

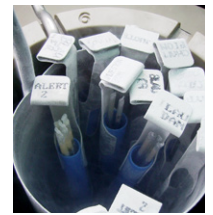
Development and implementation of genomic predictions in beef cattle

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Implications

- Beef production represents a considerable contribution to local and global economies and food security but also the environmental footprint of agricultural production systems.
- The development of accurate genomic evaluations in beef populations are more difficult than in dairy populations for reasons including the presence of multiple breeds, poor extent of phenotyping, lack of artificial insemination, and beef systems being generally a lower-margin business of poorer adopters of technology.
- Several options exist to minimize or overcome the limitations of developing accurate genomic evaluations for beef cattle.

Key words: beef, cattle, dairy, genomics, genotype, phenotype

Introduction

The global beef cattle population includes *Bos indicus*, *Bos taurus*, and their crosses and comprises almost 1 billion head (USDA-FAS, 2015) with two-thirds of this in India, Brazil, and China. Although the efficiency of beef production systems is often cited to be inferior to poultry and pig production (Wilkinson, 2011), most beef cows inhabit environments unsuitable for the production of human edible energy or protein sources (O'Mara, 2012). Once accounted for, the efficiency of beef production, defined as human edible energy ingested per human edible energy produced, is similar to pigs and poultry (Wilkinson, 2011). Beef cattle are generally finished in either feedlot systems or pasture-based systems.

Beef production is extremely important for global food security and is characterized by extreme diversity in both the production systems and germplasm used. This results in a range of breeding objectives comprising a range of traits (Amer et al., 2001). Most breeding objectives are, however, suboptimal due to a lack of accurate estimates of breeding values on some traits, most notably fertility, feed intake and efficiency, meat quality attributes, and animal health.

Natural mating is commonly used as means of generating offspring due to the extensive nature of most cow-calf production systems. Candidate sires are often selected based on visual appearance or lineages, with little cognizance of the individual's estimated breeding value. Many coun-

tries do not have national or compulsory individual animal identification systems, and parent identities are seldom recorded. These global beef production characteristics complicate the development of accurate genomic predictions and hinder the adoption of these technologies.

The development and implementation of official genomic evaluations for beef cattle has occurred later than its 2009 introduction in dairy, and here we discuss contributing reasons for this, as well as possible solutions in overcoming the barriers to implementation. Genomic information has nonetheless been used for several decades in beef breeding programs as means of parentage (in)validation or assignment, breed assignment, and screening for congenital defects or lethal mutations (e.g., Meyers et al., 2010). There has also been some use of low-density commercial marker panels (e.g., Van Eenennaam et al., 2006).

Genomic Evaluations in Dairy Cattle vs. Beef Cattle

The following factors have hindered the development and implementation of genomic evaluations in beef cattle relative to dairy cattle.

Multiple breeds and crossbreds

The Holstein-Friesian is the predominant breed in global dairy production systems in temperate climates. Its effective population size is less than 100 (McParland et al., 2007; de Roos et al., 2008). In contrast, a plethora of British and Continental beef breeds are used in temperate climates, each with effective population sizes greater than Holstein-Friesian, and each with their own breed-specific attributes. In hot environments, *Bos indicus* breeds or *taurindicus* crosses are preferred with Nellore and Brahman being the most prominent indicine breeds. Regarding the *taurindicus* crosses, Brangus and Braford are very popular, with increasing interest in composite breeds such as Senepol, Bonsmara, and Montana. However, considerable genomic differences exist between taurine and indicine breeds (McKay et al., 2008), further complicating the generation of accurate genomic predictions, especially in the crossbreds that exist in several countries (Amer et al., 1997; Berry et al., 2006).

The accuracy of genomic predictions is influenced by effective population size, number of animals with genomic and phenotypic information (Daetwyler et al., 2008), and the relatedness of the reference population (i.e., population of genotyped and phenotyped animals) to the candidate animal population (Pszczola et al., 2012). Compared with dairy cattle, achieving high accuracy of selection for all beef breeds requires larger reference

populations comprising all breeds and crosses. Genomic predictions for candidate animals of a given breed may actually be negatively correlated with their resulting phenotypic performance if that breed is not sufficiently represented in the reference population (Kachman et al., 2013). Similarly, genomic predictions developed for a breed using a reference population representing a selection of countries may be negatively correlated with performance of animals of the same breed originating from a different country (Saatchi et al., 2013). This is because estimated allele substitution effects of genotyped single nucleotide polymorphisms (SNPs) may actually differ in sign among breeds due to different linkage phases with the causal mutation(s). Purfield et al. (2015) reported that almost half of the allele substitution effects of genotyped high-density SNPs differed in sign for their association with direct calving difficulty between pairwise comparisons of Irish Holstein, Charolais, and Limousin populations.

Lack of artificial insemination

All else being equal, the greater the reliability of the phenotypic information in the reference population, the greater the accuracy of genomic predictions (Daetwyler et al., 2008; Garrick et al., 2009). Moreover, the accuracy of imputation from lower-density (i.e., lower cost) genotypes to higher-density genotypes is greatest when high-density genotypes are available on close ancestors of animals to be imputed (Berry and Kearney, 2011). A large proportion of dairy calves in most populations are offspring of a few AI sires. In contrast, a smaller proportion of beef calves are generated from AI. Less AI usage generally implies fewer bulls with highly accurate genetic evaluations. Collectively, these constraints require a larger reference population, which is more difficult and expensive to assemble. The lack of AI in beef also contributes to poor genetic connectedness (i.e., common sire families) among the same breeds in different countries.

Relatively poor international genetic connectedness

INTERBULL is responsible for international genetic evaluations in several dairy cattle breeds. Accurate international genetic evaluations rely on

strong genetic connectedness among countries achieved in dairy from similarities in national breeding objectives and thus similar families being represented across populations. The phenotypes used in many genomic evaluations of Holstein-Friesian dairy populations are multiple across-country evaluations (MACE; Schaeffer, 1994) generated by INTERBULL (Berry et al., 2009). Thus, males with no phenotyped descendants in a given country may still achieve genetic evaluations with relatively high accuracy in that country based on MACE evaluations. This facilitates the establishment of large reference populations and provides opportunities for sharing genotypes of common animals across multiple countries. BREEDPLAN and INTERBEEF undertake international genetic evaluations for beef cattle, but few breeds and countries participate in these initiatives, and all traits are not considered (e.g., animal health). Many North American breed associations pool data from USA and Canada but not from other countries.

Relatively low levels of phenotyping

Accurate genomic predictions are predicated on access to large quantities of phenotypic information (Daetwyler et al., 2008). For example, the majority of dairy cows in most developed countries have milk production recorded. To enroll in milk recording, calving dates are generally required, thus facilitating generation of fertility and survival phenotypes. Udder health information, via the measurement of somatic cell count in milk, is available from milk testing. Access to such data facilitates the achievement of accurate genetic evaluations for large populations of male and female animals for a wide range of traits. In contrast, phenotyping strategies in beef production systems tend to be poorer, especially in commercial populations. Sire recording is also generally poor in many beef production systems especially where multi-sire mating is practiced.

Lower-margin business model

Development of a genomic selection-based breeding program requires an initial investment in genotyping and phenotyping as well as necessary infrastructure (i.e., computing and personnel) to deliver routine genomic



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Sugar Loaf Farm Black Angus Cattle (source: © 2015 Wikimedia.org/Wndyfrg).

evaluations. Generation of genomic predictions at the producer level requires investment in genotyping. Anecdotal evidence suggests that beef producers tend, in general, to be slower adopters of technology than dairy farmers. This could be due to a multitude of reasons, including the lower business margin. Poor adoption rates, even in the use of measures of genetic merit as a whole (i.e., expected progeny differences, or **EPDs**), provide little incentive for investment in genomic technologies to advance genetic gain in beef. Reduced uptake, in turn, impedes the growth of the reference population necessary to improve the accuracy of prediction, and thus, the justifiable cost that can be paid per genotype by producers. In contrast, the high accuracy of genomic prediction achieved in many dairy populations, coupled with it being a generally higher profit margin business, justifies investment by producers in genotyping to aid in selection of candidate female replacements (Weigel et al., 2012). The fiscal status of the beef sector also impacts the investment strategy for the development of the initial reference populations; different countries have adopted different strategies. The reference populations globally have been funded by individual breed societies (e.g., US), breeding or other commercial companies (e.g., US and Brazil), or by subsidies available to the beef producers themselves (e.g., Ireland and Scotland). The establishment of the initial reference populations in dairy cattle has generally been funded by commercial AI companies (e.g., US, New Zealand, The Netherlands) although competitive research grants have contributed to, or been the source of funding for the establishment of reference populations in other countries (e.g., Ireland and Brazil).

National Beef Genomic Evaluations

Europe

Genomic evaluations in beef cattle are currently not official in any European country, but research on genomic evaluations or access to unofficial genomic proofs exists in many countries. Ireland will launch official genomic proofs in early 2016 for all beef breeds, based on a one-step multi-breed genomic evaluation, which includes > 100,000 animals with genotypes and phenotypes. These include a combination of sires as well as commercial (predominantly crossbred) cows. The genomic evaluations will be generated and disseminated by the Irish Cattle Breeding Federation (<http://www.icbf.com>), which is the government-appointed body responsible for national genetic evaluations in Ireland.

Genomic evaluations for UK Limousin cattle for a selection of video image analysis carcass traits are planned to be available in December 2015 based on a reference population of 720 Limousin animals with high-density genotypes and an additional 1,700 Limousin animals with medium-density genotypes. Genomic evaluations will be undertaken using a one-step approach by EGENEs (<http://www.sruc.ac.uk/info/120275/egenes>) on behalf of Genesure, a web-based company that will act as the new delivery vehicle for collecting samples and providing genomic evaluations to individual farmers.

Unofficial genomic evaluations for Charolais, Limousin, and Blonde d'Aquitaine cattle were made available in February 2015 in France based

on a two-step approach blended with traditional genetic evaluation using a selection index approach. The number of animals included in the training population varied by breed and trait but ranged from 1,029 to 5,181 animals in Charolais, 606 to 3,995 animals in Limousin, and 1,645 to 4,282 animals in Blonde d'Aquitaine. Of these animals, 8 to 35% were well proven progeny-tested bulls.

North America

National genetic evaluations of beef cattle in North America are managed by the various breed associations. The Angus society was the first national genetic evaluation to incorporate whole-genome SNP information. This occurred because of separate investments by Pfizer Animal Genetics and Merial Igenity in the development of reference populations. Due to the significant contribution of Angus cattle to the North American performance recorded population, Angus was an obvious choice for the initial investment. At that time, there was an expectation that genomic predictions developed in one breed would have predictive ability in a range of breeds. Igenity developed a low-density panel whereas Pfizer Animal Genetics marketed a competitive medium-density (i.e., 54,000 SNPs) product. The proprietary molecular breeding values (MBV) from the two companies were included as correlated traits in the Angus evaluation, with procedural modifications being made so that evaluations could be run on a regular basis. Since then, Igenity was purchased by GeneSeek/Neogen, Pfizer Animal Genetics has been restructured into Zoetis, and there has been successive retraining and rationalization. Individual breeders can undertake genotyping using reduced-density panels by Zoetis or GeneSeek, the respective genotypes being imputed to 54,000 SNPs with a single prediction equation used to generate the molecular breeding value (MBV), which can subsequently be included in national genetic evaluation as a single correlated trait for each reported EPD. Recent prototyping based on approximately 50,000 genotyped animals has been undertaken to develop single-step GBLUP for Angus with the objective of implementation by the end of 2016.

In contrast to Angus, which benefited from the external investment by animal health companies, the American Hereford Association was only able to access genotypes from a small dataset of publicly funded research. This was sufficient to demonstrate that the prediction equations being marketed for Angus cattle did not have predictive power in Herefords, forcing the American Hereford Association to develop a training population using their own funds. Other breed associations gradually followed suit, resulting in staged implementation of genomic predictions (Saatchi et al., 2011). Genetic evaluations for many of the other breeds are undertaken by International Genetic Solutions. The approaches to genomic prediction used by American Hereford and International Genetic Solutions have been to include the MBV in a post-genetic evaluation selection index procedure since their genetic evaluations are currently run only two to three times a year. Both American Hereford and International Genetic Solutions are prototyping single-step evaluations that could include up to 20,000 and up to 50,000 genotyped animals, respectively. The accuracy of genomic evaluations in a selection of US cattle populations is in Table 1 (Saatchi et al., 2011, 2012)

Australasia

Genomic information has been exploited in Australian beef genetic evaluations for several years. This began with the use of a small panel of commercial markers for meat tenderness. More recently, Angus genetic evaluations for a range of traits were supplemented using a post-BLUP blending approach for genotyped animals with genomic breeding values

developed by Pfizer/Zoetis for Angus. This has now recently been supplemented with genomic breeding values from a commercial company Genesee and genomic predictions from Australian research grants. Genomic breeding values for female reproductive performance and 200-d weight for Brahman are also generated by BREEDPLAN using a reference population of > 1,000 cows genotyped and phenotyped for age at puberty and lactation anoestus interval. Specialized beef phenotyping farms also exist in Australia, termed beef information nucleuses (BINs; Banks, 2011), in an attempt to achieve unbiased, accurate genetic (and genomic) predictions on young bulls for especially difficult-to-measure traits.

South America

The application of genomic information in beef cattle genetic evaluations in South America began in 2008 through Igenity and Pfizer Animal Health. In the taurine beef breeds (particularly Angus), these companies promoted the same approach used in North America. Success has been limited. Because countries like Brazil and Argentina have their own breeding strategies for taurine breeds, which are different from North America, combining genotypic and phenotypic information to improve outcomes on genomic selection has not been considered.

Research by Igenity and Pfizer Animal Health on genomic evaluations for Nelore (*Bos indicus*) in Brazil began in 2010. Similar to in the US, Igenity marketed a low-density genotype panel while Pfizer marketed a medium-density genotype panel. Because genetic evaluations for Nelore in Brazil are based on several large groups running independent genetic evaluations through consultant geneticists or quantitative genetics services companies, genomic evaluations were basically limited to one of the several breeding programs (ANCP), and thus restricted to only a fraction of the potential users. One of the reasons for the limited use of genomic selection in Nelore could be the particularity of the breeding market where commercial competition is extremely high, thereby generating some skepticism among breeders in new technology.

Since 2010, however, a notable increase of science in the application of genomic technologies in Brazilian beef breeding programs has occurred. Neves et al. (2014) documented the feasibility of using different genetic evaluation and validation methods for genomic selection in Nelore. Carvalho et al. (2014) proposed the best imputation strategy for increasing the power of genomic information by predicting large SNP panels (> 700,000) from panels as low as 15,000 SNPs. These results have prompted increased interest among breeders in adopting genomic technologies with a greater uptake expected in 2016. Discussions have also begun on the development of genomic evaluations for Brahman, another important indicine breed in several tropical areas of the world. A recent international

Table 1. Genetic correlations between direct genomic values and phenotype from k-fold validation in several different beef breed populations (Saatchi et al. 2011, 2012)

Trait	Red Angus	Angus	Hereford	Simmental	Limousin
Birth weight	0.75	0.64	0.68	0.65	0.58
Weaning weight	0.67	0.67	0.52	0.52	0.58
Milk yield	0.51	0.51	0.37	0.34	0.46
Rib eye muscle area	0.75	0.75	0.49	0.59	0.63
Marbling	0.85	0.8	0.43	0.63	0.65
Direct calving ease	0.6	0.69	0.68	0.45	0.52
Maternal calving ease	0.32	0.73	0.51	0.32	0.51

initiative, capitalized by the World Brahman Federation, is advocating the establishment of multi-country genomic evaluations.

Overcoming the Constraints to Achieving Accurate Genomic Evaluations in Beef

Multi-breed genomic prediction models

Multi-breed genomic predictions could potentially be useful in exploiting information from multiple breeds in improving the accuracy of genomic predictions. This may be especially true when the candidate animals are either crossbred or composite animals. Multi-breed genomic evaluations are, however, complex compared with single breed evaluations because multi-breed datasets are characterized by a greater number of haplotypes at any particular genomic location. Haplotypes are sets of alleles at nearby loci that tend to be inherited together. Since the causal mutations responsible for variation are not yet included on the currently used SNP panels, difficulties exist in capturing the effects of the variation via the collective haplotype. Any breed may have several haplotypes, some of which are associated with a favorable allele and others with unfavorable alleles. Unrelated breeds do not share the same haplotypes, so training on one breed is not typically informative for another breed. Pooling breeds increases the number of haplotypes whose effects need to be estimated. Accordingly, more data are needed in a multi-breed reference population than for a single breed. Furthermore, SNP allele frequencies vary between breeds, and this can create some challenges in constructing genomic relationships for strategies that use this approach.

Exploitation of information from other populations

Although across-country multilateral genetic evaluations do not exist for all traits in all beef breeds, international initiatives such as INTER-BEEF (Vernot et al., 2007), BREEDPLAN (Graser et al., 2005), and the

Hereford Pan-American Cattle Evaluation do exist. Incorporating estimated breeding values (EBVs) from another country within a multi-trait genomic (or genetic) evaluation could aid in augmenting the accuracy of genomic evaluations if the foreign animals were related to those in the domestic population. Collation of data from multiple sources is, however, not without its own complications such as differences in trait definitions, differences in breed representation, and genotype by environment interactions. de Haas et al. (2015) documented an improvement in accuracy of genomic prediction for dry matter intake in Holstein-Friesian dairy cow populations by exploiting phenotypic and genomic information from other populations of Holstein-Friesian cows; the within-country accuracy of genomic predictions when information from all eight countries was included in the genomic predictions was 1.04 to 1.35 (median of 1.13) that when only genomic information for the country itself was considered. International genetic connectedness allowed estimation of genetic correlations between countries; to aid in improving genetic connectedness in beef populations, an initiative to share germplasm between countries would be a prerequisite. This is particularly important for difficult-to-measure traits where recording of such traits may be confined to small populations like experimental research farms or nucleus herds.

Specialized phenotyping herds

Consideration should be given to development of specialized beef herds that are financially incentivized to undertake accurate phenotyping of genotyped animals but also to use certain semen to ensure strong connectedness to their national beef population. Such systems already exist in some countries such as the BINs in Australia (Johnston et al., 2012); national performance test stations for feed intake and other performance traits are also relatively commonplace (Crowley et al., 2010). The principles for establishing such herds for the recording of difficult-to-measure traits have been outlined in detail by Calus et al. (2013). The financial value (i.e., incentive) of such phenotypes has been described in detail by Gonzalez-Recio et al. (2014). The size of the financial incentive is a function of the value of the trait in the breeding objective and the heritability of the trait (Gonzalez-Recio et al., 2014); a strategy could also be put in place to reward early adopters since the marginal benefit of additional phenotypes (and genotypes) declines as the number of phenotypes (and genotypes) increases, all else being equal (Daetwyler et al., 2008).

Lower-cost genotyping technologies

Many genotyping platforms now exist (Berry et al., 2013) to simultaneously generate sufficient genomic information for imputation to higher genotype density for use in genomic evaluations while also providing genomic information for parentage and breed verification or assignment. These genotype platforms can also aid in the monitoring of variants in major genes or genes conferring lethal or congenital defects, as well as quantifying the contribution of (genotyped)



Ampoules of frozen bovine semen in liquid nitrogen canister (source: © 2008 Wikimedia.org/Uwemuell).

ancestral genomes to that of the genotyped individual. The commonly referred to “SNP chips” have been, and continue to be, almost exclusively used in the genotyping of large populations of cattle. Although the cost of SNP chips is continuously declining, the potential still exists to reduce this cost further. Developments in approaches for the procurement of biological samples, as well as the extraction of DNA and the time required to undertake the assay, could each contribute to cost reductions as could automation of genomic predictions. Other genotyping technologies such as genotype-by-sequencing (Nielsen et al., 2011) could potentially reduce genotyping costs further. The value proposition is directly related to what the resulting information will be used for and how accurate the genomic predictions are. To our knowledge, no financial analysis exists to guide beef breeders on how much they can afford to pay for a genotype.

Value-added genomic information

Many beef breeders are not overly concerned with measures of polygenic genetic merit (e.g., EPDs) per se. Nonetheless, many beef breeders have a keen interest in other animal-related statistics, which can be generated from genomic information such as parentage verification or assignment. Breeders are also generally interested in the genotype of an animal to determine particular variants such as myostatin (Grobet et al., 1998) or those resulting in congenital defects (e.g., Meyers et al., 2010). Other potential genotype-derived information includes the breed composition of the animal, which may be particularly useful in crossbreeding strategies, or the contributions of individual ancestors to the genome of an animal. Harnessing interest among breeders in such information, within the context of a larger genotyping strategy to also generate genomic EPDs, could be used as an approach to generate a large and relevant reference population for the development of accurate genomic predictions.

Public good investment

The contribution of the global beef herd to food security and environmental footprint has been well documented (Hume et al., 2011). The only output in beef cow herds is the calf (and cull cow), thereby resulting in a high environmental footprint per unit product (Wilkinson, 2011). Improving efficiency of beef production, through exploitation of genomic technologies for example, is therefore a public good. Such a proposal is already recognized in Ireland where beef farmers were financially incentivized to genotype a selection of their commercial cows as a means of generating a genomic selection reference population. Irish beef farmers are also financially incentivized to retain genomically tested high-index females as herd replacements. The aim of that initiative is to increase the efficiency of the national herd. A similar publicly funded initiative has also begun in Scotland.

Opportunities for Beef Genomics

The economic and social importance of beef production globally necessitates an optimal breeding strategy to be put in place. The appropriate exploitation of genomic information is key to achieving high accuracy of selection, and thus, initiatives to achieve this simply must be embarked on. The success achieved through international collaboration (mostly the exchange of genotypes) in dairying cannot be ignored; the framework, agreements, and logistics, therefore, already exist. Moreover, the skill sets and knowledge of generating genomic predictions for different population structures already exist, albeit they are constantly being improved. The ever-declining cost of generating a genotype implies that cost should soon

no longer be a barrier to implementation. Developments in low-cost sensors and associated information technology for the generation and capture of phenotypes suggest that the necessary ingredients for the development of genomic predictions in beef are indeed available.

Conclusions

Several factors have contributed to the slower development and uptake of genomic evaluations in beef cattle relative to that achieved in dairy. Within-breed genomic evaluations are, however, either already in place or are close to official implementation status. Nevertheless, several issues persist, most notably access to phenotypes (both number of animals phenotyped and range of phenotypes) from which to generate genomic predictions and low-cost genotyping for widespread adoption of the genomic predictions.

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