period by dividing by the growth period and multiplied with 365. Records of WW were corrected within the flock for sex and age of the lamb before deriving TWW as a trait of the ewe. In the case of the commercial 'Industry' group of flocks, data were available during the 1990s but had a very high level of missing records and incomplete pedigrees. Phenotypes and pedigree were thus pruned to only include records after the year 2000. Production records of the Grootfontein resource flock were available from 1968, but this was also pruned to 1986, which was the start of the Elsenburg selection experiment (Cloete et al., 2004).

Contemporary groups (CG) were derived separately for traits measured at weaning or yearling age, as well as for reproduction traits. CGs were generally derived from concatenating flock, year and season. For the Elsenburg flock, the divergent genetic trends (Cloete et al., 2004, 2017) of the H- and L-Line had a clear influence on results in the preliminary analyses, and the selection line was additionally included in CGs to account for these effects, despite being managed as a single flock. In the Langgewens research flock, CGs for the ewe reproduction data included a factor to identify ewes mated to non-Merino terminal sires and thus raised crossbred offspring. For industry data, factors for management groups were additionally included in CG definitions. CGs with less than 20 animals were excluded from the analysis. Summary statistics of the data for each flock following quality control can be seen in Table 1.

2.3 | Pedigree and genotype data

The full pedigree contained a total of 88,600 identities, which consisted of 7130 members of the base population and the progeny of 1459 sires and 23,696 dams. The pedigree size and completeness on a per flock basis is detailed in Table 1, which excludes 6108 external identities not born as a member of any of these particular flocks.

Genotypes have been collected on a range of panels, initially using the OvineSNP50 Chip (OVN; Illumina Inc) Version 1 ($n = 876$) and Version 2 ($n = 1106$), with subsequent genotypes obtained using the Geneseek Genomic

TABLE 1 Number of records and summary statistics of production, reproduction, pedigree and genotype data for all flocks.

	Production					Reproduction				Pedigree			Genotypes
Flock	**WW**	**YW**	**FD**	**CFW**	**SL**	**NLB**	**NLW**	**TWW**	**From n-ewes**	**Number IDs**	**Known sires**	**Known dams**	**Count**
Cradock	10,990	9683	9668	9629	9467	8927	8927	8927	2540	11,002	100%	100%	363
Elsenburg	6734	5575	5579	5408	4753	6203	6203	6203	1614	6876	100%	100%	516
Grootfontein	9209	7439	7491	7322	7467	9161	9161	9161	2768	9315	100%	100%	371
Langgewens	1645	–	–	–	–	1221	1221	1221	349	2115	93%	99%	79
Tygerhoek	2624	3375	3439	3088	3300	–	–	–	–	3523	97%	100%	277
Industry_1	14,050	9996	9969	9696	9782	8415	8415	8415	3198	14,247	100%	100%	272
Industry_2	9503	4933	4823	4877	4835	5277	5277	5277	1900	9741	98%	99%	320
Industry_3	8238	4816	4739	4702	4690	4998	4998	4998	1643	8604	82%	97%	234
Industry_4	10,605	6290	6190	6229	6203	6171	6171	6171	2267	11,084	83%	97%	255
Industry_5	5502	3909	3849	3845	3575	2656	2656	2656	989	5985	83%	94%	124
Total	79,100	56,016	55,747	54,796	54,072	53,029	53,029	53,029	17,268	82,492	93%	99%	2811
Trait Mean	28.05	50.03	17.85	3.643	98.46	1.344	1.177	31.94					
SD	6.532	12.43	1.953	1.298	20.17	0.6681	0.6773	19.31					

Abbreviations: Production traits: CFW, clean fleece weight; FD, fibre diameter; SL, staple length; WW, weaning weight; YW, yearling weight. Reproduction traits: NLB, number of lambs born; NLW, number of lambs weaned; TWW, total weight weaned.

Profiler (GGP) Ovine 50 K chip (Geneseek®, Lincoln, Nebraska) Version 2 ($n = 986$). Quality control measures were applied to SNPs (GenCall score >0.50 or >0.90 in >95% of samples, MAF >0.01, heterozygosity <3-SD of the mean, and a call rate >0.95) and samples (heterozygosity <3-SD and call rate >0.90) per batch using the 'snpQC' package (Gondro et al., 2014) in the R environment (R Core Team, 2020). Markers that were unmapped or on the X or Y chromosomes, mitochondrial DNA and structural variants (I/D) were removed from the analysis. Before imputation across platforms, the base pair location of each SNP was mapped to the sheep genome build OAR_V3.1.

Samples genotyped on the first OVN V1 chip were first imputed to the post-QC density (~47 K) of OVN V2 using 'Beagle' (Version 5.2; Browning et al., 2018), and as a single batch imputed across to the GGP V2 platform from a reference set of ~21 K SNP markers in common. To validate the imputed genotypes, 208 samples were genotyped in duplicate on both the OvineSNP50 and the GGP platforms, and the accuracy of imputation was determined as the Pearson correlation between the imputed and original genotypes (excluding common markers). The accuracy of imputation ranged from 0.94 to 0.99 with most cases (87%) reaching 0.98 or higher. The imputation was this considered accurate and further analyses proceeded on the GGP platform.

Following these procedures and quality control measures, data of 41,709 SNP markers were available for 2811 ($n = 277$ sires and $n = 2551$ dams) individuals. Of these, 1606 were from the five resource flocks and 1205 from five commercial flocks. Genotypes per flock can be seen in Table 1. Genotyped animals were born between 1996 and 2018, but the majority (90%) were between 2006 and 2016, averaging 237 genotyped individuals per year during this period. The distribution of genotypes according to the design of the study is shown below (Table 2).

2.4 | Statistical analysis

2.4.1 | Population structure

To identify possible influential population substructures in the dataset used in this study, an overview of genetic relationships between and within populations was visualized by the results of a Principal Component Analysis (PCA) of the genomic relationship matrix (GRM) calculated using the 'irlba' 'R' package (Baglama et al., 2019). The first and second PCs were plotted, identified by sector ('commercial' vs. 'industry') and flock (e.g. 'Elsenburg', 'Industry-1' etc.).

2.4.2 | Linear mixed models

The study was designed to compare the predictive abilities of the pedigree BLUP (ABLUP) analysis to the enhanced 'single-step' genomic BLUP (ssGBLUP) method that combined pedigree, genomic and phenotypic information into a single analysis. The inverse numerator relationship matrix ($\boldsymbol{A}^{-1}$) was built from the full pedigree of 88,600 individuals following pedigree checking with RENUMF90 from the BLUPF90 family of programmes (Misztal et al., 2014).

The method of ssGBLUP relies on combining information from the pedigree in $\boldsymbol{A}$ with relationships in the genomic relationship matrix ($\boldsymbol{G}$) by building the combined $\boldsymbol{H}$ matrix (Christensen & Lund, 2010; Legarra et al., 2009). The required inverse ($\boldsymbol{H}^{-1}$) was derived with

TABLE 2 Distribution of records and genotypes as well as genotyping rate of individuals and sires according to four periods within which data were recorded.

			Records		Of which genotyped	Progeny of	Of which genotyped
	Period	Group	(WW)	*n* animals	Number/(%)	*n* sires	Number/(%)
Production	1986_1999	Reference	11,941	11,941	2/0.02%	278	0/0.00%
	2000_2005	Reference	14,969	14,969	300/2.00%	317	2/0.63%
	2006_2013	Reference	28,186	28,186	1623/5.76%	486	68/13.99%
	2014_2018	Validation	16,746	16,746	619/3.7%	308	108/35.06%
			(NLW)				
Reproduction	1986_1999	Reference	11,733	3237	2/0.06%	275	0/0.00%
	2000_2005	Reference	9275	3034	222/7.32%	227	1/0.44%
	2006_2011	Reference	22,978	7191	1400/19.47%	442	66/14.93%
	2012_2018	Validation	9043	3806	434/11.40%	265	94/35.47%

Note: Records of weaning weight (WW) and number of lambs weaned (NLW) were used to represent the maximum of production and reproduction trait groups, respectively.

the 'PreGSF90' software (Aguilar et al., 2014) from the 'BLUPF90' family of programmes. $\boldsymbol{G}$ was scaled based on $\boldsymbol{A}_{22}$ so that mean(diag($\boldsymbol{G}$))=mean(diag($\boldsymbol{A}_{22}$)) and mean(offdiag($\boldsymbol{G}$))=mean(offdiag($\boldsymbol{A}_{22}$)) with scaling parameters of $\alpha=0.95$ and $\beta=0.05$:

$$\boldsymbol{H}^{-1}=\boldsymbol{A}^{-1}+\begin{bmatrix}0 & 0\\ 0 & \left(0.95\boldsymbol{G}+0.05\boldsymbol{A}_{22}\right)^{-1}-\boldsymbol{A}_{22}^{-1}\end{bmatrix}$$

where $\boldsymbol{A}$ is the numerator relationship matrix, $\boldsymbol{A}_{22}$ is the block of $\boldsymbol{A}$ for genotyped animals and $\boldsymbol{G}$ is the genomic relationship matrix, calculated according to VanRaden (2008) as:

$$\boldsymbol{G}=\frac{(\boldsymbol{M}-2\boldsymbol{P})(\boldsymbol{M}-2\boldsymbol{P})'}{2\sum_j(\boldsymbol{p}_j)(1-\boldsymbol{p}_j)}$$

where $\boldsymbol{M}$ is the genotypic matrix of 0/1/2 B-allele marker counts with dimensions animals by markers and $\boldsymbol{P}$ is the corresponding matrix ($m\times n$) where the jth column of $\boldsymbol{P}$ is a vector of m replicates of the allele frequency p_j within all the animals.

Analysis commenced in ASREML V4.2 (Gilmour et al., 2015). Model selection was determined for each trait in an ABLUP analysis, with only the relationship matrix changed from $\boldsymbol{A}^{-1}$ to $\boldsymbol{H}^{-1}$ for the ssGBLUP model. For production traits, the CG at weaning ($n=636$) or yearling ($n=458$) were fitted as fixed effects for WW or YW and wool traits, respectively. Additionally, weaning and yearling age (in days), sex (SEX; male or female), age of dam (AOD; 1–7+) and rearing status as a concatenation of status at birth and weaning (REAR; 1: Single-single, 2: Multiple-single and 3: Multiple-multiple) were considered. For reproduction data, the CG in which the ewe was weaned ($n=561$) and the CG of the lambing record ($n=269$), the age of the ewe (AGE; 1–7+) and the service code (SCODE; 1: natural mating, 2: artificial insemination and 3: artificial insemination with hormonal treatment) were considered as fixed effects. Fixed effects were tested for significance according to Wald statistics derived from conditional least square methods. Those observed as significant ($p<0.05$) were retained in the fixed effects model throughout subsequent analysis.

In the case of production traits, random effects considered in the model were direct (σ^2_a) and maternal (σ^2_m) genetic effects, and the maternal permanent environment (σ^2_{mc}) effect. The full single-trait model was:

$$y=\boldsymbol{X}b+\boldsymbol{Z_1}a+\boldsymbol{Z_2}m+\boldsymbol{Z_2}mc+e$$

where y is the vector of phenotypes, b is the vector of fixed effects, a is the vector of direct genetic values, m the vector of maternal genetic effects, mc the vector of maternal permanent environment effects and e is the vector of residuals. The corresponding incidence matrices for these effects were respectively represented by $\boldsymbol{X}$, $\boldsymbol{Z_1}$ and $\boldsymbol{Z_2}$.

For reproduction traits, a single-trait repeatability model was used, and random effects considered were direct genetic of the ewe (σ^2_a) and ewe permanent environmental effects (σ^2_c). The full model equation was

$$y=\boldsymbol{X}b+\boldsymbol{Z_1}a+\boldsymbol{Z_1}c+e$$

where y is vector of observations, b the vector of fixed effects, a the vector of direct genetic effects, c the permanent environmental effects of the ewe and e the vector of residuals. The corresponding incidence matrices of each effect were, respectively, represented by $\boldsymbol{X}$ and $\boldsymbol{Z_1}$. It was assumed that:

$$V(a)=\boldsymbol{A}\sigma^2{}_a \text{ or } \boldsymbol{H}\sigma^2{}_a;\ V(m)=\boldsymbol{A}\sigma^2{}_m \text{ or } \boldsymbol{H}\sigma^2{}_m;$$
$$V(mc)=\boldsymbol{I}\sigma^2{}_{mc};\ V(c)=\boldsymbol{I}\sigma^2{}_c;\ V(e)=\boldsymbol{I}\sigma^2{}_e$$

with $\boldsymbol{A}$ or $\boldsymbol{H}$ representing the relevant relationship matrix in ABLUP or ssGBLUP, respectively, I representing identity matrices and σ^2_a, σ^2_m, and the direct and maternal genetic variances, σ^2_{mc}, σ^2_c, the permanent environmental variance of the dam or the ewe, and σ^2_e the environmental (residual) variance.

Model selection was performed by testing various combinations of fixed effects and possible two-way interactions. Random terms were then added to the operational model on a step-wise basis by comparing the log-likelihood of the current model with the additional term to the simpler (nested) model. A log-likelihood ratio test (LRT) was used to test for significant differences between full and nested models. Models with significant improvements in LRT ($p<0.05$) were preferred over simpler models.

2.5 | Validation designs

The predictive ability of ssGBLUP and ABLUP analyses was examined by a cross-validation design that replicates the prediction of 'validation' candidates without phenotypes or progeny. For both ABLUP and ssGBLUP, EBVs were estimated based on the full dataset after data filtering, which was labelled as 'whole' EBVs (a_w). Subsequently, a second set of analyses were performed where all phenotypes of the validation population were set to missing, where the EBVs estimated were labelled as 'part'(a_p) EBVs.

Prediction was assessed according to the to the 'LR-method' (Legarra & Reverter, 2018), including accuracy (ACC_{LR}), bias (β_0), and dispersion (β_1) of breeding values

depending on the derived part (a_p) and whole (a_w) EBVs of animals in the validation set:

$$\mathrm{ACC_{LR}} = \sqrt{\frac{\mathrm{cov}(\hat{a}_w \hat{a}_p)}{(1 + \overline{F} - 2\overline{f})\sigma_g^2}}$$

Where a_p and a_w are the (G)EBVs as described above, $\overline{F}$ is the average inbreeding coefficient, $2\overline{f}$ is the average relationship between individuals and σ_g^2 the genetic variance derived from the ABLUP analysis of the partial dataset. As also described by Legarra and Reverter (2017), $\beta_0 = \overline{\hat{a}_p} - \overline{\hat{a}_w}$ and $\beta_1 = cov(\hat{a}_w \hat{a}_p) / \mathrm{var}(\hat{a}_p)$, indicating the difference between mean breeding values and the regression slope of whole on part estimates, respectively.

Validation sets were assigned according to two Scenarios (I and II). In Scenario I, ABLUP and ssGBLUP models were compared in a 'forward' cross-validation of all candidates born after a certain time point. The cut-off points were chosen to result in roughly a 25% partition of records in the validation set, resulting in different cut-off points for the validation set for production data (born between 2014 and 2018) and reproduction data (born between 2012 and 2018; Table 2). Records of animals born after 2018 were retained in the 'full' analysis to contribute as progeny records to candidates in the validation set, but were not used as validation animals themselves, for two reasons: (1) to allow for some accumulation of records of designated validation candidates (born between 2012/2014 and 2018) in the 'whole' dataset and (2) there was no genotyping after 2018, thus little reason to compare these year cohorts between the ABLUP and ssGBLUP methods. The design of Scenario I is detailed in Table 2, showing the distribution of records, individuals, and genotypes according to four periods within which data was recorded. For both production and reproduction traits, the entire period between 1986 and the respective 2013 or 2011 cut-off points contributed to the reference set, but it can be seen that the bulk of the records linked to genotypes was from animals born after 2006.

For Scenario II, the animals were split up into 'across-flock' validation cohorts. In general, for the nine flocks (excluding Langgewens), the analysis was repeated nine times, each in turn with a dataset where all the records of a particular flock were set to missing. However, some specific adjustments were necessary in selected cases. Since it was common for unselected Elsenburg ewes to join the Langgewens research flock, it was necessary to also set Langgewens data to missing in the analysis where the Elsenburg flock was the target. In turn, the Langgewens flock was not used as a validation set. In the case of Scenario II, the number of genotypes and records partitioned into the validation set was highly variable, as can be deduced from flock totals in Table 1.

3 | RESULTS

3.1 | Population structure by principal components

Inspection of the first (PC1) and second (PC2) principal components of the GRM showed some evidence of population structures (Figure 1), but no sub-populations were completely segregating. For some flocks, PC1 and PC2 suggested useful relationships existed across sectors, such as the homogenous grouping of the Grootfontein and Langgewens resource flocks with Industry-1 and Industry-5. Generally, however, most animals from resource flocks tended to higher values of PC1, with the greatest distance between the Tygerhoek/Cradock flocks and the Industry-3 and -4 flocks. According to PC1 and PC2, the genetic architecture of these flocks also appeared better defined with little within-flock variation. The space between the Elsenburg flock and other flocks included genotyped progeny of external sires in the Elsenburg flock as well as genotyped progeny of Elsenburg sires also used at Langgewens. It should be noted, however, that while flock of origin appeared important to derived values of PC1 and PC2, these first and largest PCs explained only a small proportion of the total variation in the GRM, supporting the high dimensionality of genotype data in sheep.

3.2 | Fixed effects

The effects REAR, SEX and AOD were all significant ($p < 0.01$), with better performance for singles, rams and dams of intermediate age. For reproduction traits, both SCODE and AGE were significant ($p < 0.01$), with the best performance for ewes of intermediate age and for artificial mating with hormonal treatment. These factors were included in the models used for genetic analysis, but the values were in line with what is expected and are not explored further in this study.

3.3 | Variance components

The variance components and ratios for production and reproduction traits can be seen in Tables 3 and 4, respectively. It is clear that ABLUP and ssGBLUP derived values were very similar, with no need to further differentiate

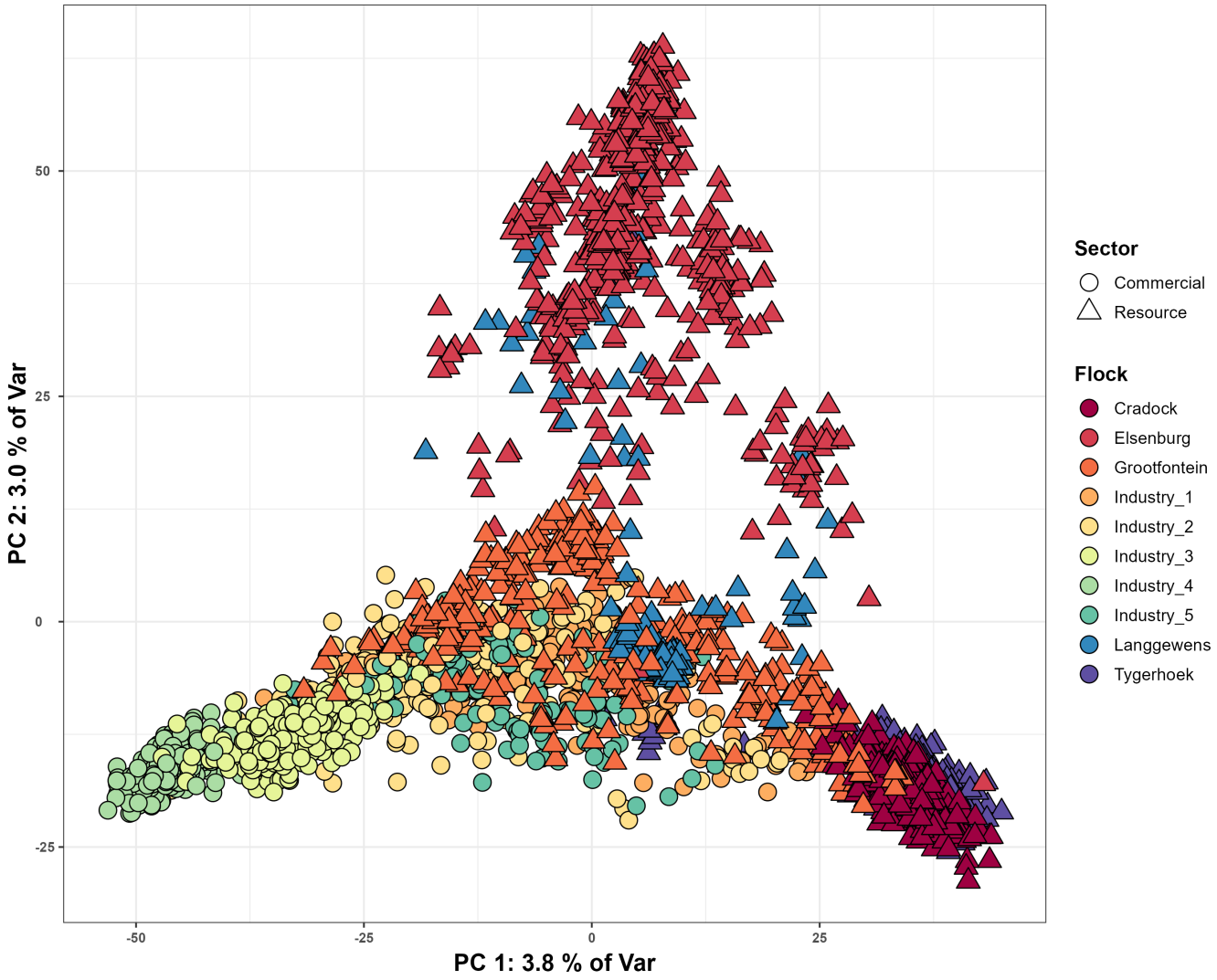

FIGURE 1 The first (PC1) and second (PC2) principal components of animals identified by flock and sector of origin. [Colour figure can be viewed at wileyonlinelibrary.com]

between these results. According to the LRT, the additive genetic effect (σ^2_a) was significant ($p < 0.05$) in all traits considered. The addition of maternal genetic effects (σ^2_m) also improved the Log-Likelihood ($p < 0.05$) of all production traits (Table 3), but the influence of the maternal permanent environmental effect (σ^2_{mc}) was only observed as influential in the case of WW and YW. For reproduction traits, the permanent environmental (σ^2_c) and genetic (σ^2_a) effect of the ewe was significant in all cases (Table 3). The heritability (h^2) was low to very low for reproduction traits (0.03–0.04, Table 4), low to moderate for WW (0.14), SL (0.23) and YW (0.27) and high for FD (0.57; Table 3). The maternal genetic component (m^2) was low for WW (0.05), CFW (0.04) and YW (0.03) and significant, but <0.02 for the remaining traits in Table 2. The permanent environmental component of the ewe (c^2) was low (0.05–0.06) for the reproduction traits, but generally larger than the corresponding direct genetic effects (Table 3).

3.4 | Accuracy, bias and dispersion of breeding values

The accuracy (ACC_{LR}) of (G)EBVs for production and reproduction traits derived from validation designs I and II can be seen in Figure 2. The ACC_{LR} was generally moderate to high in the case of Scenario I but varied considerably across traits from the ABLUP derived ACC_{LR} of 0.31 for CFW to 0.67 for FD from the ssGBLUP analysis. In comparing the methods, ssGBLUP delivered higher accuracies of prediction for all production traits, but this difference also varied and ranged from only marginal gains for FD (+8%) to substantial gains for WW (+44%). For reproduction traits, slightly smaller gains were associated with ssGBLUP if compared to the production traits. In the case of NLB, there was no difference in ACC_{LR}, but a notable increase in accuracy for TWW (+12%) as well as NLW (+18%). In the case of Scenario II, it was apparent that the lack of 'within-flock'

TABLE 3 Variance components and ratios (±SE) of all production traits estimated from both ABLUP and ssGBLUP analysis.

	WW		YW		FD		CFW		SL	
Effects	**ABLUP**	**ssGBLUP**	**ABLUP**	**ssGBLUP**	**ABLUP**	**ssGBLUP**	**ABLUP**	**ssGBLUP**	**ABLUP**	**ssGBLUP**
Variance components										
σ^2_a	2.84 ± 0.18	2.84 ± 0.18	10.15 ± 0.47	10.69 ± 0.48	0.78 ± 0.02	0.78 ± 0.02	0.12 ± 0.01	0.13 ± 0.01	38.24 ± 1.91	37.59 ± 1.89
σ^2_m	0.94 ± 0.11	0.96 ± 0.11	1.07 ± 0.19	1.08 ± 0.18	0.02 ± 0.005	0.02 ± 0.005	0.02 ± 0.002	0.02 ± 0.002	2.13 ± 0.62	2.26 ± 0.62
σ^2_{mc}	1.67 ± 0.10	1.64 ± 0.10	0.44 ± 0.18	0.39 ± 0.17	–	–	–	–	–	–
σ^2_e	14.51 ± 0.13	14.48 ± 0.13	26.3 ± 0.32	25.9 ± 0.32	0.57 ± 0.01	0.56 ± 0.01	0.29 ± 0.004	0.29 ± 0.004	125.87 ± 1.38	126.08 ± 1.38
σ^2_p	19.95 ± 0.12	19.92 ± 0.12	37.96 ± 0.28	38.05 ± 0.28	1.37 ± 0.01	1.36 ± 0.01	0.43 ± 0.003	0.44 ± 0.003	166.25 ± 1.18	165.93 ± 1.17
Variance ratios										
h^2	0.14 ± 0.009	0.14 ± 0.009	0.27 ± 0.01	0.28 ± 0.01	0.57 ± 0.01	0.57 ± 0.01	0.29 ± 0.01	0.29 ± 0.01	0.23 ± 0.01	0.23 ± 0.01
m^2	0.05 ± 0.005	0.05 ± 0.005	0.03 ± 0.005	0.03 ± 0.005	0.02 ± 0.004	0.01 ± 0.003	0.04 ± 0.005	0.04 ± 0.005	0.01 ± 0.004	0.01 ± 0.004
mc^2	0.08 ± 0.005	0.08 ± 0.005	0.01 ± 0.005	0.01 ± 0.005	–	–	–	–	–	–

Note: Empty cells indicate effects not included in the model.

Abbreviations: Variance components refer to direct genetic (a), maternal genetic (m), maternal permanent environmental (mc), residual (e) and phenotypic (p) variance. Ratios present the direct genetic (h^2), maternal genetic (m^2) and maternal permanent environmental (mc^2) effects. See Table 1 for trait abbreviations.

information resulted in an overall reduction in ACC_{LR} across all traits for both methods of analysis. For production traits, accuracy was moderate between 0.18 for WW (ABLUP) and 0.54 for FD (ssGBLUP). For reproduction, values of ACC_{LR} were generally low and ranged between 0.12 (ABLUP) for TWW and 0.22 (ssGBLUP) for NLW. In Scenario II, however, there were considerably larger proportional gains (%) for ssGBLUP compared to ABLUP, especially for production traits. Interestingly, for traits WW, YW, CFW and SL, the ACC_{LR} derived from ssGBLUP in Scenario II equalled or exceeded the accuracy obtained from ABLUP in Scenario I, that is, from results derived from 'within-flock' information. This pattern was not visible in the reproduction trait group, but the relative gain (up to +29% for NLW) made by the ssGBLUP analysis was favourable for traits with a low to very low h^2 (see Table 4).

The prediction parameters for bias (β_0) and dispersion (β_1) can be seen in Table 5 for all traits. In Scenario I, there was little indication of strong bias in either trait group while absolute values of β_0 were generally low. A possible exception could be WW where the EBV of unproven candidates (a_p) tended to be slightly overestimated, even more so in the case of ssGBLUP ($\beta_0 = 0.25\sigma_g$). In turn, EBVs for FD proved slightly underestimated with $\beta_0 = -0.14\sigma_g$. For reproduction traits, the negative values of β_0 pointed to consistent underprediction, for this trait group but not to a large extent. In the case of Scenario II, there was some indication of underprediction of WW, YW and CFW, but also with little difference between the methods of analysis. This pattern of negative values was more pronounced for reproduction traits, with the most extreme value of $\beta_0 = -0.23\sigma_g$ for NLW. For TWW, ssGBLUP notably improved bias ($\beta_0 = -0.03\sigma_g$ from $-0.17\sigma_g$), but the opposite was true for NLB and NLW, where ssGBLUP was more biased (Table 5).

There was apparent over-dispersion of EBVs (a_p) for production traits in Scenario I, with β_1 well below 1 for most traits except for FD ($\beta_1 = 0.91$–0.93). In turn, all reproduction traits had β_1 values >1, indicating consistent under-dispersion. In Scenario II, a generally similar pattern was observed for production traits, with FD again having β_1 values close to 1. For reproduction traits, however, all values of β_1 were below 1, and low for NLB ($\beta_1 = 0.59$–0.60) and very low for TWW ($\beta_1 = 0.35$–0.47). Analysis of the production traits dataset thus tended to exhibit more consistent behaviour across validations designs, but breeding values for reproduction traits were subject to both under- or over-dispersion, depending on whether the reference originated from 'within' or 'across-flock' information, respectively. There was little to no evidence of improved metrics of dispersion associated with ssGBLUP. In fact, less desirable outcomes were seen in

TABLE 4 Variance components and ratios (±SE) of all reproduction traits estimated from both ABLUP and ssGBLUP analysis.

	NLB		NLW		TWW	
Effects	**ABLUP**	**ssGBLUP**	**ABLUP**	**ssGBLUP**	**ABLUP**	**ssGBLUP**
Variance components						
σ^2_a	0.02 ± 0.002	0.02 ± 0.002	0.01 ± 0.002	0.01 ± 0.002	8.52 ± 1.28	9.1 ± 1.29
σ^2_c	0.02 ± 0.002	0.02 ± 0.002	0.02 ± 0.002	0.02 ± 0.002	17.63 ± 1.52	17.16 ± 1.51
σ^2_e	0.35 ± 0.003	0.35 ± 0.003	0.35 ± 0.003	0.35 ± 0.003	239.13 ± 1.73	239.12 ± 1.73
σ^2_p	0.39 ± 0.002	0.39 ± 0.002	0.39 ± 0.002	0.39 ± 0.002	265.28 ± 1.67	265.38 ± 1.68
Variance ratios						
h^2	0.04 ± 0.005	0.04 ± 0.005	0.03 ± 0.005	0.03 ± 0.005	0.03 ± 0.005	0.03 ± 0.005
c^2	0.05 ± 0.006	0.05 ± 0.006	0.06 ± 0.006	0.06 ± 0.006	0.07 ± 0.006	0.06 ± 0.006

Abbreviations: Variance components refer to direct genetic (a), ewe permanent environmental (c), residual (e) and phenotypic (p) variance. Ratios present the direct genetic (h^2) and ewe permanent environmental (c^2) effects. See Table 1 for trait abbreviations.

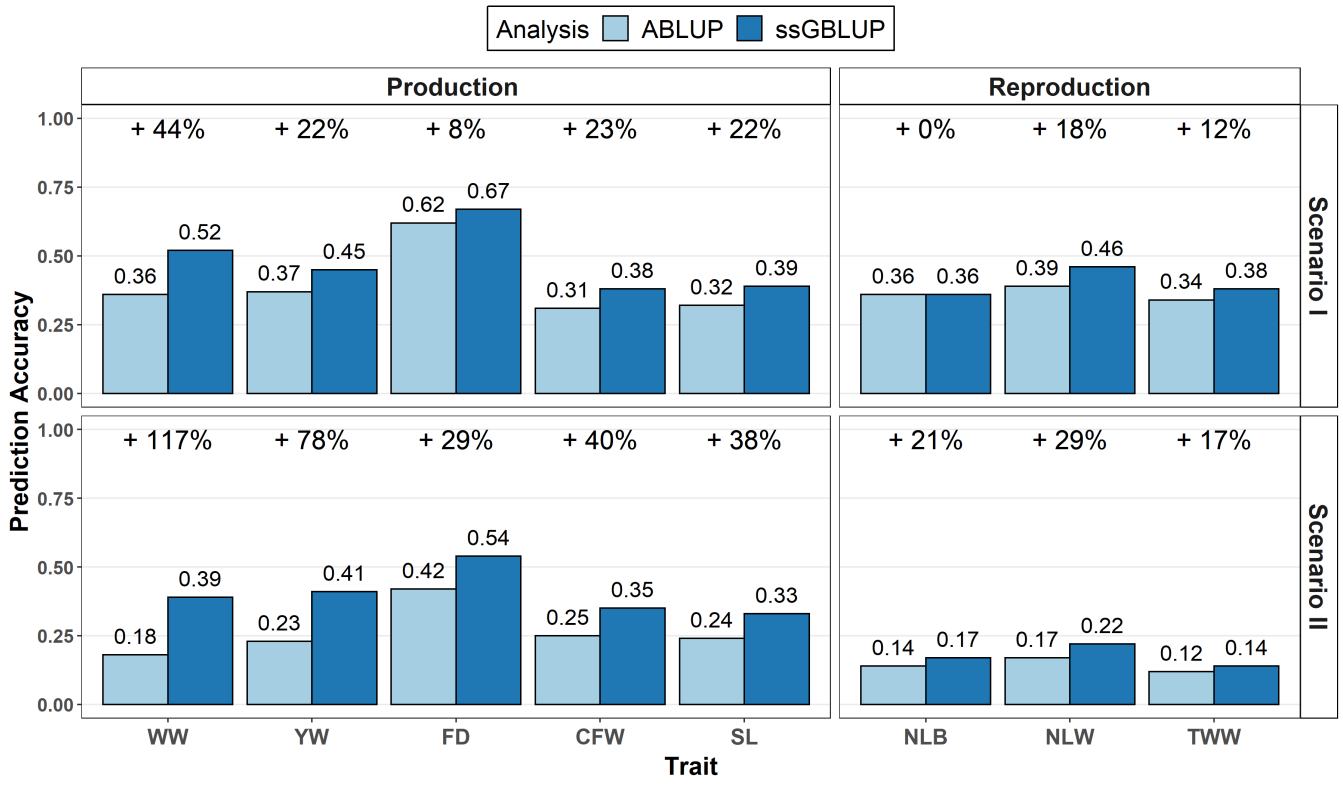

FIGURE 2 Accuracy of prediction (ACC_{LR}) and gains made (%) for production and reproduction traits using ABLUP and ssGBLUP for both validation designs I and II. See Table 1 for trait abbreviations. [Colour figure can be viewed at wileyonlinelibrary.com]

multiple cases for bias and dispersion according to the expected measures of $\beta_0 = 0$ and $\beta_1 = 1$.

4 | DISCUSSION

This study is the first to report on the use of genomic SNP data to enhance the prediction of production and reproduction traits in SA Merinos. To our knowledge, it is the first study of its kind for SA sheep in general. It is also the first across-flock analysis of the SA Merino resource flocks (Schoeman et al., 2010) and combination of data originating from both the commercial and resource sectors. According to the variance components in Tables 3 and 4, the concatenation of these datasets delivered generally reliable results. For most production traits, the estimated variance components were generally in line to what is expected according to the review by Safari et al. (2005) as well as more recent studies on Merinos (Huisman et al., 2008; Mortimer et al., 2017; Safari et al., 2007; Swan

TABLE 5 Bias (β_0) and dispersion (β_1) from ABLUP and ssGBLUP analysis for production and reproduction traits evaluated according to validation designs Scenarios (I) and (II).

	Production										Reproduction					
	WW		YW		FD		CFW		SL		NLB		NLW		TWW	
	ABLUP	ssGBLUP	ABLUP	ssGBLUP	ABLUP	ssGBLUP	ABLUP	ssGBLUP	ABLUP	ssGBLUP	ABLUP	ssGBLUP	ABLUP	ssGBLUP	ABLUP	ssGBLUP
β_0																
I	0.12	0.25	0.01	0.01	−0.14	−0.14	0.01	0.07	0	0.06	−0.05	−0.02	−0.06	−0.08	−0.1	−0.1
II	−0.13	−0.11	−0.16	−0.17	0.02	0.04	−0.13	−0.12	0.02	0	−0.14	−0.17	−0.16	−0.23	−0.17	−0.03
β_1																
I	0.69	0.69	0.59	0.73	0.91	0.93	0.66	0.68	0.78	0.79	1.09	1.06	1.18	1.17	1.29	1.16
II	0.63	0.83	0.67	0.66	1.04	0.97	0.57	0.62	0.77	0.76	0.6	0.59	0.93	0.92	0.47	0.35

Note: Bias was standardized to units of genetic standard deviation (σ_g) for a particular trait. See Table 1 for trait abbreviations.

et al., 2008, 2016) An exception could be the low values for WW, for which multiple studies support a considerably higher h^2 (Huisman et al., 2008; Safari et al., 2005, 2007; Swan et al., 2008). The derived h^2 for SL was also low compared to multiple values reported as exceeding 0.5 (Huisman et al., 2008; Swan et al., 2008, 2016). For reproduction traits, a low h^2 has become well accepted, with values commonly below 0.05 and very unlikely to exceed 0.10 (Bunter et al., 2016; Bunter & Brown, 2015; Newton et al., 2014; Pickering et al., 2012; Walkom & Brown, 2017). A more detailed treatment of the fixed effects can be seen elsewhere (Nel, 2022) and will not be discussed here.

With a high level of genetic diversity for sheep (Kijas et al., 2009), and especially Merinos (Al-Mamun et al., 2015; Ciani et al., 2015; Nel, Gurman, et al., 2022; Prieur et al., 2017), it is expected that a large reference population is needed to achieve useful levels of accuracy by genomic selection (GS). However, despite a relatively modest reference population size in this study, the use of genomic information benefited the accuracy of prediction meeting or exceeding the expected gain amounting to between +5 and +15% for sheep (van der Werf et al., 2014).

The 2811 individuals represented in the GRM represents only a very small proportion if weighed against the total size of the pedigree (88,600 animals), or the 79,100 of animals with WW records. However, while the genomic dataset used in this study is limited, the useful gains in ACC_{LR} in Scenario I could have depended on having the bulk of the genotypes originating from animals born after 2006 (Table 2). The most valuable information is derived from the most recent, and implicitly the genetically closest, animals in the reference population (Habier et al., 2007, 2010), and the design of Scenario I aligned the most recent animals in the reference population with the peak genotyping rate (Table 2) Also, it is important to note that validation animals in Scenario I were not restricted from being born from sires with progeny also in the reference set, thus having the benefit of being connected by close relatives such as half sibs for better prediction accuracy (Clark et al., 2012).

The results varied across traits, however, and gains in accuracy were more marginal for the reproduction trait group (Figure 2). This was true especially for NLB, the only example in this study where the use of genomic data did not improve ACC_{LR} in Scenario I. For low h^2 (Table 4), sex limited traits such as NLB or NLW, a larger reference population size, or higher genotyping rate, would improve results (Daetwyler et al., 2008; Li et al., 2017). However, issues with reproduction datasets could also influence prediction parameters. For example, the failure to submit and/or process mating lists, or to accurately report lamb mortality, is a common problem for flocks participating

in the NSIS. Consequently, composite traits like NLW can fail to capture the underlying components of reproduction. This would affect accuracy (Olivier, 2022), and could result in bias when different phenotypic means (due to a failure to express NLB/NLW = 0) is confounded by industry data as a genetic group (Figure 1). It also prohibits for NLW to be decomposed into its underlying components such as conception, litter size and ewe rearing ability (Nel, Swan, et al., 2022; Swan & Bunter, 2021), traits that would otherwise have been an attractive target for GS methods in future studies.

It is important that such issues are investigated prior to wide-scale investment into generating genomic data, since the real-world benefit of genomic methods reported in Figure 2 are most applicable to reproduction traits. Currently, it is standard protocol for stud flocks participating in the NSIS to deliberately keep selection candidates until yearling age, at which time point most of the key production traits are recorded. Naturally, this is not the case for reproduction traits, and candidates must be considered for selection without records of their own.

In the literature, most previous studies evaluating GS in Merinos were based on 'genomic-BLUP' (GBLUP) methods that directly replaced $\boldsymbol{A}$ with $\boldsymbol{G}$. From these, Moghaddar et al. (2014) reported the accuracy of prediction (Pearson correlation between a_p and a_w) of GEBVs in Australian Merinos for WW (0.52), YW (0.58), CFW (0.65), FD (0.72) and SL (0.56) as slightly higher compared to those reported here (Figure 2). Very high prediction accuracies of 0.73 for GFW and 0.79 for FD were reported from the earliest GBLUP results for Merinos (Daetwyler et al., 2010), but results for meat traits were lower and highly variable (−0.04 to 0.57). Also from GBLUP analysis, Moghaddar et al. (2019) reported reasonable accuracies for CFW (0.35) and post-weaning weight (0.40), but a comparatively low estimate for FD (0.38). The study by Brito et al. (2017) reported similar accuracies for WW (0.46) and live weight at 6 months (0.41) from a multi-breed population in New Zealand. Using a two-step blending approach, accuracies were also high (0.75–0.87) from blended 'multi-step' GEBVs in Merino sires for both weight and wool traits, commonly with gains between 0.05 and 0.07 compared to standard ABLUP analyses, but also higher than GBLUP results from the same study (Swan et al., 2012). Applying ssGBLUP, Gurman et al. (2018) reported a favourable mean increase of ~0.10 in accuracy across a variety of traits including liveweight, carcase and worm egg count measurements in Australian terminal sheep, but the values were based on changes in genotyped individuals. Similarly, Kaseja et al. (2023) reported a range between 0.07 and 0.09 gain in accuracy (square root of reliability) for weight and carcase traits in genotyped Texel lambs, but also based on only genotyped candidates. Kaseja et al. (2023) also reported a negligible gain in population wide accuracy when the validation set also included non-genotyped animals. The authors explained that only a very small proportion of the large group of animals in the pedigree would have had useful links genotyped individuals with records. For the major sheep breeds in New Zealand, Lee et al. (2021) reported up to a 10% average increase in accuracy associated with ssGBLUP for yearling fleece weight, but results varied widely across breeds.

For reproduction traits, Daetwyler et al. (2014) reported GBLUP accuracies from 0.06 to 0.12 for NLB, NLW and litter size in Merinos when predicting strictly across sire families, but with a much higher range of 0.21–0.40 when the validation sets were assigned at random. A similar pattern was reported by Bolormaa et al. (2017), but with a slightly higher GBLUP accuracy (0.32–0.54) for reproduction traits when predicting across randomly assigned groups. In other examples of sex limited traits, Legarra et al. (2014) reported an increase in accuracy of between 0.05 and 0.30 for milk yield derived from ssGBLUP in Western Pyrenees dairy sheep breeds. They also reported results to be highly variable across breed groups, and in selected instances, better results were obtained from ABLUP. In Lacaune dairy sheep, Baloche et al. (2014) reported an increased accuracy of roughly 0.10 across a variety of milk type traits.

In addition to this study, the majority of literature results support the benefit of genomic data in small stock breeding. Differences in methodology, design, trait types and size of datasets make direct comparison difficult, but the importance of connectedness between reference and target animals is a clear pattern across studies. Accordingly, the 'across flock' design of Scenario II would have markedly reduced the number of close relatives in the reference population, resulting in much lower overall values of ACC_{LR} (Figure 2). However, this design was also in place when the ssGBLUP model delivered the largest relative gains (Figure 2), and in selected cases, capable of matching or exceeding the accuracy of ABLUP in Scenario I. GS was capable of moderate accuracies in relatively unrelated populations when ABLUP predictions were very low (Clark et al., 2012). If reliable breeding values can be derived for a flock where the particular trait is not recorded, it points to promising potential for the objective of genetic selection for 'difficult-to-measure' traits, outlined as one of the primary benefits of GS methods (van der Werf et al., 2014). Genetic selection within a limited scope, such as sole emphasis on production or 'output' traits, risks detrimental effects in metabolic, reproductive, metabolic or behavioural traits in farm animals (Rauw et al., 1998). In turn, genetic selection to the benefit of animal health and welfare (Jensen et al., 2008; Rauw, 2016) can also deliver

indirect economic benefits by reducing input costs and reproductive wastage.

In contrast to the developments of Sheep Genetics Australia (Brown et al., 2007, 2018) or Sheep Improvement Limited in New Zealand (Newman et al., 2000, 2010), no traits indicative of animal resilience or fitness are currently recorded by the National Small Stock Improvement (NSIS) in South Africa (Cloete & Olivier, 2010). Currently, the recording of difficult to measure traits is limited to within resource flocks only, reporting useful components of genetic variation for traits such as faecal worm egg count (Cloete et al., 2007; Matebesi-Ranthimo et al., 2014), absence of breech strike (Scholtz et al., 2010), lamb survival (Cloete et al., 2009), or maternal behaviour (Cloete et al., 2021).

If breeding objectives in the wider SA industry were to consider these or similar fitness traits, the application of GS methods such as ssGBLUP could facilitate genetic progress. Some promising gains in accuracy has been reported, for example, for faecal worm egg count (Gurman et al., 2018) or footrot and mastitis (Kaseja et al., 2023) when comparing ABLUP with ssGBLUP. Following this, the most attractive strategy for SA is outlined by the question: 'can we use GS methods to predict the performance of industry animals from data recorded in the resource sector?' However, preliminary analysis showed the success of an 'across-sector' design (reference = only resource animals, validation = only commercial animals) to be very low, sometimes with $\mathrm{cov}(\hat{a}_w, \hat{a}_p) < 0$, and only marginal gains from the ssGBLUP model (Nel, 2022). The PCA results suggested limited linkage between research and industry sectors for SA Merinos (Figure 1), and genomic prediction has limited penetration across distant populations (Habier et al., 2007, 2010). Also, it should be noted that the industry flocks in this study were selected because of at least some known links to resource flocks, and the prospect of predicting across sectors will become even less feasible if they were picked at random from the NSIS database.

Genomic information can be a useful tool to enhance genetic gain but will be best exploited if combined with strategies to address these limitations. A centralized reference population recording difficult to measure traits for prediction in the commercial sector can be a viable strategy (Alexandri et al., 2022) but needs to be specifically designed for this purpose (van der Werf et al., 2010). The useful results reported for Scenario II depended on information being available from both sectors, and it is likely that at least some commercial flocks will have to participate in the recording scheme if new traits were to be considered for genetic selection on a wide scale.

Additionally, future genotyping for SA Merinos should commence strategically, and not based solely on increasing the size of the reference population. Examples of large reference populations have underperformed compared to the expected accuracy for their size (van der Werf et al., 2014) whereas numerically small genomic datasets have delivered useful results for a well-connected population (Legarra et al., 2014). An average per-flock genotyping rate is arguably a more sensible guide compared to simply targeting many genotypes. This would account for any genetic groups that could exit due to isolated flocks or strains, and allow a good chance of at least some close relatives in the reference set (Clark et al., 2012).

There was little indication of strong bias (β_0) favouring either proven 'old' or unproven 'new' animals (Table 5). There was also no clear trend across traits, except that reproduction traits tended to all be underestimated ($\beta_0 < 1$). Over dispersion ($\beta_1 < 1$) of some traits tended to be a bigger concern in this dataset. The realistic expectation of β_1 is in fact below 1, since a_w is only an approximation of the 'true' accuracy (Legarra & Reverter, 2018), but in some cases the values of β_1 was very low (<0.50; Table 5). For animals ranked at the 'better' end of the distribution, over-dispersion leads to overestimating 'new' candidates and bias against the retaining candidates in the current breeding flock. From a single trait point of view, the practical impact of this issue is arguably limited because breeding flocks tend to have a standard number of replacements selected each year, at roughly 20–25%. However, if animals are ranked according to a multi-trait index, it will be problematic given that the dispersion of some traits are inflated more than others (Table 5). Models incorporating genomic information improved slopes (β_1) elsewhere (Baloche et al., 2014; Legarra et al., 2014), but there was no clear pattern to suggest that the ssGBLUP model improved either bias or dispersion in this study. With composite reproduction traits such as TWW being the most susceptible to over dispersion (Table 5), it would be interesting to see the behaviour of component traits (Nel, Swan, et al., 2022; Swan & Bunter, 2021) according to these prediction metrics.

It should be noted that this study has not exhausted all the methodological options. Measures of accuracy and bias are sensitive to particular cut-off points in a (Scenario I) cross validation design (Macedo et al., 2020). Repeated analysis with different time or year cohorts could improve the reliability, but a larger dataset with a more uniform genotyping programme is needed for this approach. In addition, the scaling parameters α and β heavily weighted information in $\boldsymbol{G}$ when deriving $\boldsymbol{H}^{-1}$ and alternative scaling parameters could potentially yield better results (Lee et al., 2021; McMillan & Swan, 2017).

Finally, there is an opportunity to facilitate development of genomic reference populations by including genotype and phenotype data from Australian Merinos

(Nel et al., 2019; Nel, Swan, et al., 2022). The reference populations and pipelines for analysis has already been well established for these breeding programmes (Brown et al., 2018; Swan et al., 2014), but across country genomic prediction (e.g. de Oliveira et al., 2021) is yet to be investigated for Merino sheep.

5 | CONCLUSIONS

This study was the first to deliver a validation of the benefit of genomic information in South African Merinos and is the first for any South African sheep breed. It has shown potential for genomic data to enhance genetic prediction in South African Merino breeding programmes, assuming that continuous genotyping of new candidates can be incorporated into routine management of stud flocks. Reproduction traits are likely to be an important target of GS methods, but results were more mixed for this trait group. Some prediction parameters were also not improved by GS methods, and it is important that some underlying issues with recording are addressed prior to large-scale investment into generating marker data. There is potential for GS to facilitate broadening the scope of selection objectives for SA sheep breeds, but it will require a deliberate effort to establish genetic links and more widespread recording of difficult to measure traits in at least selected commercial flocks.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonablerequest.

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