Implementation of single-step genomic BREEDPLAN evaluations in Australian beef cattle

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Summary

Single-step GBLUP (ssGBLUP) procedures have now been implemented into Australia's BREEDPLAN genetic evaluation system for beef cattle. This major remodelling required the development of many new features and modifications to existing procedures. The first requirement was the construction of a flexible but robust set of procedures for handling and processing of raw SNP genotypes to enable the construction of suitable genomic relationship matrices. The analytical processes were modified to replace with and for the explicit fitting of genetic groups. A new accuracy algorithm was developed and the solver was revised. Examples from Australian Angus and Brahman breeds comparing current BLUP evaluation with ssGBLUP are presented to show the resultant changes and effects of implementing the new genomic evaluations.

Keywords: genomic evaluations, single-step, beef cattle.

Introduction

Genomic selection is rapidly changing dairy breeding (Garcia-Ruiz *et al.* 2016) with rates of genetic progress increasing 2-4 fold for most dairy traits. This phenomenal change was made possible with the advent of low-cost, high density SNP microarrays and the application of genomic selection (Meuwissen *et al.* 2001). However, for beef cattle the impact of genomic selection has been less pronounced to date. The BREEDPLAN analytical software (Graser *et al.* 2005) developed by the Animal Genetics and Breeding Unit (AGBU) has evolved over the past decade to include a range of DNA marker-based predictions. Single-step procedures (Legarra *et al.* 2014) have recently been implemented into several livestock evaluations, including US Angus (Lourenco *et al.* 2015), and this paper presents the implementation of single-step procedures in the routine BREEDPLAN genetic evaluation, and closely parallels developments in Australian sheep genetic evaluations.

Progression of including DNA based predictions in BREEDPLAN

DNA based predictions have been included in BREEDPLAN since 2008 with the inclusion of GeneSTAR meat tenderness gene marker predictions, with effects estimated from Beef CRC data (Johnston and Graser 2010). Genomic values were included as additional predicted phenotypes in the multi-trait BLUP evaluations using a 0.28 estimated genetic correlation (Johnston *et al.* 2009). Development of the bovine 50K microarray in 2008 saw the first genome-wide SNP based predictions from Pfizer Animal Genetics for Angus cattle in 2011.

These predictions, called MVPs, were included in Angus BREEDPLAN in 2011 using a post-BLUP blending method. Genomic accuracies were estimated in an independent dataset and ranged from 0.21 to 0.44 for a limited number (N=9) of traits (Johnston *et al.* 2010). This was shortly followed by an increased number of genomic predictions and an expanded number of products and traits e.g. Igenity and Beef CRC direct genomic values (DGV) (Boerner and Johnston 2013, Boerner *et al.* 2014a,b). These new genomic predictions were incorporated into BREEDPLAN using a modified blending algorithm that enabled multi-source genomic information. In 2014, genomic accuracies for blending in Angus were re-estimated for 12 traits and the genomic accuracies ranged from 0.27 to 0.62 (Boerner *et al.* 2014c). In the same year, Brahman BREEDPLAN was modified to include the blending of Beef CRC DGVs for weaning weight and the female fertility EBV, days to calving with accuracies of 0.27 and 0.35, respectively.

New procedures for implementing ssGBLUP

Adoption of wide-scale SNP genotyping in beef cattle breeding is currently low and represents a very small proportion of the total animals in current evaluations. Therefore evaluations need to utilise existing pedigree information as well as efficiently use genomic information from the small numbers of genotyped individuals. Current blending approaches have limitations with regard to calibration and implementation but the development of single-step procedures (Legarra *et al.* 2009, Christensen and Lund 2010) allowed the simultaneous use of genotypes, all phenotypes and pedigree information into existing genetic evaluations. The following developments and modifications were required to include ssGBLUP into the routine BREEDPLAN multi-trait linear model evaluations.

Construction of a genomic pipeline

Processing raw SNP genotypes into a genomic relationship matrix (**G**) for a given breed required the development of several data processing and quality assurance steps. The resulting genomics pipeline developed for beef cattle was recently documented by Connors *et al.* (2017). In brief, the procedure developed takes industry-recorded genotypes, from multiple labs and genotyping platforms, and processes them through a series of databases, enabling matching, merging and quality assurance checks to be performed.

Building the G matrix

After initial quality control of genotypes described above, only purebred individuals (Boerner 2017) were selected for parentage testing. The opposing homozygote (OH) approach for parentage (Hayes *et al.* 2011) was used to exclude individuals with extra numbers of OH with any of their parents. The approach was slightly modified to use the number of OH divided by number of loci that are homozygous in both parent and offspring. In addition, individuals were excluded that resulted in too many heterozygotes in their sire as the result of too many OH with other individuals in a half-sib family (Ferdosi *et al.* 2014). A possible sire was assigned to some individuals with unknown sire, or individuals with incorrect pedigree identified in previous steps. Then the original pedigree for individuals with genotypes was rebuilt using the parentage information to yield a corrected pedigree (CPed). The CPed was used to impute sire haplotypes and phase offspring in half-sib families (Ferdosi *et al.* 2014, 2016). The new sire haplotypes were converted to genotypes and were added to original genotypes. Sire and half-sib haplotypes were then added to the haplotype library. The

haplotype library and the CPed were used to impute missing genotypes in all individuals that were purebreds and passed the parentage test (Sargolzaei *et al.* 2014). The genomic relationship matrix (G) was built by following VanRaden's (2008) first method using the imputed genotypes.

Modified mixed model equations

Implementation of ssGBLUP required replacing the traditional inverse of the numerator relationship matrix (with However, in an analysis with millions of individuals, H can become very large and its inversion could become impossible. Thus Aguilar *et al.* (2010) suggested a new method to build directly using the following formula:

where, $\mathbf{A}^{22}$ is the inverse of the numerator relationship matrix for individuals with genotypes and was built using the method explained in Colleau (2002).

When building a modified G matrix was used, using a weighting factor λ to regress genomic relationships towards pedigree relationships. The derivation of appropriate values of λ were determined using an empirical approach described by Zhang *et al.* (2017) for a range of beef traits. In general, the results found that a λ value of 0.5 to weight genomic and pedigree information in was most appropriate, and this has been implemented in the current ssGBLUP BREEDPLAN evaluations.

All current BREEDPLAN evaluations include genetic groups as additional random effects to account for genetic differences in sub-populations of founder animals, and are included using an *implicit* model in which groups are included as dummy ancestors in . However, this does not work when using in ssGBLUP. Therefore, for implementation of ssGBLUP into BREEDPLAN the genetic groups were removed from the animal breeding value block of the mixed model equations and fitted *explicitly* as separate effects (Misztal *et al.* 2013). All other fixed and random effects remain unchanged, and includes all other features of the BREEDPLAN evaluations (Graser *et al.* 2005) e.g. sire x herd interactions, heterogeneous residual variance adjustment, importation of overseas EPD, and inclusion of crossbred animals.

New accuracy and solver algorithms

The accuracy of an EBV is important accompanying information from genetic evaluation systems. Traditionally these have relied on approximations based on effective progeny number (EPN) because of computational limitations in inverting the mixed model equations in large evaluations is not feasible (Graser and Tier 1997). Similarly for implementation of ssGBLUP, a new approximation algorithm was required to include the contribution from genomics to the EPN approach. The new procedure to compute genomic EPN and then add them to the existing EPN from phenotypic data is described by Li *et al.* (2017) and compared the approximation with actual accuracies derived for both sheep and beef traits.

The solver currently used for the new ssGBLUP is a modified version of the original BREEDPLAN solver. The new system includes the explicit fitting of genetic groups and as a fully stored dense matrix. Acceleration of the processing time was achieved by using multi-threading MKL and OMP. In the next few months, the BREEDPLAN evaluations will move to AGBU's next generation solver that has the capacity to solve more than 450 million equations in less than 24 hours and will help meet the challenge of increased size of genomic

evaluations and demands for more frequent runs.

Implementation of ssGBLUP in Australian Angus and Brahman

Data

September 2017 data extracts of Australian Angus and Brahman breeds were used to compare standard multi-trait linear model BREEDPLAN BLUP evaluations (without blending) with new ssGBLUP evaluations. The evaluations included 23 traits, with 2 maternal effects, and permanent environmental effects. The ssGBLUP evaluations included **G** matrices containing 29,441 and 10,905 animals for Angus and Brahman, respectively. Total number of animals not genotyped were 2,215,744 and 420,532 for Angus and Brahman, respectively. For Brahmans, the evaluations included two new female reproduction traits to enable ssGBLUP to emulate the existing evaluation that was blending genomic values derived from heifer age at puberty and lactation anoestrous interval phenotypes.

Results

Comparison of EBVs and accuracies from standard BLUP versus ssGBLUP evaluations are presented in Tables 1 and 2 for genotyped and non-genotyped individuals in the two breeds for a sub-set of traits. The EBV means in both breeds for ssGBLUP evaluations were similar to conventional BLUP runs but had increased variance, and this was more so for genotyped animals compared to non-genotyped. The extent of the increase in variance of EBVs varied between traits. Similarly, mean EBV accuracies from ssGBLUP increased compared to BLUP runs, but had lower variance, and was more evident in the genotyped animals.

Table 1. Angus mean EBVs (Ebv_) and accuracies (Acc_) for a sub-set of traits for standard evaluation (BLUP) and new ssGBLUP for genotyped (IN G) and non-genotyped (NOT G) animals.

		BLUP				ssGBLUP			
Run	Trait[1]	Mean	Std	Min	Max	Mean	Std	Min	Max
IN G	Acc_BW	71.8	11.0	0	99	73.6	6.6	14	99
	Acc_YW	66.7	10.9	0	99	69.2	6.9	11	99
	Acc_DC	40.4	10.6	0	98	42.3	9.6	4	98
	Acc_CIMF	53.9	11.8	0	98	58.5	8.7	13	98
	Ebv_BW	4.1	1.6	-2.9	12.0	4.2	2.0	-4.5	12.3
	Ebv_YW	73.9	14.2	-3.7	126.5	74.1	16.4	-14.6	129.2
	Ebv_DC	-3.9	2.3	-14.0	8.9	-3.8	2.4	-13.9	8.0
	Ebv_CIMF	1.7	1.0	-1.9	6.1	1.7	1.1	-2.1	6.2
NOT G	Acc_BW	62.9	17.1	0	99	63.1	16.9	0	99
	Acc_YW	60.4	15.3	0	99	60.6	15.2	0	99
	Acc_DC	37.3	14.2	0	98	37.5	14.2	0	98
	Acc_CIMF	40.0	17.4	0	99	40.9	17.5	0	99
	Ebv_BW	3.7	1.7	-5.0	12.8	3.7	1.7	-5.1	12.8
	Ebv_YW	54.1	19.9	-26.7	155.0	54.1	20.2	-27.2	154.9
	Ebv_DC	-1.8	2.5	-17.2	12.3	-1.8	2.5	-17.6	12.5
	Ebv_CIMF	0.7	0.9	-3.0	6.4	0.8	0.8	-2.9	6.4

[1]BW=birth weight direct (kg); YW = yearling weight (kg); DC = days to calving (days); CIMF = carcase intramuscular fat (%)

The BLUP and ssGBLUP evaluations in both breeds included the same configuration of genetic groups and the correlations between the solutions for Angus were greater than 0.99. Similar correlations were observed for the majority of traits for Brahmans except for some traits with very low numbers of records. The genetic trends (not presented) between BLUP and ssGBLUP were essentially identical both for genotyped and non-genotyped animals. However, in both breeds the mean EBVs were generally higher for genotyped animals, reflecting on average the sampling of genetically superior animals for genotyping.

Table 2. Brahman mean EBVs (ebv) and accuracies (Acc) for a sub-set of traits for standard evaluation (BLUP) and new ssGBLUP for genotyped (IN G) and non-genotyped (NOTG) animals.

		BLUP				ssGBLUP			
Run	Trait[1]	Mean	Std	Min	Max	Mean	Std	Min	Max
IN G	Acc_BW	59.6	15.8	0	96	62.0	11.5	25	96
	Acc_YW	66.3	16.5	0	98	69.0	11.1	11	98
	Acc_DC	40.6	17.8	0	96	47.2	13.7	6	96
	Acc_CRIB	39.8	14.2	0	92	44.8	11.0	18	92
	Ebv_BW	1.9	1.7	-4.5	7.2	1.8	1.9	-5.7	7.6
	Ebv_YW	21.6	9.8	-23.6	72.2	21.1	10.6	-23.5	68.4
	Ebv_DC	-1.2	5.0	-34.9	21.4	-1.5	6.1	-35.6	22.1
	Ebv_CRIB	-0.2	0.7	-3.2	3.9	-0.2	0.8	-3.2	4.3
NOT G	Acc_BW	46.6	17.5	0	96	47.1	17.3	0	96
	Acc_YW	53.3	19.8	0	97	53.8	19.5	0	97
	Acc_DC	26.2	14.7	0	93	27.8	15.1	0	93
	Acc_CRIB	27.3	12.4	0	86	28.5	12.8	0	86
	Ebv_BW	1.7	1.6	-5.3	7.9	1.7	1.6	-5.4	8.0
	Ebv_YW	17.6	10.2	-40.4	86.3	17.7	10.2	-40.7	86.6
	Ebv_DC	0.4	3.3	-30.7	19.2	0.5	3.7	-32.1	18.6
	Ebv_CRIB	0.0	0.7	-3.1	4.8	0.0	0.7	-3.0	4.7

[1] BW = birth weight direct (kg); YW = yearling weight (kg); DC = days to calving (days); CRIB =carcase rib fat depth (mm)

Discussion

In both breeds the implementation of ssGBLUP resulted in the largest changes in EBVs and accuracies in those animals with genotypes, with smaller changes observed in non-genotyped animals. ssGBLUP increased the spread of EBVs and increased EBV accuracies but the magnitude of the changes differed across traits. This likely reflects differences trait genetic architecture and heritability, and also the number of animals in the breeds with genotypes and the trait recorded. Changing configuration of genetic groups did not affect the evaluations and implementation of the revised solver resulted in similar run times, and therefore the ssGBLUP is commercially viable to implement. The genomic pipeline allows for timely processing of genotypic data; however, issues of matching animal identifications across systems is not trivial and handling discrepancies of parentage identified using genomics also requires considerable effort to resolve.

Future research and development

Including additional breeds

Single-step BREEDPLAN is available for implementation in all breeds however the timing will primarily depend on a breed having sufficient animals genotyped to build a stable **G** matrix. Currently, several Australian breeds are increasing the number of animals genotyped and it is expected that these breeds will transfer to ssGBLUP evaluations in the next 12 months. However another constraint to the implementation of effective genomic selection is the number of phenotyped and genotyped animals in a breed, commonly referred to as the size of the reference population. This is particularly important for traits that are difficult or costly to record or are lowly heritable, and therefore are the traits that will benefit most from genomic selection. This limitation is being addressed through several industry and research initiatives in Australia. For example, in northern Australia a large project is underway in tropically adapted beef breeds (Johnston *et al.* 2017) recording female reproduction phenotypes to drive future ssGBLUP in those breeds. Also in several temperate breeds, there are collaborative projects (called BINs) collecting feed intake, abattoir carcase and meat quality traits to increase the size of genomic reference populations for those traits. However, with the implementation of ssGBLUP the breeding sector of the beef industry will need to consider how to fund ongoing collection of phenotypic data and genotyping.

Future developments

Over time it is expected that the ssGBLUP implemented will need to be modified, especially as the numbers of genotyped animals' increase. Currently building of is not a constraint but it is anticipated as the number of genotyped animals increases we will need to modify the evaluation. This may require implementing hybrid-type models (e.g. Fernando *et al.* 2014) or use techniques such as recursive algorithm for inversion of **G** when the number of genotyped animals exceeds around 150,000 (Misztal *et al.* 2014) or methods for updating the inverse of **G** (Meyer *et al.* 2015). It is also anticipated these ssGBLUP evaluations will need to be expanded to include more than one breed and crossbred animals in the construction of **G**. This is likely to require the inclusion of procedures such as meta-founder models as proposed by Legarra *et al.* (2015) or possible use of sequence data to enable accurate across-breed genomic predictions (van den Berg *et al.* 2017). Work is also underway to develop single-step procedures for existing threshold model analyses for calving ease and docility.

Conclusions

Implementation of ssGBLUP heralds a new era for genetic evaluation in Australia. With the more effective use of genomic information, the resulting increases in accuracy, and potential to evaluate more animals in our breeding populations, presents opportunity to increase rates of genetic gain, particularly for traits currently with low accuracy. However the challenge exists to increase levels of genotyping: certainly the implementation of ssGBLUP should increase the value proposition but the relative high cost of genotyping is still likely to be a constraint.

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