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Genomic Evaluations in the Australian Sheep Industry

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ABSTRACT: The main benefit of genomic selection for Australian sheep is to increase the accuracy of hard to measure traits including carcass, adult wool and reproduction traits. A genotyped reference population has been established to measure these traits, and genomic predictions from this population show moderate accuracies, in the range 0.2 – 0.5. Genomically enhanced breeding values for traits in the current evaluation system have been delivered to breeders using the "blending" selection index method to combine genomic predictions with pedigree based estimated breeding values, and for carcass traits using the "single step" method. The goal for genomic evaluation is to move to single step analyses for all traits. One of the challenges is to accommodate breed and strain within breed structure, particularly for animals with unknown pedigree and no data. Marker information can be used to define genetic groups which correlate reasonably well with genetic groups defined from pedigree information.
Keywords: Sheep; genomics; Estimated Breeding Values

Introduction

The Australian sheep industry has a well-developed genetic evaluation system (Brown et al., 2007) featuring three separate analyses: Merinos, maternal sires (with the major breeds being Border Leicester, Coopworth, and more recently maternal composites), and terminal sires (dominated by the Poll Dorset and White Suffolk breeds). The Merino is dominant in commercial production systems, and while wool is a key component of farm income, most of the sheep meat produced in Australia is from progeny of Merino or Merino cross dams. Maternal and terminal sire breeds on the other hand are used in crossing systems for meat production. The three analyses are all conducted across-flock, and there are currently 1.7 million animals in the pedigree for Merinos, 1.5 million for maternal sires, and 2.3 million for terminal sires, with approximately 125 thousand, 70 thousand, and 130 thousand new animals entering the system each year respectively.

Significant genetic gains have been made, particularly in the terminal and maternal sire sectors (Swan et al., 2009), and from 2007 the industry has invested heavily in research to develop genomic selection to further increase rates of gain. Unlike in dairy cattle where genomic selection has a major impact through shorter generation intervals made possible by more accurate evaluations of bulls with less progeny testing (Schaeffer, 2006), sheep are typically evaluated with reasonable accuracy from an early age in both sexes, at least for traits which are easy to measure. This means that the gains from genomic selection in sheep are predicted to be more modest (van der Werf, 2009), and likely to be derived mainly from increased accuracy of hard to measure traits including carcass and meat quality, disease resistance, reproduction, and adult wool production. Because these are typically not measured in industry breeding programs, much of the effort to develop genomic selection for the Australian sheep industry has been in establishing a comprehensively phenotyped reference population to develop genomic predictions.

In this paper we describe how this reference population has been used to develop genomic predictions for a range of traits, and how these predictions have been incorporated in genetic evaluations to deliver genomically enhanced estimated breeding values (GEBVs). One of the key issues has been how to deal with the multi-breed nature of the data because there are a number of influential breeds in the terminal and maternal sire evaluations, and strains within Merino evaluations.

Development of the Reference Population

The main reference population is the Information Nucleus (IN) flock established in 2007 (Van der Werf et al., 2010). This flock was run at 8 locations representing the major sheep production environments across Australia. Approximately 5,000 mainly Merino ewes were mated annually to Merino (n≈40), maternal (n≈20), and terminal sires (n≈40) selected on the basis of industry relevance and to represent the diversity of the respective populations (Banks et al., 2006). An earlier research flock with phenotypes and genotypes (Oddy et al., 2007) also contributes to the reference.

An extensive measurement program was conducted in the IN flock, including measurement of carcass and meat traits on slaughter progeny, a comprehensive wool measurement program, growth and ultrasound scanning of muscle and fat, resistance to gastrointestinal nematodes (worm egg count, or WEC), visually assessed traits for wool and body conformation, and reproduction data collected on female progeny of the Merino and maternal sires. Progeny were genotyped using the Ilumina 50K ovine SNP chip (Illumina Inc., San Diego, CA). The number of proge-

ny in the reference with both genotypes and phenotypes for different trait groups is shown in Table 1.

Table 1. Approximate size of genomic reference populations for Merino, maternal and terminal sire breeds for wool traits, body weight and ultrasound muscle and fat scanning (WT/SCAN), worm egg count (WEC), and carcass traits, as of March 2014.

Trait group	Merino	Maternal	Terminal
Wool	5,100		
WT/SCAN	3,800	2,200	5,800
WEC	4,200	2,000	5,200
Carcass	2,800	1,300	6,100

In addition to the reference population, a pool of widely used industry sires with accurate estimated breeding values (EBVs) from the main genetic evaluation analyses were also genotyped as a resource for validating genomic predictions. At the time of writing there were 536 Merino validation sires, 130 maternal sires, and 618 terminal sires. Seedstock breeders in each sector have also begun to genotype young male selection candidates, and it is these animals which are of interest for genomic evaluation.

Accuracy of Genomic Predictions

Genomic predictions of breeding value (GBVs) have been calculated using GBLUP, from the model $y = X\beta + \mathrm{Z}Q\mathrm{g} + \mathrm{Z}\mathrm{a} + \mathrm{e}$ where y is a vector of trait measurements for reference population animals only (and excluding progeny from validation sires for example), β is a vector of fixed effects, g is a vector of random genetic group effects, a is a vector of GBVs for all animals of interest including the reference population, validation sires, and young male selection candidates, and e is a vector of random residuals distributed as $N(0, I\sigma_e^2)$. X is an incidence matrix for fixed effects, Z is an incidence matrix aligning animals with records and their GBVs, and Q is a matrix describing the genetic group content for all animals with GBVs. Elements of Q are fractions of each genetic group for each animal, with rows (corresponding to animals) summing to 1. Distributions for g and a are $N(0, I\sigma_g^2)$ and $N(0, G\sigma_a^2)$ respectively, where G is the genomic relationship matrix (VanRaden, 2008) calculated from SNP genotypes following Yang et al. (2010). Note that this model is a modified version of the "genetic groups" model (Quaas, 1988) used in many genetic evaluation systems, the modifications being that the covariance structure for animal genetic effects is modelled using genomic rather than pedigree information and that genetic groups are fitted as random rather than fixed effects. While genetic groups are often considered to be fixed effects, treating them as random is a pragmatic approach to assist with estimability issues which can result from confounding between genetic groups and environmental classifications such as management groups or small numbers of records contributing to genetic groups.

Although breed and Merino strain structure can be identified in the 50K SNP genotypes of this population (Daetwyler et al., 2012a; Brown et al., 2013), genetic groups are derived from the extended pedigree, and are defined for maternal and terminal sires by breed (e.g. Border Leicester, Coopworth, Poll Dorset, White Suffolk, Texel) and for Merinos by strain (Ultra-fine wool, Fine-medium wool, and Strong wool).

For traits in the main genetic evaluation analyses, accuracies of genomic predictions have been calculated by correlating GBVs for validation sires with their independently estimated EBVs (Moghaddar et al., 2013a). Accuracies estimated for these traits have generally been moderate, in the range 0.2 to 0.5, although for some traits in Merinos initial estimates were very high (fleece weight, 0.63 to 0.75; fibre diameter, 0.65 to 0.72; and body weight, 0.49 to 0.63). This runs counter to expectations that accuracy in Merinos would be lower than in maternal and terminal sire breeds due to the larger effective population size of Merinos (Kijas et al., 2012). We have shown that this is due to population structure and the large differences in trait performance between strains of Merino. When accuracies for validation sires are calculated within strains for these traits they fall within the 0.2 to 0.5 range (Moghaddar et al., 2013a).

Inflated accuracy estimates suggest that GBVs are not free of population structure even though we have used a genetic groups model. It seems likely that this is because the genetic groups defined from the pedigree are somewhat arbitrary, and not fully consistent with the genetic architecture described by the SNP genotypes.

We have also used bivariate REML analyses to estimate accuracies with reduced influence from population structure effects, fitting progeny records of validation sires as the first trait, and GBVs of validation sires as the second trait. Reference progeny are excluded from the first trait, and population structure is accounted for by fitting the genetic groups model described above in bivariate form (while population structure effects are still present within GBVs, when the genetic groups model is fitted to both traits in this analysis population structure effects are reduced). Genomic prediction accuracies are then estimated as the genetic correlation between traits. Accuracies estimated using this approach are shown in Table 2 for body weight, ultrasound muscle and fat scan traits, gastrointestinal parasite resistance (worm egg count, WEC), and wool traits. These results are similar to the within strain estimates reported by Moghaddar et al. (2013a).

Table 2. Accuracies of genomic predictions for Merino, maternal and terminal sire breeds for body weight, ultrasound muscle and fat scanning, worm egg count, and wool traits.

Trait[1]	Merino	Maternal	Terminal
bwt	0.54	0.41	0.19
wwt	0.19	0.47	0.23

pwt	0.48	0.62	0.23
ywt	0.58	0.33	
hwt	0.55	0.22	
awt	0.47	0.45	
pemd	0.33	0.34	0.41
pfat	0.27	0.34	0.37
pwec	0.26	0.10	0.32
ygfw	0.37		
ycfw	0.34		
yfd	0.52		
ydcv	0.32		
yss	0.32		
ysl	0.42		

[1] bwt = birth weight, wwt = weaning body weight, pwt = post-weaning body weight, ywt = yearling body weight, hwt = hogget body weight, awt = adult body weight, pemd = post-weaning eye muscle depth, pcf = post-weaning fat depth, pwec = post-weaning worm egg count, ycfw = yearling clean fleece weight, yfd = yearling fibre diameter, ydcv = yearling CV of fibre diameter, yss = yearling staple strength.

GBLUP genomic predictions have also been developed for carcass and meat quality traits, including carcass weight, muscle and fat depth, lean meat yield, shear force and intramuscular fat. Because there is no existing data outside the reference population, the validation sire approach to estimate accuracy is not possible, and internal cross validation has been used instead (Daetwyler et al., 2012b). Accuracies estimated for these traits were in the range 0.15 to 0.20 for the three breed groups.

Female reproduction traits are classic candidates for genomic selection because they are economically important in breeding objectives, lowly heritable, sex limited, expressed late in life, and are often not recorded in seedstock flocks in Australia. Developing genomic predictions for reproduction has been difficult precisely because it is hard to record, and there are limited records in the reference population. In order to maximise the available data, Daetwyler et al. (2013) developed a GBLUP analysis combining Trait Deviations (corrected phenotypes) from genotyped females in the IN reference population with Daughter Trait Deviations calculated from phenotypes of daughters of genotyped validation sires recorded in industry flocks. Accuracy was estimated by cross validation, and although estimates were low they were always higher than accuracy from pedigree BLUP models. Updated estimates of these accuracies are presented in these proceedings (Daetwyler et al., 2014), and are in the range 0.11 to 0.31 for Merinos and 0.05 and 0.15 for maternal breeds.

The ability to develop genomic predictions across breeds is highly desirable in all livestock populations, to make best use of available reference populations and to provide predictions for small breeds. At the current 50K SNP density the IN reference population is not able to predict across breeds (Daetwyler et al., 2010; Moghaddar et al., 2013b), and there is some evidence that including animals from another breed can decrease the accuracy for the target breed.

Within breeds there is evidence in the IN population that accuracies are higher for animals which are more closely related to the reference (Clark et al. 2012). The implications of this are that at the current SNP density the reference population needs to be maintained because reference animals born in the early years of the program will be less related to current selection candidates, and that seedstock breeders should ensure that they have adequate relationships to the reference population.

Genomic selection with the accuracies estimated in the current reference population is predicted to increase genetic gain in the overall breeding objective in the order of 15 to 20% (van der Werf, 2009). These are gains from within flock (and within breed) selection, but as noted above, higher accuracies in Merinos are possible if across flock effects due to population structure are considered. However, these will rarely be useful to breeders, firstly because for those making the fastest rates of genetic gain who have typically been the early adopters of genomic testing, finding superior animals outside their own flocks is uncommon, and secondly, for breeders within the current evaluation system the existing benchmarking information from pedigree and performance data is already highly accurate. The main beneficiaries of these higher levels of accuracy arising from across flock effects are therefore likely to be breeders outside the evaluation system, or breeders with limited trait recording programs.

Genomic Evaluations

The methods used to produce genomically enhanced EBVs (GEBVs) for the Australian sheep industry have been described by Swan et al. (2012). For traits currently in the genetic evaluation analyses, the "blending" approach is used, in which GEBV is an index of the EBV and the genomic prediction, $GEBV = w_1 EBV + w_2 GBV$ where the weights w_1 and w_2 are derived from the accuracies of GBVs and EBVs. For GBVs the accuracies used are derived from the population estimates summarised in Table 2 for wool, weight and scan traits, and worm egg count, while for EBVs individual animal accuracies from the genetic evaluation analyses are used. An assumption of the blending method implemented is that EBVs and GBVs are independent. This is not strictly true because data from the IN reference population are included in the genetic evaluation analyses, but it is likely that potential effects of double counting are reduced because the selection candidates of interest are not part of the reference population, or reference population sires. They can have relatives in the reference population who contribute information through both EBVs and GBVs, but not in large numbers relative to the total size of the reference population.

A key issue for blending is that GEBVs for genotyped animals must be compared relative to the same genetic mean as the EBVs of their un-genotyped contemporaries, particularly in the current situation in which the proportion

of the total animals entering the genetic evaluation system which have been genotyped is small. In fact flocks involved to date have typically genotyped 10 – 20% of available selection candidates. To ensure GEBVs are comparable in this situation, they are centred on the genetic group effects from the main evaluation, and the blending equation implemented is $GEBV = Q\hat{g} + w_1(EBV - Q\hat{g}) + w_2 GBV$, where $Q\hat{g}$ are the estimates of genetic group effects from the main evaluation. As described above genetic group effects are fitted in GBLUP models but are not included in GBVs for blending. Use of estimated genetic group effects from GBLUP models in blending can cause difficulties in comparing GEBVs for genotyped animals with EBVs of their un-genotyped contemporaries because GBLUP genetic groups are estimated with lower accuracy from the reference population, and are not always defined with the same level of detail as genetic groups in the main evaluation (van der Werf et al., 2013).

GEBVs for carcass traits are computed using the single step method (Misztal et al., 2009; Aguilar et al., 2010) with the genetic groups model. Although carcass phenotypes are available only from the reference population, a number of slaughter animals have not been genotyped. The benefit of the single step analysis in this situation is that all records can be included whether animals are genotyped or not. Initially, six carcass traits have been included in single trait analyses. Accuracies calculated from prediction error variances for young male selection candidates outside the reference population (i.e. without measurements) increased by 0.14 – 0.24 compared to equivalent pedigree only BLUP analyses (Swan et al., 2011).

Genetic Groups from Marker Information

One of the opportunities for the use of genomic information in sheep is to extend evaluations to flocks outside the current system which may have limited phenotypic data and pedigree linkage. While it is straightforward to make genomic predictions from reference population data for animals in these flocks, in order to make their GEBVs comparable a genetic group effect needs to be included. The issue for these flocks is that most will not have sufficient data and linkage to estimate their own genetic group effects. One possibility is to use genomic information to identify genetic groups.

Techniques including principal components analysis have been used to identify population structures from marker genotypes (Price et al., 2010), and have been used to study strains within the Australian Merino (Brown et al., 2013) and to identify breeds within the New Zealand sheep population (Dodds et al., 2013). The Merino is an interesting case because there is a very large range in trait performance between flocks in the evaluation system. Genetic groups are essentially defined by flock, and flocks are allocated into three strains for EBV reporting purposes: Ultra-fine wool, Fine-medium wool, and Strong wool. These allocations are partly based on trait performance and partly arbitrary.

The Merino portion of the genotyped population including reference, validation sires and young rams is highly representative of the genetic diversity within the breed. The ADMIXTURE software (Alexander et al., 2009) was used to identify four sub-population genetic groups (GG1 – GG4) within 9,945 genotyped Merinos. A subset of 11,922 markers corresponding to a low density SNP panel currently in use by the industry was selected from the 50K SNP genotypes for this analysis.

ADMIXTURE gives estimates of the fractions of each of the four groups for each animal (referred to below as admixture fractions). The separation of animals between the groups is demonstrated in Figure 1, which shows the first two principal components of the genomic relationship matrix, and animals plotted by group when their admixture fraction for the largest group is greater than 0.5. Comparing the admixture fractions with the allocation of animals to strains in the evaluation system, all Ultra-fine strain animals had a very high GG3 fraction, while animals with high GG4 fractions were almost all from the Strong wool strain. However, approximately half of animals that were classified as Strong wool in the evaluation system had significant contributions from GG1 – GG3. The Fine-medium strain is the largest in the evaluation system, and around half of the animals classified as such had very high fractions of either GG1 or GG2. The remaining Fine-medium animals were a mixture of GG1 – GG3 with very little contribution from GG4.

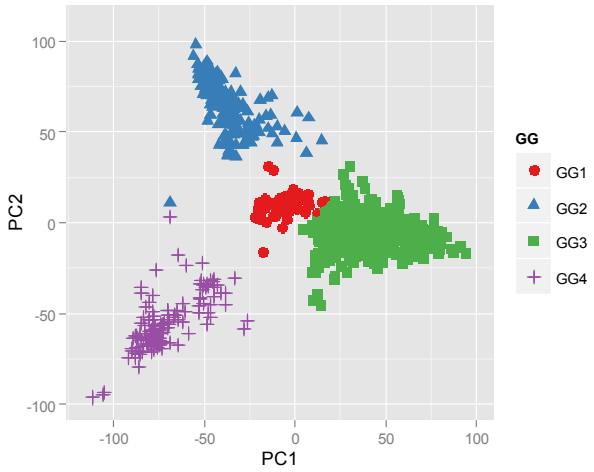

Figure 1: First two principle components (PC1 and PC2) of the genomic relationship matrix for Merino animals with high content of ADMIXTURE sub-population groups GG1 - GG4.

The ADMIXTURE sub-population groups GG1 – GG4 were fitted as genetic group effects using admixture fractions as the genetic groups matrix Q_m. Estimates of the effects for a range of traits measured on reference population animals are shown in Table 3. As expected, GG3 (more

Ultra-fine wool animals) and GG4 (more Strong wool animals) represent the extremes of performance, with GG3 having the lowest fleece weight (ycfw), fibre diameter (yfd), and body weight (ywt), and GG4 having the highest fibre diameter and body weight. GG1 and GG2 (more Fine-medium animals) were intermediate, with GG1 closer to GG3 and GG2 closer to GG4. Correlations between admixture genetic group and pedigree genetic group effects for individual animals were also estimated and are shown in Table 3 ($r_q = r[ZQ_m\hat{g}_m, ZQ_p\hat{g}_p]$). For most traits the correlations were moderate, in the range 0.45 – 0.71. A correlation of 0.05 for staple strength (yss) is not unexpected given that there is very little variation in performance between flocks and strains for this trait. Fibre diameter traits (yfd and ydcv) on the other hand do show considerable variation between flocks and the low correlations (0.12 for both) were therefore unexpected. These correlations were reduced by a cohort of animals in which the pedigree group effects were opposite to the marker group effects. This could be due to poor allocation of animals to pedigree groups, or alternatively that the marker information at this density is not sufficient to detect variants with a significant effect on trait performance.

Table 3. Estimates of ADMIXTURE sub-population genetic group effects GG1 – GG4 and correlation between allocation to genetic groups by marker and pedigree information (r_q).

Trait[1]	GG1	GG2	GG3	GG4	r_q
ycfw	0.25	0.21	-0.62	0.16	0.52
yfd	-0.90	1.28	-2.25	1.87	0.12
ydcv	1.78	0.20	-1.58	-0.39	0.12
yss	-0.93	-0.23	1.77	-0.60	0.05
ysl	-6.48	4.41	-12.04	14.11	0.49
ycuv	-6.45	-0.04	20.13	-13.64	0.71
ybdwr	1.16	-0.05	0.04	-1.14	0.45
ywt	-4.23	5.40	-8.17	6.99	0.65

[1] ycfw = yearling clean fleece weight (kg), yfd = yearling fibre diameter (microns), ydcv = yearling CV of fibre diameter (%), yss = yearling staple strength (Newtons per ktex), ycuv = yearling fibre curvature (degrees), ybdwr = yearling body wrinkle (1 – 5 visual score), and ywt = yearling body weight (kg).

In summary, use of genomic information to define genetic groups is a realistic proposition. Agreement between estimated marker and pedigree based genetic group effects is reasonable across a range of traits but not perfect. Particularly in single step analyses for sheep it will be necessary to further develop methods to define genetic groups using both pedigree and marker information to ensure that genetic group information from un-genotyped animals can be used alongside genetic group differences derived from genomic data.

Development of Single Step Evaluations

The ultimate goal for genomic evaluation of Australian sheep is to implement single step analyses for all traits. The benefits of single step in Australian sheep are that genomic information can be propagated to more animals, the size of reference populations can be increased, and the potential for double counting inherent in blending methods can be avoided.

In the Misztal – Aguilar single step method the sub-matrix of the inverse numerator relationship matrix (A^{-1}) in the BLUP equations for genotyped animals is replaced by $G^{-1} - A_{22}^{-1}$ where G is the genomic relationship matrix and A_{22} is the numerator relationship matrix for genotyped animals, with the resulting modified inverse relationship matrix denoted as H^{-1}. Forming H^{-1} is more computationally demanding than A^{-1} because of a large matrix multiplication necessary to build G and the need for direct inversion of G and A_{22}. Solving the single step BLUP equations with H^{-1} is also more demanding because of the increased density of equations for genotyped animals. Using highly optimised versions of the BLAS (Dongarra et al., 1988) and LAPACK (Anderson et al., 1999) matrix libraries it has been possible to solve problems with several tens of thousands of genotyped animals on a routine basis. The method has been implemented on a small scale in single trait models for carcass traits as described above. At the time of writing these models included approximately 20,000 genotyped animals, 60,000 animals in the extended pedigree, with the equations solved by direct inversion in order to obtain accuracies for GEBVs from prediction error variances. In addition, test analyses have been conducted on data sets with up to one million animals in the pedigree, 5 traits, and 5,000 animals genotyped. These analyses converged within an acceptable time frame, but as the number of genotyped animals grows this will become increasingly challenging for the Misztal – Aguilar single step method. It is likely that as the number of animals genotyped and density of marker information increases new computing strategies and analysis models will be required in the not too distant future.

Fitting genetic groups in the single step method requires special consideration. Traditionally groups have been fitted in genetic evaluations using the "implicit" model in which groups are included as dummy ancestors in the A^{-1} matrix (Quaas, 1988). However, this does work when using H^{-1} in the single step method (Misztal et al., 2013). We have observed that GEBVs are biased by incorrect genetic group effects when using the implicit model with the single step method. This can be addressed by fitting groups as separate effects outside the H^{-1} matrix.

Population structure can also be included when building the genomic relationship matrix for example by using allele frequencies calculated per breed or strain group (Harris and Johnson, 2010). Experience to date in our data is that this has a small impact on the accuracy of genomic

predictions (Moghaddar et al., 2013b), or on GEBVs from single step analyses, provided the genomic relationship matrix is scaled appropriately to be compatible with the numerator relationship matrix.

Conclusion

Considerable progress has been made in the incorporation of genomic information into genetic evaluations for Australian sheep. Reference populations have been established and provide genomic predictions with moderate accuracy, and genomically enhanced breeding values have been available to seedstock breeders since 2011. The next challenge is to develop single step analyses for all traits so that the benefits of genomic selection can be maximised.

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