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BEEF CATTLE GENETIC EVALUATION IN THE GENOMICS ERA

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SUMMARY

Genomic selection is rapidly changing dairy breeding but to date it has had little impact on beef cattle breeding. The challenge for beef is to increase the accuracy of genomic predictions, particularly for those traits that cannot be measured on young animals. Accuracies of genomic predictions in beef cattle are low, primarily due to the relatively low number of animals with genotypes and phenotypes that have been used in gene discovery. To improve this will require the collection of genotypes and phenotypes on many more animals. Several key industry initiatives have commenced in Australia aimed at addressing this issue. Also, unlike dairy, the beef industry includes several major breeds and this will likely require the use of very dense SNP chips to enable accurate genomic prediction equations that are predictive across breeds. In Australia genotyping has been performed on all major breeds and research is underway to ascertain the effectiveness of a high density SNP chip (800K) to increase the accuracy of prediction. However, at this stage it is apparent, even in dairy breeding, that genomic information is best combined with traditional pedigree and performance data to generate genomically-enhanced EBVs, thus allowing greater rates of genetic gain through increased accuracies and reduced generation intervals. Several methods exist for combining the two sources of data into current genetic evaluation systems; however challenges exist for the beef industry to implement these effectively. Over time, as the accuracy of genomic selection improves for beef cattle breeding, changes are likely to be needed to the structure of the breeding sector to allow effective use of genomic information for the benefit of the industry.

INTRODUCTION

The advent of powerful genomic information from high density SNP (single nucleotide polymorphism) chips on large numbers of individuals is radically changing dairy cattle breeding (Hayes *et al*. 2009) and has the potential to change the way beef cattle are selected. Genomics has the potential to increase the accuracy of EBVs for traits which currently have little information thus enabling greater rates of genetic gain. Currently there are several challenges to increasing the accuracies of genomic predictions in beef cattle and developments are needed for their inclusion into existing genetic evaluation schemes. Genetic evaluation of beef cattle in Australia has been through the BREEDPLAN system (Graser *et al*. 2005) since the mid 1980's. This is a flexible system, continually changing to accommodate new traits, advances in computational capacity and development of new methods and models. Recently methods for including the effects of a few gene markers into BREEDPLAN have been developed (Johnston *et al*. 2009), however the system needs to continue to adapt to accommodate the ever expanding volume and power of genomic information. This paper discusses 3 key areas including: recent developments in the generation of genomic information; changes to genetic evaluations to include genomic information; and the implications of genomic selection on future genetic improvement.

GENOMIC INFORMATION

Genotyping of individuals for many thousands of SNPs is now a reality and will soon be routine, and individual whole genome sequencing on large numbers of animals is fast approaching.

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The testing of gene markers has been occurring for more than a decade and we have witnessed a progression of the technology from the early days of single linked markers, to direct markers, to very low density SNP panels. Then a major development occurred when the mapping of the bovine genome sequence identified thousands of SNPs distributed across the genome. This led to the development of bovine SNP chips containing many thousands of SNPs which could be simultaneously tested on an individual. In the past 12 months high density chips with more than 777,000 SNPs (800K) have become commercially available. This revolution in genotyping and the associated reduction in cost have resulted in large numbers of individuals with comprehensive genotypic data from whole genome scans, leading to the development of the concept of genomic selection (Meuwissen *et al*. 2001).

The aim is to use the power of genomics to cost effectively enhance our genetic evaluations systems. This requires an understanding of the various types of genomic information and how it can be used to explain genetic variance of traits of interest. To generate genomic information currently involves genotyping large numbers of animals, performing association studies with phenotypes and assessing the accuracy of the resultant genomic predictions.

Association studies. The use of gene markers as information in breeding relies on the ability to determine significant associations between marker alleles and variation in a given trait. With the advent of high density SNP chips containing SNPs from across the genome it is now possible to test for associations of tens of thousands of SNPs and phenotypes, in what is termed genome-wide association studies (GWAS). The aim of a GWAS is to determine the set of SNPs that are significantly associated with the genetic variation of a trait, and this set is associated with a resultant estimated accuracy (i.e. the square root of the % variance explained). Commonly the estimated SNP effects are combined into a prediction equation that is applied to genotyped animals outside the training set of animals. The predictions are called marker breeding values (MBVs) or genomic breeding values (GEBVs) with several other variations in names including those trade-marked by companies (e.g. Pfizer MVP®). Many statistical methods (e.g. Moser *et al.* 2009) have been used to perform GWAS and to predict MBVs and differ mainly in their assumptions regarding the distribution of SNP effects.

Australian beef GWAS. In Australia, the Beef CRC phenotypic databases have been used to perform GWAS. Early experiments were performed using a 10K chip followed by large numbers (N>7000) genotyped with the Illumina Bovine SNP50 BeadChip (50K) array (Illumina Inc, Hayward, California). The focus has been particularly on female reproduction and feed intake traits but includes other trait complexes across a range of temperate and tropically adapted breeds. Most animals have been recorded for one or more trait complexes including carcase and meat quality (N=3670), feed intake and efficiency (N=2520), female reproduction (N=3950) and male reproduction (N=1100). A majority of the animals also have comprehensive weight and live animal carcass ultrasound scan records, along with a variety of other traits (e.g. flight time).

Some GWAS results have been published (e.g. Zhang *et al.* 2010) but much of this work is still ongoing, including the genotyping of validation populations. Over the next 12 months a subset (N=1720) of animals with 50K genotypes will be genotyped with the high density 800K Illumina chip. This will allow for the imputation of 800K genotypes from the 50K genotypes and this is expected to increase the power to perform association studies of the pooled breed dataset, with the goal of increasing the accuracy of all MBVs. Pfizer Animal Genetics have also performed GWAS using Angus BREEDPLAN EBVs on several hundred Angus sires with 50K genotypes and validation studies have enabled the predictions to be included in BREEDPLAN (see below).

Accuracy of genomic predictions. The theoretical accuracy of genomic predictions as proposed by Goddard (2009) and Goddard *et al.* (2010) depends on 2 main parameters: the proportion of genetic variation explained by the SNPs and the accuracy of estimating the SNP effects.

i) The proportion of genetic variation explained by the SNPs. This is due to the SNPs being in linkage disequilibrium (LD) with the causal mutations and can be approximated by M/N_eL, where **M** = density of SNP markers, **L** = length of the genome, and $\mathbf{N_e}$ = effective population size.

ii) Accuracy of estimating SNP effects. This can be approximated by Th^2/ N_eL, where **T** = number of animals with genotypes and phenotypes and $\mathbf{h^2}$ = trait heritability.

Therefore accuracies of genomic predictions are higher with increased SNP density, more records, for traits with higher heritabilities, and for populations with smaller genome sizes and lower effective population size. To date, dairy breeding programs have been most successful with GWAS and have reported accuracies of GEBV of 0.7, averaged across 27 traits, compared to a 0.5 mid-parent accuracy (VanRaden *et al.* 2009). Hayes *et al.* (2009) also reported significant improvements in accuracies from Australian dairy studies and predicts that the impact of genomic selection in the dairy industry will be a doubling of the rate of genetic gain. However for the majority of dairy results the reported accuracy (or reliability) of GEBVs included a mid-parent polygenic component. Also for both the US and Australia, the improvement in accuracies for the lowly heritable female fertility traits were much lower than for production traits.

In beef, the commercial GeneSTAR® gene markers where shown to generally have low accuracies to predict their target traits, with the exception of the tenderness markers (Johnston and Graser 2010). Progression to genomic predictions with 56 SNPs also had relatively low accuracy (full results at http://www.beefcrc.com.au/Assets/572/1/DJ_Pfizer_MVP_Report-3toCRC.pdf). Recent predictions using the 50K chip in Angus have been available and Australian results (Johnston *et al.* 2010) show accuracies of 0.01 to 0.45, while a study in US Angus (MacNeil *et al.* 2010) reported accuracies of 0.50 to 0.65 for a range of carcass traits from subsets of SNPs from the 50K panel. An example of the progression of results from various marbling MBVs with Australian abattoir carcass intramuscular fat (IMF) phenotypes is presented in Table 1. The accuracies of the marker predictions have increased over time, but are still relatively low compared to dairy results. This most likely reflects the training data (i.e. BREEDPLAN IMF EBV) which is predominantly driven by live animal ultrasound records and is only moderately genetically correlated (0.6 to 0.8) with the abattoir carcass trait.

Table 1. Results of the accuracy (r_g) and additive variance explained ($\%V_a$) for marble score (MS) markers or MS MVPs with abattoir carcass intramuscular fat %.

Marker or MVP	Source*	Validation data#	Number phenotyped	Number genotyped	r_g	$\%V_a$
GeneSTAR M1,M2, M3, M4	A	1	3594	2518	*ns*	*ns*
GeneSTAR MS MVP	A	1	3594	703	0.05 (0.06)	<0.01
Pfizer Angus 50K MS MVP	U	2	4028	901	0.16 (0.07)	0.03
Pfizer Angus 50K MS MVP	A	2	3557	1031	0.20 (0.08)	0.04

*1= pooled Temperate breeds; 2 = Angus only; # U = US derived MVP predictions; A = Australian derived markers or MVP predictions; ns = marker effects not significant

The most likely reason for the difference in MBV accuracies between dairy and beef cattle, according to the formulas of Goddard (2009) is simply differences in **T**, $\mathbf{h^2}$ and $\mathbf{N_e}$ between the 2 types of cattle. Therefore if considering traits of similar $\mathbf{h^2}$ then the difference reduces to **T** and $\mathbf{N_e}$. For beef to increase accuracy of MBVs it needs to increase **T**. Dairy WGAS use highly accurate

progeny test sires with many hundreds of daughters recorded, is working in a single dominant breed, and has a relatively small effective population size. Whereas in beef, far fewer sires have high accuracy EBVs, there are many more breeds and effective population sizes are slightly larger. Alternatively in beef, the accuracy could be improved by increasing **M** thus enabling the detection of SNPs that are in LD across breeds, though there will be some trade off through increased $\mathbf{N_e}$.

Validation of genomic predictions. It is becoming common practice in the process of developing genomic selection to include a validation step by testing the predictions in a population outside the training set of animals. This is recognised as important since the estimates obtained from the training set can be population specific and the sizes of effects are often over estimated. Therefore a validation study is required to estimate the accuracy of genomic predictions in a population outside the discovery set of animals. This process measures the predictive powers of the MBVs and provides estimates for their incorporation into genetic evaluations. Validation requires large numbers of additional animals with genotypes and phenotypes for the traits of interest. In some experiments it is possible to split datasets into training and validation sets, but pedigree relationships can still remain across sets. The number of animals required for validation is less than required for training and depends on the heritability of the trait and the accuracy of the MBV from the initial training set.

In Australia, the large database of Beef CRC phenotypes has been used for numerous validation studies, including the Pfizer tests mentioned above and IGENITY® MBVs from Merial. However this resource is being used in discovery by the Beef CRC and therefore new populations of genotyped and phenotyped animals are required. Efforts are underway with international cooperation but differences across countries in breed composition, trait definitions and recording times can reduce the effectiveness of the validation. Two initiatives have commenced specifically addressing the need for animals with extensive phenotypes and a DNA sample for genotyping.

*BIN schemes***.** Beef information nucleus (BIN) schemes have been implemented in 5 Australian beef breeds and will generate approximately 5700 progeny from 285 sires over 3 rounds of mating. There are also other breeds under consideration for BIN projects, and if implemented, these will almost double the total number of progeny generated. The primary function is to create large amounts of phenotypic data to enable validation of genomic predictions developed by the Beef CRC or industry. It is planned these will include difficult to measure carcase traits, feed intake, meat quality and female reproduction traits depending on the trial. The progeny test design of the BINs will produce approximately 20 progeny from high $Index merit young sires, thus providing additional capacity to increase rates of genetic gain in the industry.

Industry sire genotyping. The Beef CRC is currently genotyping approximately 1,300 sires from 8 breeds with a range of BREEPLAN trait accuracies. Semen samples have been provided and assembled by the cooperating breed societies. The aim of this project is to provide a resource, across major breeds in Australia, for the validation of genomic prediction equations developed by the Beef CRC for related traits. The sires genotyped will represent a broad cross-section of each breed, and could be used in the future to construct genomic relationship matrices (see section below). All sires will be genotyped with the 50K chip and a subset will also be genotyped with the 800K chip. In the US, a similar project is also underway (Garrick 2010) where a repository of DNA from more than 2000 influential sires or upcoming bulls across 16 breeds has been assembled and will be used to validate genomic prediction equations developed from their research populations. To increase the number of sires with high density genotypes available in each country sharing arrangements are in place across countries.

Traits needed. It is important for the beef breeding sector to work together to collect traits of high economic importance that are difficult or costly to routinely collect, particularly on young bulls that are the candidates for selection. For beef cattle these would include traits that can only be recorded on daughters (e.g. maternal calving ease, days to calving, maternal weaning weight, and mature cow weight) or steer progeny (e.g. abattoir carcase and meat quality) or those traits costly to measure on the animal itself (e.g. feed intake). Female reproduction is a key profit driver in many beef production systems but the development of future genomically-enhanced EBVs will rely on collecting large number of phenotypes, including cow survival information. It will also be important to consider which additional traits may benefit from genomic selection, with particular focus on traits currently deemed too difficult or costly to measure. In the future it may be possible to have genomic predictions for traits such as methane emissions, chemical attributes of meat, animal health and welfare. Such predictions will require the collection of suitable phenotypes and these may need to be considered in future BIN schemes.

Future genomic information. Already higher density SNP chips (800K) are commercially available and it is predicted they will be dense enough to provide predictions that can be used across breeds if LD is maintained between the SNP and the QTL in different breeds. This will allow pooling of training data across beef breeds, thus increasing the accuracy of genomic predictions and the possible extension of the technology to other breeds with limited information.

Imputation of genotypes from small chips to larger densities (i.e. 50K up to 800K) has been shown to be accurate. This will greatly increase the number of animals with high density genotypes and may also enable the development of small chips that are cheaper and could be used to genotype large numbers of cows. In beef, if cost effective, these could be used to genotype large numbers of carcases, although to perform WGAS effectively requires additional management group information that is not usually available on commercial cattle.

Whole genome sequences will also become more readily available and less expensive as a result of recent developments in next generation parallel sequencing (Perez-Enciso and Ferretti 2010). Not only will this allow genome sequence association studies, but these data will provide new information on copy number variants and RNA sequences. Gene expression arrays have been available to beef cattle but to date have had limited application. The availability of denser SNP chips and whole genome sequences will lead to the discovery of genes and gene pathways; although at this stage it is unclear how this will impact on genetic evaluation or selection.

GENETIC EVALUATION

Massively expanding genotyping capacity and improving genomic predictions provides the opportunity to greatly increase the accuracy of EBVs of young beef animals. This will be most effectively achieved by combining the genotypic information with traditional sources of data in genetic evaluations (e.g. BREEDPLAN) to generate genomically-enhanced EBVs. Methods are being developed for incorporating genomic information into existing evaluations and suitable databases will be required for effective storage of large volumes of genotypic data.

Methods for incorporation. Including genomic data into existing genetic evaluation systems presents the challenge of correctly weighting the contribution of genomic information to the prediction of EBVs. Issues also exist regarding the heterogeneity of data (i.e. genotyped versus un-genotyped animals) and the need for commercially viable systems. Listed below are 3 methods that current exist for incorporating genomic data into EBVs.

a) Genomic predictions as additional traits. This method is a simple extension of the multiple trait model where the genomic predictions (i.e. MBVs) are included in the evaluation as an additional

trait. The MBV for an individual is considered as a phenotypic record with a heritability close to one. The genetic variance and covariance matrix between the MBVs is required and this allows the MBV to contribute to the EBV of the target trait and other traits through the specified covariances. This method requires estimates of genetic correlations between traits in the genetic evaluation and each of the MBVs. The estimated genetic correlation in this calibration step may differ in magnitude to estimates from the training and validation due to population differences, especially if different breeds are involved, but also due to differences in trait definitions or models used (e.g. inclusion of maternal effects), and through accounting for selection and genetic trend.

The multiple trait approach was used to include genomic predictions from GeneSTAR® tenderness markers into a trial shear force EBV for the Australian Brahman breed (Johnston *et al.* 2009). However, an extension of this method to a larger breed with several MBVs proved computationally difficult and will require changes to the method of solving mixed model equations currently used in BREEDPLAN. In the US, Kachman (2008) also outlined a multiple trait method to incorporate marker scores into national cattle evaluation. In 2010, the American Angus Association reported incorporating IGENITY® genomic predictions into their genetic evaluation (Northcutt 2010).

b) Post analysis combining. It is also possible to include genomic predictions into the BLUP EBVs using selection index theory. This requires deregressing the EBVs using the accuracy and including the genomic prediction using a variance/covariate matrix similar to those required for the multiple trait method. This selection index approach has been used in dairy in a multi-step process to include 50K genomic predictions into US (VanRaden *et al.* 2009), Australian (Hayes *et al.* 2009) and New Zealand (Harris and Johnson 2010) dairy estimated breeding values.

In beef, a multiple-trait selection index approach has been developed to include 7 Pfizer 50K MVPs genomic predictions into Angus BREEDPLAN EBVs and accuracies. This required construction of variance and covariance matrix between the MVPs and traits using results from Johnston *et al.* (2010). BREEDPLAN multi-trait EBVs were de-regressed using their accuracies and the 7 MVPs were added to individuals' EBVs.

c) Genomic relationship matrix. The use of genomic data to build a genomic relationship matrix (GRM) between animals is emerging as an alternate approach for including genomic information into genetic evaluations without the need for WGAS or the development of prediction equations. The GRM has been proposed to replace the existing pedigree-based relationship matrix (e.g. Legarra *et al.* 2009, Hayes *et al.* 2009). However due to the presence of both genotyped and un-genotyped individuals in evaluations the GRM needs to be augmented with the existing relationship matrix. Misztal *et al.* (2009) proposed computation methods to handle this new matrix and Swan *et al.* (2011) applied the methodology to an Australian sheep genetic evaluation example.

Future benefits. Genomic data on individuals will allow the determination of more exact pedigrees, benefiting the EBVs of relatives. In the longer term it could also contribute to more accurate heritability estimates. Genomic information would also benefit the accuracies of EBVs for animals that have not been performance recorded or those in small management groups, especially those in single animal groups.

Genomic information on single gene effects (e.g. recessive diseases or horns) would allow these conditions to be effectively managed in a breeding program. Future applications of genomic information to manage inbreeding and determine breed composition could be very useful and genomic predictions may assist in the further development of across breed EBVs. In the longer

term, genomic technology will be applied to understanding the genetic architecture of imprinting, dominance and epigenetic effects.

Database requirements. For genomic data to be included in genetic evaluation schemes it will require storage and access for routine use. If the computation of prediction equations is necessary then a database is required that stores an individual's genotypic (e.g. 50K) and phenotypic records. Alternatively, if the GRM is the method for including genomic information then only the genotypes would need to be stored. Storage of MBVs from DNA companies will require correct unique animal identification along with version details of the prediction equation used, as they are likely to change over time. Currently, a national genotype database has been developed at AGBU as part of Beef CRC, and it is being populated with genomic (genotypes and MBVs) and phenotypic data. Significantly, over time the capacities of this database will need to be expanded to allow storage of 800K genotypes and future whole genome sequence data.

GENETIC IMPROVEMENT

Genomic selection clearly offers a major advancement in modern animal breeding methodology. With the widespread availability of genotyping and the continued development of genomically-enhanced EBVs the opportunity exists to significantly accelerate rates of genetic gain across our livestock species, including beef. The main advantage will come through increased accuracy of selection particularly for difficult to measure traits, those that are sex limited, expressed later in life, and on animals previously not recorded. But the cost effectiveness to the beef industry of genotyping currently relies on the accuracies of genomic predictions and the price of genotyping. Results of Van Eenennaam *et al.* (2010) also suggests industry structure and strong price signals through the beef production chain will be necessary to make genomic selection successful.

Breeding structure. Genomic selection is likely to change the breeding industry structure. This has been seen in dairy where genomic selection of young sires is greatly reducing the size of the annual progeny test team thus reducing cost, and it is also changing the way young bulls are selected and used. Currently the beef seedstock sector uses a combination of higher accuracy AI sires and relatively low accuracy young bulls. However, with the advent of higher accuracy genomically-enhanced EBVs a breeder will have the opportunity to increase rates of gain by selecting their own young bulls. In the commercial sector, natural service is likely to continue to dominate and thus the impact of genomic information will be through increased accuracy on young bulls allowing more targeted matching of genetics with market-production systems. Genomic selection may have utility in the bull multiplier sector of pastoral companies in northern Australia, but again will depend on the cost effectiveness of genotyping versus the accuracy of prediction.

As the accuracy of genomic prediction and the amount of genotyping increases, the need for pedigree and performance recording may reduce. This will lead to questions such as what level of recording will be sufficient, who in the industry will continue to performance record, which animals and traits should be targeted, and who will pay for the cost of improvement? In the future there will also be a need for ongoing collection of phenotypes. Firstly to allow genomic selection for new traits but also to allow the re-estimation of prediction equations for existing traits due to the expected decline in accuracy over generations or as genomic technologies improves. Certain sectors of the industry may require higher accuracies than can be obtained from genomic predictions. This will require a level of ongoing performance recording, also needed to maintain a base level of accuracy of the mid-parent EBV on which genomic information can significantly improve.

Breeding Objectives. Increased accuracy of EBVs, and importantly of objective traits, is currently where genomics prediction has the potential to increase rates of gains but we still require the correct weighting of traits in the breeding objective. Barwick *et al.* (2011) argue that current forms of genomic information should not require any fundamental changes to the development of breeding objectives, although as the technology develops there may be the opportunity to more accurately define traits and the need to include genomic tests for genes of large effect (e.g. diseases, horns) directly into breeding objectives.

CONCLUSIONS

For the beef industry to benefit from genomic information, investments in the collection of many more phenotypes, particularly for feed intake and female reproduction traits will be required. Genotypic data can then be used in genetic evaluations to build genomic relationship matrices or to generate genomic predictions that can be combined with existing phenotypic information to lift the accuracy of breeding objectives, thus allowing greater rates of genetic gain for the beef industry.

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