Evaluating the effect of ssGBLUP on a composite beef cattle population with limited pedigree completeness

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Abstract

To improve the accuracy of estimated breeding values (EBV), correct parentage assignment remains a cornerstone of BLUP. Genomic evaluations can alleviate constraints experienced during the assessment of young animals in large populations, especially for animals with limited pedigree depth and for traits of low heritability. South African (SA) Beefmaster (BMA) breeders mostly are prone to using multiple sires in their herd, with a low parentage verification rate resulting in a larger proportion of young animals with at least one unknown parent. Upgrading of first acceptance cows with blank pedigrees, was common in the establishment of the SA BMA breed. The completeness of a 451,009 animal pedigree, consisting of 187,448 males and 263,561 females dating back to 1937 was assessed. Records for birth weight (BW) and adjusted weights at 205, 365 and 540 days of age (WW, YW, M18W) were collated for the growth multi-trait model, while the fertility multi-trait model included records for adjusted weight at 205 days of age (WW), heifer fertility (HF) and the first three inter-calving periods (ICP). Breeding values and trait reliabilities for registered animals, were either estimated traditionally (BLUP) or with the inclusion of genomic information (ssGBLUP). Genomic profiles of 1,397 recorded animals, genotyped across five commercial single nucleotide polymorphism (SNP) arrays of varying densities, were imputed to a reference genotype of ~132,000 SNPs. Animals with varying proportions of known ancestry allowed for a comparison of genotyped animals across the herd book status of upgrading. The assessment of pedigree completeness indicated a substantial decay in pedigree depth, higher in females compared to males, after the grand-parent generational equivalent. The ssGBLUP accuracies were higher across all traits (0.01 – 0.89), with equal increases observed for animals with limited pedigree depth (only 1 or 2 generations) as to young animals with minimal to no measured phenotypes. The change between conventional and genomic breeding values decreased as the depth of pedigree increased. The results obtained indicate the knowledge of genetic relationships through ssGBLUP allow for increased reliability of predictions for foundation animals with limited or unknown pedigree structure.

Key Words: pedigree completeness, genetic evaluation, single-step GBLUP, multiple sires

Introduction

To improve the accuracy of estimated breeding values (EBV), correct parentage assignment remains a cornerstone of BLUP. Genomically enhanced breeding values (GEBVs) are increasingly being used to predict values for all animals in the pedigree using single step mixed model equations (MMEs) (Legarra et al. 2014). GEBVs are calculated using a genomic relationship matrix (GRM) in conjunction with MMEs (Taskinen et al. 2013). Genomic evaluations can alleviate constraints experienced during the assessment of young animals in large populations, especially for animals with limited pedigree depth (Clark et al. 2012; Gowane et al. 2022) and for traits of low heritability (Hayes and Goddard 2010; Kluska et al. 2018).

The South African (SA) Beefmaster (BMA) was established through the importing of live semen and live animals from Lasater's herd and purebred herds associated with the Beefmaster Breeders United (BBU) (Beefmaster SA

Website). The SA BMA was ratified as an established breed in 1987 and is currently the second largest stud beef cattle breed being serviced by the SA Stud Book and Animal Improvement Association (SASB). SA BMA breeders are distributed throughout the country, utilise a mix of extensive farming in conjunction with available crop fodder or crop residues, with average herd sizes of around 450 animals and commonly use multiple sires on their cow herds. The SA BMA has a low parentage verification rate, resulting in a larger proportion of young animals with at least one unknown parent. Breeders from a commercial background were prone to upgrading first acceptance (FA) and Section A cows with blank pedigrees alongside Stud Proper (SP) BMA bulls when establishing their SA BMA herd. These cows will also lack production and fertility related measurements themselves as they can come into the herd at any age. Progeny of Section A cows mated with SP, Section C or Section B bulls are allocated Section B herd book status. SP progeny can only arise from Section C or SP parents. The use of multiple sires introduces a high percentage of Section B calves that have an unknown sire pedigree coupled with the upgrading of cows with poor pedigree depth results in lower accuracies when predicting the genetic merit of these animals (Clark et al. 2012; Gowane et al. 2022).

The objectives of this study were to firstly assess the level of pedigree completeness across the levels of upgrading in the SA BMA and to identify any changes in breeding value estimation and accuracy of measured growth and fertility traits when using genomic data on a breed with limited pedigree completeness.

Materials and Methods

Data

The phenotypic data were acquired from the LOGIX Genetic Evaluation System (SA Stud Book / SA Stamboek). Records for birth weight (BW) and adjusted weights at 205, 365 and 540 days of age (WW, YW, M18W) as well as fertility records for heifer fertility (HF) and the first three inter-calving periods (ICP1, 2 and 3), are summarised in Table 1.

Table 1. Total number of weight and fertility records for birth weight (BW), weaning weight (WW), yearling weight (YW), weight at 18 months (M18W), heifer fertility (HF) and the first three inter-calving periods (ICPs).

Trait	Number of Male Records	Number of Female Records	Total Number of Records
BW	146,501	143,522	290,023
WW	132,022	135,323	267,345
YW	41,750	77,299	119,049
M18W	29,804	54,801	84,605
HF	-	68,089	68,089
ICP1	-	46,795	46,795
ICP2	-	33,078	33,078
ICP3	-	23,821	23,821

Pedigree information on 451,009 animals, consisting of 187,448 males and 263,561 females dating back to 01 September 1937 including the phenotypic data and herd book upgrading status, is reported in Table 2.

Table 2. Pedigree information on the South African Beefmaster based on by herd book upgrading status.

Herd Book Population	Number of Males	Number of Females	Total
Total	187,448	263,561	451,009
Stud Proper	32,339	32,149	64,488
Section C	38,728	38,316	77,044
Section B	99,836	108,575	208,411
Section A	3,281	67,971	71,252
FA	0	9,511	9,511
Pending	1,718	1,624	3,342
NFR	11,347	5,140	16,487

FA: first acceptance; NFR: not for registration.

Genomic profiles of 1,797 SA BMA animals, genotyped across five commercial single nucleotide polymorphism (SNP) arrays of varying densities, were used in this study. Much of the genomic population was initially genotyped on the GeneSeek Genomic Profiler (GGP) 150K or GGP 80K primarily through funding from the SA Beef Genomics Project (BGP). After the BGP ended in 2018, genotyping was done on commercial variants of the Illumina BovineSNP50 v.3; namely the ICBF IDB v.2, SASB 50K or the Versa 50K.

Quality control of genomic SNP data, done

in PLINK v1.9 (Purcell et al. 2007), consisted of keeping only autosomal SNPs with a known base pair position, a call rate≥0.90, a MAF≥0.10 and did not significantly deviate from Hardy-Weinberg equilibrium (p>0.001). Animals required a call rate ≥90% while individuals with ≥0.95 identical genotype were discarded. Population stratification of the post-QC genomic data allowed for the possible detection of outliers and returned a final set of 1,397 SA BMA genotypes. Genotypes were imputed alongside pedigree information with FImpute v3 (Sargolzaei et al. 2014) to a density of ~130,000 SNPs.

Models

Using R version 4.2.3 (RStudio Team 2015), the optiSel R package (Wellmann, 2019) was utilized in conjunction with Poprep (Groeneveld et al. 2009), to assess the complete generation equivalent (CGE), pedigree completeness index (PCI) and F_{PED} coefficients (Meuwissen and Luo 1992) of the total and genotyped BMA populations. The total pedigree consists of all 451,009 animals in the BMA pedigree, while the fully traced back genotyped pedigree contains 7,630 animals (1,974 males and 5,683 females) related to the core 1,397 animals in the genomic population. Grouping for the calculation of the mean (standard error) of CGE, PCI and F_{PED} occurred at a whole population level, sex level, genotyped pedigree level and herd book allocation in order to compare across levels of upgrading.

In order to predict estimated breeding values, two multi-trait animal linear models were assessed. The growth and fertility models were defined as follows:

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Zu} + \boldsymbol{e},$$

where **y** is the vector of phenotypes, **b** is a vector of fixed effects, **u** is a vector representing the direct additive-genetic effects, with **u** ~ N(0,A σ_u^2), where A is the pedigree-based matrix and σ_u^2 is the direct-genetic variance, **e** represents the residual, where e ~ N(0,I σ_e^2), with σ_e^2 representing the residual variance, **I** the identity matrix while **X** and **Z** are incidence matrices for **b** and **u** respectively.

Fixed effects in **b** for the growth trait model were herd x year x season x treatment group x birth status, sex, age, dam parity (1 or >1) and linear (α) and quadratic (α^2) regression coefficients for age of dam. Fixed effects in **b** for the fertility trait model were herd x year x season x treatment group x birth status for WW which was used as an anchor trait, herd x year x season for HF and herd x year x season x previous calving group for each ICP.

Estimation of variance components for the two animal models stated above were calculated using restricted estimated maximised likelihood (REML) optimised with quasi-Newton procedure using analytical gradients in Variance Component Estimation (VCE) (Groeneveld, 2010) software. MiX99 (MiX99 Development Team, 2017) was used to predict both traditional EBVs and GEBVs using the same models in the estimation of variance components. The ssGBLUP model utilises the inverse of the joint relationship matrix $\mathbf{H^{-1}}$ (Aguilar et al. 2010; Legarra et al. 2014).

$$\boldsymbol{H}^{-1} = \boldsymbol{A}^{-1} + \begin{pmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{G}^{-1} - \boldsymbol{A}_{22}^{-1} \end{pmatrix},$$

where $\mathbf{A}^{-1}$ is the inverse of the pedigree-based matrix, $\mathbf{A}_{22}$ is the overlapping part of A for the genotyped animals and **G** is the genomic relationship matrix (GRM). The GRM was constructed among all animals using the RelaX2 HGInv program (Strandén, 2014).

Pedigree-based and genomic reliabilities were calculated utilising the program ApaX99 (Lidauer et al. 2017) implementing the Misztal and Wiggans approach (Misztal and Wiggans 1988), where the Misztal approximation method 1 (Misztal et al. 2013) accounts for full genomic information. These reliabilities were subsequently transformed into accuracies.

Results and Discussion

At a population level, 33.9% of SA BMA animals in the pedigree are demarcated as “Sire

Unknown", with a further 16.7% of animals having "Both Parents Unknown". The mean, interquartile range (IQR), and median years of birth for the whole BMA population was 2008, 1994 to 2009 and 2011, respectively and 2001, 1994 to 2009 and 2003 for the genotyped BMA population. A slightly higher pedigree depth of 16 generations for the whole BMA population was noted against the genotyped BMA populations pedigree depth of 15 generations. Assessment of pedigree depth indicated a mean pedigree completeness index (PCI) and mean complete generational equivalent (CGE) of 0.298 (SE = 0.347) and 1.975 (SE = 1.720) for the whole BMA population and 0.381 (SE = 0.350) and 2.067 (SE = 1.753) for the genotyped BMA population. Table 3 indicates the mean pedigree completeness of the genotyped pedigree to be higher than that of the whole pedigree born. Females are observed to have a shallower pedigree completeness, as SA BMA breeding bulls must have known parentage in order to upgrade cows with limited pedigree completeness.

Table 3. The mean six-generation deep pedigree completeness of the SA Beefmaster for A) the whole pedigree (451,009 animals) and B) the genotyped pedigree (7,630 animals) born within the period 2011 to 2021 and split on a sex level

	Whole		Genotyped	
GD	Male	Female	Male	Female
1	1	1	1	1
2	0.792	0.568	0.886	0.614
3	0.518	0.366	0.677	0.423
4	0.365	0.257	0.491	0.293
5	0.263	0.183	0.349	0.192
6	0.184	0.128	0.239	0.117

GD: generation depth.

The inbreeding coefficients (F_{PED}) observed ranged from 0 to 0.2995 with a mean of 0.007 for both the whole and genotyped BMA population. The CGE and PCI were seen to be lower in the whole BMA pedigree (1.975 and 0.298) in comparison to the genotyped BMA pedigree (2.067 and 0.381). Genotyped Stud Proper animals had the highest F_{PED} (0.021), CGE (4.466) and PCI (0.859), across all the levels of upgrading, with genotyped Section A animals having the lowest CGE (0.470) and PCI (0.056), respectively (Table 4).

Table 4. Pedigree statistics including the birth year range, mean (μ) and standard error (SE) for various groupings of the South African Beefmaster population which include level of inbreeding (F_{PED}), pedigree completeness index (PCI) and complete generational equivalents (CGE)

Group	Birth Year Range	F_{PED}	PCI μ (SE)	CGE μ (SE)
WP	1937–2021	0.007	0.298 (0.35)	1.975 (1.72)
GP	1956–2021	0.007	0.381 (0.35)	2.067 (1.75)
GA	1985–2021	0.012	0.603 (0.32)	3.148 (1.58)
GSP	1999–2021	0.021	0.859 (0.13)	4.466 (0.92)
GSC	1994-2021	0.012	0.660 (0.17)	3.445 (0.95)
GSB	1985-2021	0.001	0.241 (0.24)	2.095 (1.19)
GSA	1997-2013	0.002	0.056 (0.20)	0.470 (1.16)

WP: whole pedigree; GP: genotyped pedigree; GA: genotyped animals; GSP: genotyped stud proper animals; GSC: genotyped section C animals; GSB: genotyped section B animals; GSA: genotyped section A animals.

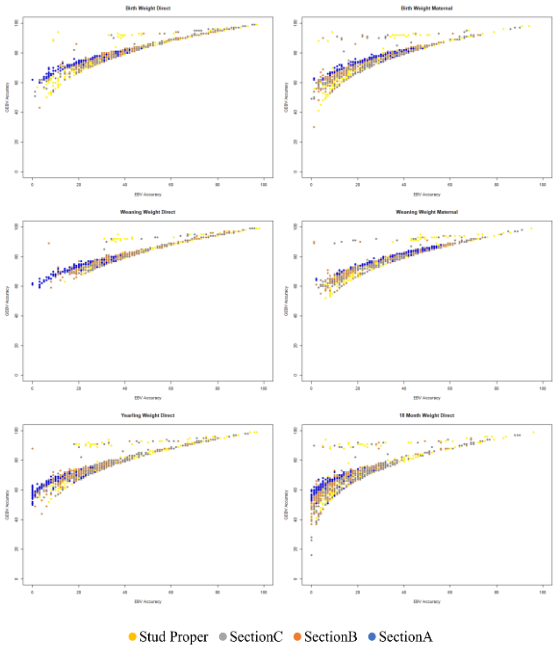
The generated solutions of the genotyped animals were extracted and compared for the various traits in the growth and fertility models. Observed coefficients of determination (R^2), between the EBVs or accuracies and their corresponding genomically enhanced solutions were lowest for Section A animals across all directly measured traits (Table 5). The biggest differences were observed for maternal traits, especially the WW_{MAT} of the genotyped SP animals ($R^2 = 0.888$), and the ICP1 ($R^2 = 0.843$) and ICP3 ($R^2 = 0.861$) of the total genotyped population.

Trait reliabilities were transformed into accuracies and plotted against their genomically enhanced counterparts. Animals were identified according to the herd book level of upgrading and compared accordingly. Increases in accuracy (0.01 – 0.89) when using genomic information were seen across all growth traits (Figures 1-6).

Table 5. The coefficient of determination (R^2) between estimated breeding values and genomically enhanced breeding values derived from the growth and fertility models for the South African Beefmaster population.

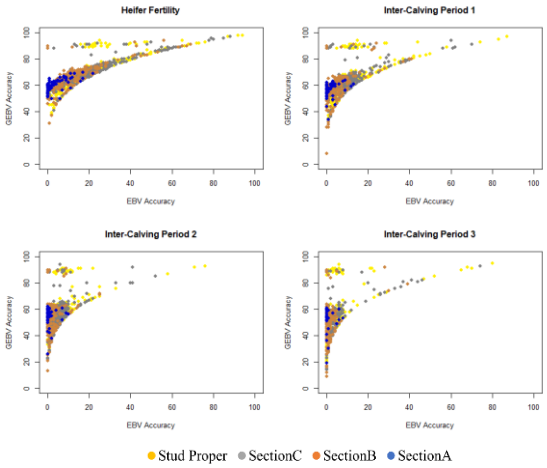
Trait	R^2				
	GA	GSP	GSC	GSB	GSA
BW_{DIR}	0.914	0.898	0.915	0.942	0.843
BW_{MAT}	0.869	0.858	0.843	0.904	0.849
WW_{DIR}	0.929	0.907	0.940	0.952	0.728
WW_{MAT}	0.907	0.888	0.907	0.930	0.928
YW	0.929	0.917	0.941	0.946	0.668
M18W	0.928	0.917	0.940	0.944	0.672
HF	0.896	0.882	0.899	0.917	0.874
ICP1	0.843	0.819	0.852	0.904	0.734
ICP2	0.879	0.842	0.898	0.929	0.844
ICP3	0.861	0.857	0.849	0.910	0.699

GA: genotyped animals; GSP: genotyped stud proper animals; GSC: genotyped section C animals; GSB: genotyped section B animals; GSA: genotyped section A animals.



Figures 1-6: The direct estimated breeding value (EBV) plotted against the direct genomically enhanced breeding value (GEBV) accuracy for the traits included in the growth model.

Higher average increases of 10% in accuracy were observed for traits included in the fertility model (Figures 7-10) in comparison to growth traits. The traits of low heritability ICP2 (0.13-0.90) and ICP3 (0.09-0.90) having the highest observed increases in accuracy.



Figures 7-10: The direct estimated breeding value (EBV) plotted against the direct genomically enhanced breeding value (GEBV) accuracy for the traits included in the fertility model.

The SA BMA had an estimated pedigree CGE of 1.975, which is similar to the CGE that were observed in local indigenous beef breeds such as the Afrikaner (2.81; Pienaar et al. 2018) and the Bonsmara (2.19; Santana et al. 2012). (Gutiérrez et al. 2003) observed low CGEs, ranging from 0.81 to 2.97, in eight Spanish beef cattle breeds, while a low CGE of 1.79 was observed in Istrian cattle (Ivanković et al. 2022). In comparison to pure and composite beef and dairy breeds with robust pedigree records such as the Lidia cattle (5.5; Cortés et al. 2019), Marchigiana cattle (4.52; Santana et al. 2012), Mexican Charolais cattle (7.86; Ríos-Utrera et al. 2021), American Brangus (6.8; Paim et al. 2020) as well as the SA Ayrshire (9.74), SA Holstein (11.70), and the SA Jersey (10.05) populations studied by Visser et al. (2023), the SA BMA showed a substantially lower mean CGE. This can firstly be attributed to the prevalent use of multiple sires in herds with low parentage verification rate, increasing the number of Section B animals with at least one unknown parent. Secondly, the upgrading process introduces foundation cows (first acceptance and Section A) with limited to no pedigree information, further contributing to a shallow pedigree depth. Stud Proper and Section C animals were observed to have a higher average CGE and PCI in comparison to Section A and B animals, which is a

consequence of these animals requiring established pedigrees through known parentage.

The low inbreeding estimates (F_{PED} = 0.007) calculated in the SA BMA, in comparison to the SA Ayrshire (F_{PED}=0.051), Holstein (F_{PED}=0.064) and Jersey (F_{PED}=0.062) populations (Visser et al. 2023) and Lidia cattle (F_{PED} = 0.13; Cortés et al. 2019), indicate an inaccurate reflection of inbreeding at a population level, that can be attributed to the observed low pedigree completeness in the SA BMA (PCI = 0.298). Similar results in other smaller populations such as Afrikaner (F_{PED} = 0.0183; Pienaar et al. 2018) the Creole Blanco Orejinegro breed (F_{PED} = 0.0132; Gallego et al. 2020), Argentinian Brangus (F_{PED} = 0.0240; Garrido et al. 2008), the SA Brangus (F_{PED} = 0.0139; Steyn et al. 2012), Bonsmara (F_{PED} = 0.0026) and Marchigiana (F_{PED} = 0.0133) (Santana et al. 2012), and F_{PED} of eight Spanish beef cattle breeds ranging from 0.0025 to 0.0313 (Gutiérrez et al. 2003) have been previously reported. These breeds have either a small population size and/or poor pedigree depth due to the behaviour of pedigree recording on a breed level, which are the two primary contributing factors to lower estimates of inbreeding (Nielsen and Slatkin 2013).

The observed changes in breeding values when including genomic information occurred at multiple levels. At a population level, the traits where genomics had the highest influence were BW_{MAT} (R^2 = 0.869) and WW_{MAT} (R^2 = 0.907) for the growth model, and ICP1 (R^2 = 0.843) and ICP3 (R^2 = 0.861) in the fertility model. Maternal traits are well-known to be lowly heritable (Olasege et al. 2021; Saatchi et al. 2012) and the accuracy of these traits traditionally increase as an animal's progeny-performance records increase. Fertility traits are sex-limited and measured later in animals' life which contributes to the lower prediction accuracies and heritability's estimated in these multi-trait models (Facy et al. 2023; Hayes et al. 2019). Progeny-performance records coupled with pedigree linkages act as a feedback mechanism that enable a more accurate prediction of a bull's or cow's genetic potential. At a herd book level, Section A animals experienced the greatest observed changes in EBV, especially as Section A animals may have no growth or fertility performance records if they are foundation cows. Interestingly, the change in WW_{MAT} for Section A animals (R^2 = 0.928) is an outlier of the previous statement and is a consequence of these foundation cow's progeny calves and great-progeny calves being measured for WW. On an individual basis, animals that can be seen as a separate bubble in Figures 1 to 10, the greatest changes were observed in Section B, C and Stud Proper bulls that were used as multiple sires but were never allocated to progeny on a known parentage basis. This resulted in these bulls never being allocated progeny-performance records. Although these multiple sires may not be linked to the broader SA BMA population through the pedigree, they are well-represented on a genetic basis through the genomic population with other genotyped animals with numerous progeny-performance records. Young Section C and Stud Proper animals also experienced similar increases in prediction accuracy and was observed to be for traits that they had yet to be measured for, were sex-limited and lowly heritable.

The assessment of pedigree completeness indicated a substantial decay in pedigree depth, higher in females compared to males, after the grand-parent generational equivalent. The ssGBLUP accuracies were higher across all traits, with equal increases observed for animals with limited pedigree depth as to young animals with minimal to no measured phenotypes. The change between conventional and genomic breeding values decreased as the depth of pedigree increased.

Conclusions

The results obtained indicate the knowledge of genetic relationships through ssGBLUP allow for increased reliability of predictions for foundation animals with limited or unknown pedigree structure.

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