

Notes

Uses of Genomics in Livestock Agriculture

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Knowledge of the genomics of livestock will be useful to agriculture in many ways which can be broadly divided into improving the genotype of livestock and improving their management. Ongoing genetic improvement relies on selecting animals according to their breeding value and this is traditionally practiced by using performance and pedigree data to estimate the breeding values of selection candidates. Data on the alleles that an animal carries at individual loci can be used to increase the accuracy of these EBVs. In a few cases we know the mutation that causes a phenotypic change, but in most cases we do not know the causative mutations but can still use a panel of random genetic markers covering the whole genome to estimate the breeding value of each animal. This method, called genomic selection, is already being implemented in dairy cattle and will, no doubt, be used in all livestock industries in the near future. In addition to long term genetic improvement, the genetic merit of the next generation can be improved by utilising non-additive genetic variation by optimising mate allocation within the selected animals.

Uses of genomic knowledge to improve management of livestock can be divided into exploiting genotype by environment interactions and the development of new products such as pharmaceuticals. Assigning each animal to the environment, management and market in which it will be most profitable could use genetic information about the animal. The discovery of genes that affect economic traits might identify gene products that might be targets for new pharmaceutical products. This is only one possible way in which new biological knowledge derived from genomics might be exploited in the future.

Accelerating genetic improvement with SNP chips

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The development of a variety of single nucleotide polymorphism (SNP) platforms is having a profound impact on genetic progress in the U.S. dairy industry and creating new international data alliances. In slightly more than three years since its initial availability, the Illumina BovineSNP50 BeadChip has been used to genotype hundreds of thousands of cattle globally. In the U.S. Holstein breed, over 80,000 animals have been genotyped using various density SNP assays. These genomic data were included for the first time in the official national dairy cattle genetic evaluation published by the USDA in January 2009. More recently, in December 2010, data from a reduced panel, the Illumina Bovine3K, was incorporated into the evaluation system using imputation. Substantial increases in genetic improvement have been predicted through the implementation of genome enabled selection. Currently, however, validation results are available only from the analysis of historic data, where populations have somewhat arbitrarily been divided into past and "future" populations. Availability of lower-density SNP assays could also dramatically impact genetic improvement by reaching even a larger fraction of populations. Moderate-density SNP data are currently used to validate reported parentage and correct pedigree errors, but more comprehensive genotyping is needed. These data are also being used to discover parentage and to more accurately characterize the degree of relatedness among animals in the population using genomics-based relationship coefficients. By accurately charactering the fractions of the genome inherited from each grandparent, genetic similarity that is currently described by statistical averaging using the pedigree can be

refined to more accurately predict genetic merit early in life. Finally, individual animal genome sequencing is on the scientific horizon. Availability of such data could have implications beyond genetic improvement, and result in deeper understandings of basic biology, consequences of selection, and even animal and human health. Our ability to fully utilize these data will present enormous statistical and computational challenges.

The role of sequencing in livestock breeding

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DNA sequencing has been a critical part of livestock breeding since the advent of genomics over 20 years ago. Initially it was used solely to identify and provide probes for testing DNA variants, primarily SNPs and microsatellites. These probes provided the tools to create linkage and RH maps and the ability to map monogenic traits. In a proportion of cases the causal mutant was also identified. Perhaps less acknowledged has been the use of DNA sequence in comparative mapping across species. More recently sequencing has advanced to the stage where it can not only map variants, but can also order and orientate them. With next generation sequencing this has now advanced to where not only SNPs, but also indels and CNVs are being “genotyped” and haplotyped in many individuals where a prior high quality genome assembly is available. This information can be cascaded to relatives genotyped with SNP chips via imputation. However, the current analysis methodologies and sequencing technology still make this process rather tedious and resource intensive. *De novo* sequencing to create a whole genome assembly is still a major challenge for these newer technologies and “reasonable” next generation mammalian assemblies that do not rely heavily on external information, such as linkage and RH maps and traditional Sanger BAC end sequence, are now only just becoming possible. Critically, the process depends on read length and the ability to create a variety of insert sizes rapidly and cheaply. In the interim, complexity reduction, using pools of BACs and next generation sequencing shows potential for improvement of *de novo* assemblies. The longer term goals of DNA sequencing are to rapidly, cheaply and accurately sequence single strands of at least 500 kilobases in length in a single reaction. This will allow direct assembly of haplotypes. The concurrent ability to transparently decode the methylation status of the nucleotides would allow investigation into the effect of variants on haplotype specific gene expression.

QTN modulating the transcription rate of a chromosome domain encompassing PLAG1 control bovine stature

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We will report the mapping on bovine chromosome 14 of a Quantitative Trait Locus (QTL) with major effect on stature in an F2 cross between Holstein-Friesian and Jersey cattle. We refine the map position of the QTL to a ~780 Kb interval after adding 925 markers and by simultaneously exploiting linkage and linkage disequilibrium using a novel Hidden Markov Model-based approach. We confirm the QTL localization in an independent outbred population genotyped for a distinct high-density marker set. We use high-throughput technology to resequence the ~780 Kb interval in six sires with QTL genotype inferred by marker assisted segregation

analysis, and identify 13 clustered candidate Quantitative Trait Nucleotides (QTN) out of > 9,572 discovered polymorphisms. We identify recombinant haplotypes in a breed diversity panel and eliminate five candidate QTN by studying the phenotypic effect of one of these haplotypes in Simmental. We use quantitative RT-PCR and allelic imbalance tests to demonstrate that QTN genotype influences the expression level of seven of the nine genes mapping to the ~780 Kb in multiple fetal tissues. We conclude that the QTN modulate the activity of cis-acting regulatory elements controlling the transcription rate of an evolutionarily conserved chromosomal domain encompassing PLAG1. We demonstrate that two of the eight candidate QTN, mapping to a highly conserved sequence element in the PLAG1-CHCHD7 intergenic region, influence bidirectional promoter strength in a luciferase reporter assay and affect the formation of complexes with nuclear factors in an electrophoretic mobility shift assay. By performing expression QTL (eQTL) analyses in the same F2 cross, we identify a splice site variant in the CHCHD7 gene. We exploit this naturally occurring null allele to exclude CHCHD7 as single causative gene.

Chicks and SNPs – an entrée into identifying genes conferring disease resistance in chicken

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With high-density chicken rearing, control of infectious diseases are critical for economic viability and maintaining public confidence in poultry products. Among poultry diseases, Marek's disease (MD), a lymphoproliferative disease caused by the highly oncogenic herpesvirus Marek's disease virus (MDV), continues to be a major concern. The fear of MD is further enhanced by unpredictable vaccine breaks that result in devastating losses. The field of genomics offers one of the more exciting avenues for enhancing control of MD. By identifying genes that confer genetic resistance, it should become possible to select for birds with superior disease resistance. Genetic resistance to MD is a complex trait controlled by many genes. Most genome-wide efforts for complex traits rely on linkage between the causative gene and a genetic marker, which results in limited detection power and resolution of gene location. An alternate method is to screen for allele-specific expression (ASE), a simple yet powerful approach, where the expression of each gene allele is compared within an RNA sample. When the expression of the alleles is not equal, then one can unequivocally declare ASE and the presence of a polymorphic cis-acting (genetic) element for that gene as linkage disequilibrium (LD) is confined to the transcriptional unit. The only requirements for ASE to work are: (1) the assumption that variation in expression between alleles of a gene are responsible for part of the phenotypic variation, and (2) the existence of a cSNP to monitor the alleles. Response to MDV infection in chickens was evaluated using next generation sequencing on a limited number of samples to query for ASE followed by Illumina GoldenGate assays to validate and expand the number of samples. Our results clearly demonstrate that ASE is an efficient method to identify potentially most or all of the genes for this complex trait. The identified cSNPs can be further evaluated in resource populations to determine their size of effect on genetic resistance to MD as well as be directly implemented in genomic selection programs.

Dissecting the genetics underlying reproduction rate in tropically adapted beef cattle

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Reproduction rate is a key trait affecting profitability of beef production systems. Improvement of reproduction rate using traditional selection practices has been slow due to low heritabilities of industry measured traits. In an attempt to provide genetic marker technology to the beef industry for the improvement of reproduction rate we have performed a genome wide association study (GWAS) on Brahmans and Tropical Composite cattle, sourced and bred in northern Queensland. Key reproduction traits measured on these cattle included age at puberty (defined as age at first corpus luteum) and post partum anoestrus interval (interval from bull-in date to first detected corpus luteum). In addition, many other traits were measured on these cattle including weight, subcutaneous fat depth, serum IGF 1 concentration, hip height, and condition score. Results indicate that BTA14 is the key chromosome in Brahmans, and BTA5 is the key chromosome for Tropical Composites for almost all traits measured (reproduction and other traits). Furthermore, there is little overlap of significant markers between breeds. This may indicate that either the biology of reproduction rate traits is different between breeds, or that a higher density genome scan is required to identify common genes underlying reproduction rate in beef cattle breeds.

Patterns of genetic variation and signatures of selection in the sheep genome

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In order to understand the genetic history of sheep, the International Sheep Genomics Consortium assembled and genotyped over 2,800 sheep from 74 diverse breeds using the ovine SNP50 BeadChip. The results provide unprecedented insight into the population structure, diversity and domestication of this important livestock species. Levels of SNP diversity were compared between populations sampled across seven major geographic regions. High diversity in sheep from the Middle East (Turkey and Iran) supports existing molecular evidence indicating this was the center of sheep domestication. Global patterns of genetic structure were inferred by principal component analysis of relatedness. This revealed clustering according to geographic origin and the identification of breeds with mixed origin. Interestingly, the majority of breeds retain high effective population size. This suggests domestication occurred from a broad genetic base and that the resulting genetic bottleneck was not as severe for sheep as for other animal domesticates such as cattle. The experiment also sought to characterise the legacy of selection and adaptation on the sheep genome. Analysis revealed 31 regions with evidence for recent positive selection containing genes for coat pigmentation, skeletal morphology, body size, growth and reproduction. Together, the results provide the first in depth view of genetic diversity for this livestock species.

How accurate can we make genomic selection?

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In order to maximize the accuracy of genomic selection we need to understand which components affect this accuracy, how important are these components and whether we can improve these components. The components that determine the accuracy of genomic selection are the marker density, and thus the extend of linkage disequilibrium between the markers and the genes, the effective number of segments in the genome, the number of training animals and their relationship with the selection candidates, the heritability of the trait, the number of genes in the genome and the distribution of their effects, and the method used for the estimation of marker effects. The GBLUP method is often used for the estimation of marker effects which assumes a normal distribution with constant variance across the markers. In simulation studies, GBLUP is found to be insensitive to the number of genes and the distribution of their effects. However, GBLUP does not take advantage of the ever increasing marker densities since it does not give extra weight to the most important markers. Use of more realistic prior distributions of marker effects, such as the double exponential, the t-distribution or a spike-and-slab mixture distribution, do result in extra weight for the most important markers. The latter type of distribution was found to yield accuracies of 0.83 – 0.97 in whole genome sequence data where GBLUP only reached an accuracy of 0.5. A drawback of the latter is that they require computationally intensive Monte Carlo Markov Chain methods to estimate marker effects. Fast iterative methods that use spike-and-slab or other more realistic prior distributions, such as fastBayesB, are discussed.

How Ireland is capturing the benefits of genomic selection in its cattle population

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Genomics is a technology for increasing the accuracy which the genetic merit of young potential breeding animals can be determined. It enables earlier selection decisions thus reducing generation intervals and gives rise to more rapid annual rates of gain. Recently, the cost of genomics has reduced to the point where it enables breeding program costs to be reduced substantially. Ireland has been a rapid adopter of genomics technology in its dairy cattle breeding program with 40% of dairy cow artificial inseminations in 2010 being from bulls selected on genomic information. This rapid adoption has been facilitated by: ICBF's comprehensive database of phenotypes, strong public funding support for applied genomics research, an international network of collaborators, a short path between research and application, an overall selection index, the EBI, which farmers use in making breeding decisions and a motivated and informed breeding industry. The shorter generation interval possible with genomic selection strategies also allows exploitation of the already accelerating rate of genetic progress in Ireland, as elite young dairy bulls are considerably superior to the small numbers of bulls that entered progeny test six years ago. However, genomics is having a dramatic impact on the AI (artificial insemination) industry by substantially reducing the cost of entry, the cost of operation and shifting the focus of breeding back to cows, from bulls. We believe that the current industry structures must evolve substantially if Irish cattle farmers are to realise the full benefits of genomics and be protected from related risks. Our model for future dairy breeding envisages a small number (1,000 cows) of "next generation" research herds, some 1,000 (100,000 cows) "bull breeder" herds and an AI sector using some 30 bulls per year to breed the bulk of replacements in commercial milk producing herds. Imputation from a 3K to a 50K SNP chip is a key element of our strategy to enable dairy farmers to have direct access to genomic technology at an affordable price. This model is capable of delivering high rates of genetic gain, realising cost savings, and protecting against the risks of increased inbreeding and inappropriate breeding goals. Our strategy for exploiting genomic selection for beef

breeding is currently focused on genotyping, using the Illumina HD SNP chip, a training population with Irish phenotypes of some 1,000 bulls representing all the main beef breeds in Ireland. We recognise the need for a larger training population and are seeking collaboration with organisations in other countries and populations.

Genome sequencing of African and Indicine cattle for SNP development

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The Brahman and other tropically adapted breeds of cattle have so far not been well characterised at the level of DNA variation, and consequently do not form a large part of current genotyping arrays. These cattle are an important part of the Australian cattle industry so it will be necessary to characterize their DNA variation if genomic selection of these animals is to occur. In this study, a Brahman, a Tuli and a high grade Africander animal from Australia were genome sequenced. In excess of 16 Gb of Illumina GA-II sequence was obtained for each animal, in the form of 75 bp paired end reads. A total of 6.35 million single nucleotide polymorphisms (SNP) were discovered in the three animals, with the Brahman animal having nearly twice as many SNP as either the Tuli or the Africander. Development of new arrays that contain some of these SNP will aid in providing new tools to speed up the rate of genetic gain and will have been constructed with information from Australian cattle, making them more relevant to Australian conditions.

Finding genes for economically important traits: Brahman cattle puberty

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Age at puberty is a key component of reproductive performance in Brahman cattle. Brahman cattle are on average older at puberty than *Bos taurus* cattle and so it is of economic relevance to select for early age of puberty within this breed. To assist selection and elucidate the genetics underlying puberty, we performed a genome-wide association study (GWAS) using the bovine SNP50 chip in 843 cows and 1,115 bulls, all Brahman. The traits that defined age of puberty were: age at which the first corpus luteum was detected (AGECL, $h^2 \sim 0.57$) in cows and age at a scrotal circumference of 26 cm (AGE26cm, $h^2 \sim 0.70$) in bulls. At puberty, cows were on average older (751 ± 142 days) than bulls (555 ± 101 days). There were 169 SNP associated to AGECL and 235 SNP associated to AGE26cm ($P < 0.001$). Over 30% of associated SNP were located on chromosome 14 (BTA14), including the most significant SNP for both traits ($P = 4.52E-10$ for AGE26cm and $P = 2.45E-09$ for AGECL). The region between 21.95 Mb and 32.19 Mb of BTA14 contained 51 SNP that were associated ($P < 0.001$) with age at puberty in both female and male cattle. These results indicate that the genes underlying the QTL in BTA14 play a role in defining age at puberty in Brahman cattle. There are over 20 annotated genes underlying the QTL in BTA14 and these are the subject of current research. Information

about specific genes and markers adds value to genomic selection. Therefore, identifying this QTL contributing to genetic variation in AGECL and AGE26cm can assist with the selection for early onset of puberty in Brahman cattle.

The accuracy of genomic prediction when using information from Distantly related animals

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Genomic selection was originally based on the prediction of the effects of quantitative trait loci (QTL) in linkage disequilibrium (LD) with markers. However, there is increasing evidence that genomic selection also relies on relationships between individuals to accurately predict genetic value, as genomic predictions tend to be more accurate in closely related populations. This study aimed to examine the relative importance of information on unrelated individuals on the estimation of breeding value when using gBLUP and BLUP.

Analysis was undertaken using a simulated population of 20000 animals. Three reference populations were formed, each contained 1750 animals and the accuracy of prediction was assessed for the remaining 250 animals that formed the test population. Three test populations were constructed such that one included 5 half siblings from 50 families, another included 10 families that had no family members in the reference population and the final test population contained unrelated animals (maximum pedigree relationship of 0.05). The gBLUP method more accurately predicted breeding value than BLUP in all test populations. The highest accuracy was achieved when gBLUP was used to predict the breeding value of closely related animals. However, gBLUP was still able to predict breeding value accurately even when animals were distantly related and genomic predictions remained accurate when animals were unrelated through pedigree.

Identifying pathways significant for milk production traits in livestock

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Dairy cows vary in milk production traits at various stages of lactogenesis in response to hormonal and genetic factors expressed in mammary gland. Identifying the genes involved allows us to understand the mechanisms driving protein synthesis and identify the source of variation. This knowledge can be applied to selection programs, feeding and maintenance strategies and helps us understand the effect of individual mutations on correlated traits, such as fertility. Genome wide association study (GWAS) has become a popular statistical method to identify individual polymorphisms associated with a trait but lacks where there are many genes of small effect and does not adequately identify relationships between genes. Multiple testing also results in a large number of false positive results. Pathway analyses overcome these issues by using candidate gene sets. We compiled and analysed novel pathways associated with regulation of ribosome synthesis, including RNase5. Linear regression analysis was then used to identify the relationships between the pathway gene SNP sets and a series of milk and protein production traits. The significant relationship seen between these SNP and the milk production traits protein percent and protein yield, suggest a role of these ribosomal RNA synthesis regulation genes in regulating protein synthesis in the mammary gland. We also identified an efficient method of pathway selection for complex traits that can be applied to any pathway or gene set.

The use of genomics in the management of livestock

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Variation between animals exists at all stages of the beef supply chain, in contrast to most manufacturing supply chains where there is generally no unintended variation within each segment of the chain. This variation is generally an unwanted nuisance, but when properly managed it can provide opportunities to dynamically target multiple product end-points and turn-off dates. Moreover, good management can lead to high degrees of compliance with the needs of the next segment of the supply chain and/or end-users. Management decisions can be divided into initial group formation (mating groups, feedlot entry groups, etc.) and ongoing changes to the management plan in the light of new information (including market forces, weather and the genetic status of animals). In both cases, the best pattern of decision making depends, explicitly or implicitly, on the predicted effect of these decisions on future animal performance. This paper gives an overview of some of the factors that impact on these predictions, and hence on optimal management, and emphasises the potential role of genetic and genomic information for increasing focus and improving profitability in the beef supply chain.

Application of livestock genome technologies for genetic improvement in the developing world

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Sustainable genetic improvement has proven difficult in many developing country situations, notwithstanding a number of outstanding success stories. Many failures of genetic improvement can be attributed to attempts to make genetic improvement without making other system improvements and to overoptimistic application of genetic and reproduction technologies to systems that have insufficient human, physical or financial capacity to support the technologies after external expertise and support are withdrawn. Genomic technologies offer some promise, particularly where they need only to be applied for a short period or in a restricted setting, where the required expertise, infrastructure and financial support can be provided. Examples include, a) use of marker technologies to map genetic diversity to guide decisions on conservation and breed characterization, and b) use of dense marker assays (or custom designed reduced marker assays) to determine breed composition in existing populations with no pedigree records, coupled with assessment of performance in the field to determine optimum breed composition in the field. GWAS and its application to genetic improvement might also be feasible because, in contrast to the developed world, there will rarely be an existing phenotype-based improvement program against which it has to compete or add value. The need for ongoing genotyping required to practice selection could, however, be a substantial challenge in terms of the technical and financial capacity required. Other approaches, such as detection and analysis of signatures of selection, may be useful to identify breed-specific genome regions for longer-term use in introgression or synthetic breed formation.

Designing dairy cattle breeding schemes under genomic selection - a review of international research

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Higher rates of genetic gain can be achieved through 1) more accurate predictions of breeding values; 2) higher selection intensity and 3) shorter generation intervals. Implementation of genomic selection may positively influence all three of these terms. Genomic selection can predict breeding values in juveniles with around 60% reliability. This allows for more accurate selection of animals as soon as DNA is available and has opened opportunities to radically re-design breeding schemes. While most research in the last decade focussed on the feasibility of genomic selection, more recently, the application of genomic technology to breeding schemes has generated a lot of interest. In this paper we review published research into breeding scheme design using genomic selection and evaluate their effect on genetic gain and the rate of inbreeding. The schemes range from low risk designs, some of which have already been implemented, where bulls are screened genomically before entering progeny-testing, to more ambitious schemes which screen large numbers of bull calves to be used widely at sexual maturity. More radical genomic selection schemes that apply reproductive technologies and nucleus herds have also been described. A key driver of genetic gain was a potential reduction in sire generation interval from 5 to as little as 1.5 years by using young bulls. Generally, the rate of genetic gain in the schemes evaluated was between 12% and 100% more than conventional progeny-testing, while the rate of inbreeding per generation tended to be reduced due to less co-selection. However, short generation intervals can lead to higher annual inbreeding rates.

Genomics and the global livestock industries

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After two decades devoted to the quest of developing tools for selection that are based on information obtained directly from the bovine genome, we find ourselves at an interesting juncture. On one hand, application of the technology has essentially eliminated the potentially large negative impact of spontaneous single mutation genetic defects, as the management of recent examples of those defects has demonstrated. We also now have the ability to perform more accurate selection based on Molecular Breeding Values for animals that are closely related to the discovery population used to establish the associations of genetic markers with phenotypic measures or genetic evaluations used as phenotypic data; dairy example. Yet the amount of genetic variation explained by the DNA tests falls short of the expectations held for the technology; current tests are less effective in distant relatives within a breed and are not robust enough to be used across breeds. It is hypothesized that the new “larger SNP panels” will help extend the effective use of tests to more distantly related animals, including across breeds. Beyond the application of the new “larger panels” looms sequencing and imputing sequences across individuals with the hopes of being able to find causative mutations or SNPs in perfect harmony with the mutation.

However, the investment to revisit discovery populations will be large. We can ill afford to duplicate genotyping or sequencing activities for prominent individuals. Hence, the concept of a global strategy for genotyping and sequencing becomes an attractive proposition, since many of our livestock populations are related. As we have learned more of the complexities of the genome, the number of animals in discovery populations necessary to achieve high levels of predictability has grown dramatically. No one organization has the capacity or resources to assemble the animals needed, especially for novel, expensive or hard-to-measure phenotypes. Therefore, consolidating dataset or meta-analysis of like data results will be necessary to help map sources of variation.

Thinking beyond the genome to additional complex areas of exploration invites initiatives in proteomics and phenomics (defined here as phenotypes at the biological level that contribute to the architecture of our complex traits). These areas would also be fertile ground for strategic international collaborations as, by nature, it will be difficult and expensive for any one organization to accumulate the data required to enable discovery at the desired level. Current activities and future opportunities relating to international collaborations will be presented as examples.

Genomic selection in French dairy cattle

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A characteristic of the French model for genomic selection is the use of haplotypes, instead of single SNPs, in order to maximize LD between markers and QTL. For each trait, 20-40 large QTL are accounted for in a QTL BLUP and traced by haplotypes of 4-5 SNPs. To maximize the variance explained by markers and account for relationships, the model also includes 300-700 trait-dependent chromosomal regions selected by elastic-net. This model was found to be the most efficient one among all tested ones. It requires a tuning effort to phase genotypes, detect QTL, select SNP. Genomic selection is implemented in Holstein, Montbéliarde, and Normande breeds (75, 16, and 12% French dairy cows). QTLs are defined within breed and many of them were found to be breed-specific. Reference populations include 1800 and 1400 bulls in Montbéliarde and Normande breeds. In Holstein, the very large reference population of 18,300 bulls originates from the EuroGenomics consortium. Since 2008, ~55,000 animals have been genotyped with the 54k chip by Labogena for selection. Bulls GEBV were made official in June 2009. In the following year, the market share of the young bulls reached 30%. Advertising actions have been undertaken to recommend a time-restricted use of young bulls with a limited number of doses. In January 2011, genomic selection has been opened for females to all farmers. The choice of one unique provider, Valogene, simplifies INRA's evaluation activity and improves the negotiation capacity to obtain the lowest cost for chips.

Comparison of genomic selection across species

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The rate of genetic gain can be increased by increasing the accuracy of selection, decreasing the generation interval or increasing the intensity of selection. In the dairy industry, the availability of genomic estimated breeding values (GEBVs) offers the opportunity to substantially reduce generation intervals, through selection of young bulls rather than five to six year old bulls following progeny testing. This will lead to an almost doubling of the rate of genetic gain in dairy cattle. In both sheep and beef cattle, the main opportunity with genomic selection is to increase the accuracy of selection for breeding objective traits which are difficult or expensive to measure, such as feed conversion efficiency, lean meat yield and carcass quality traits, and number of lambs born in the case of wool sheep. The gains achieved could be substantial – a recent study predicted that genomic selection could increase genetic gain by 158% in beef cattle (Van Eenennaam et al. 2011).

In all industries additional gains can be achieved by combining genomic selection with advanced reproductive technologies such as JIVET (Juvenile Invitro Embryo Transfer) to reduce generation intervals. With these schemes attention must be paid to the rate of inbreeding. This can be managed with tools which use genomic information to avoid matings which would result in progeny with excessive homozygosity.

Finally, particularly in the beef and lamb industries, genomic selection offers the opportunity to increase the efficiency of development of composite lines which capture the most desirable characteristics from contributing breeds.

Applied genomic selection in layers

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In poultry breeding programmes owned by private companies, selection is done within closed populations based on comprehensive phenotypic data recording in both pure and cross line birds under standardised housing conditions. Due to sex limited data recording, male selection for egg quality and production traits is based mainly on female sibling tests.

Early selection of the most promising male within full sib families will improve the rate of genetic progress and can substantially reduce generation interval.

Several studies based mainly on microsatellites have identified QTLs for production and quality traits. The identification of a single nucleotide mutation in brown layers has been used to eradicate mutant variants with the consequence of a non-restricted use of canola in layer diets.

Genome wide selection is still in the initial stages in which 10 to 40 K SNP chips have been used so far. Due to sequencing of all major pure lines from DNA pools, a customised 600K chip has been developed for comprehensive genotyping of all commercial lines. Small scale line-specific SNP chips will be developed afterwards in order to reduce costs for genotyping of male progeny during rearing periods. Only most promising young males will be transferred to the breeding farm for performance testing and pedigree reproduction. Parental generation will still be genotyped with the comprehensive SNP chip and used for retraining and for input.

The first results using 30K chips were obtained from a commercial line used for training, validation and selection, which have shown improved accuracy of prediction at a young age and so resulted in increased genetic gain. Genome wide marker-assisted selection must prove its advantages over traditional methods including cost benefits.

Genomic selection in sheep

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Genomic selection can increase the accuracy of estimated breeding value, particularly for traits that are difficult to measure on-farm or those that cannot be measured early in life. Modeling of sheep breeding programs has shown that the predicted additional rates of genetic gain could be 30% for wool sheep and 20% for meat sheep. The advantage in wool sheep is mainly an increased accuracy of predicting merit for life time production (wool and lambs) when selecting at an early stage. The advantage in meat sheep is mainly the prediction of carcass and meat quality traits that cannot be measured on breeding animals. The CRC for sheep industry innovation in Australia has used more than 7000 records from the Information Nucleus Flock as well as from the Sheep Genomics Project to predict genomic breeding values which were compared with Australian Sheep breeding values (ASBVs) from progeny tested industry rams. The prediction accuracy was shown to be highest for merino sires, with accuracies of ~0.6 for wool and ~0.5 for meat traits, because the reference population was mainly based on a merino genetic background. Prediction accuracies were between 0.2 and 0.5 in maternal and terminal sire breeds. Further work is ongoing to add additional data on phenotypes and genotypes. The genetic resources used for this whole genome association study reflect the Australian sheep industry, and a challenge is how to

handle the genetic diversity across breeds as well as within breeds. Work is ongoing to consider accuracy of prediction of breeds as well as lines within breed that have a low genomic relationship with the reference population. This will result in recommendations for constituting future reference populations to support genomic selection in sheep industry breeding programs. The commercial delivery of genomic information to breeders in Australia can be via the existing genetic evaluation system (OVIS) where various methods have been explored to combine genomic and phenotypic information into predicted breeding value. This has recently been tested in a pilot project and breeders have received estimated breeding values for young rams for existing traits but with improved accuracy, as well as for new traits that are not routinely measured.

Genetic variation in the bovine myostatin gene and its effect on muscularity

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Retail beef yield (RBY) refers to the amount of saleable meat on the carcass, and is an economically important trait in the beef cattle industry. Muscle mass is a primary component of RBY, which is a heritable trait influenced by many genes. One gene in particular, known as myostatin (MSTN), encodes a protein that is a potent negative regulator of muscle mass. Loss-of-function mutations have been discovered in MSTN that are responsible for extraordinary increases in muscle mass in cattle; a phenotype referred to as double muscling. These double muscling mutations have commanded the most attention within a gene that contains high genetic variability.

In this study, we examined the effects of a series of MSTN genetic variants on muscle mass. Eighteen polymorphisms were identified in a small Angus cattle cohort, which included the 821del11 double muscling mutation. In a larger Angus cattle population, genotypes were determined at 6 tag SNP, which captured the genetic variation at each of the 18 sites. Haplotypes were inferred from the genotypic data and tested for their association with quantitative indices for muscling traits. The results demonstrated that the non-disruptive MSTN polymorphisms were also contributing to differences in muscle mass; albeit milder effects compared to the 821del11 double muscling mutation.

The effects of the MSTN haplotypes showed similar trends in an independent cattle population, comprising multiple cattle breeds. Associations were also found between the MSTN haplotypes and other traits of industry value, suggesting a more expansive role for MSTN in other tissue types.

This study has contributed new findings about the genetics influencing muscle mass in beef cattle. Moreover, the milder effect of the MSTN haplotypes investigated provide more practical alternatives for Australian beef producers focusing on improved muscle content. The association with multiple traits provides further use for improving estimates that predict the genetic potential of cattle.

The accuracy of genomic prediction for novel traits in sheep

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Genomic prediction methods make use of reference populations with both phenotypic records and genetic marker information to predict genomic breeding values in individuals without phenotypes. This increases genetic gain through early selection of juveniles and produces opportunities to improve traits which are hard and expensive to measure, so called novel traits. These novel traits could be measured and analysed in a reference population, which then could be used predict genomic breeding values in the general population without incurring additional phenotyping costs. The novel traits currently targeted by the sheep industry to maintain or increase market share for lamb include breeding objective traits that directly affect carcass value, such as lean meat yield and carcass fat, and traits that are associated with meat quality, such as shear force, intra-muscular fat and Omega-3 content. Phenotypic data for these carcass traits was collected on up to 4000 sheep in the information nucleus scheme of the Cooperative Research Centre for Sheep Industry Innovation and the Sheep Genomics project. The multi-breed reference population was made up mainly of crosses of Merino, Border Leicester, Polled Dorset and White Suffolk sheep. Genomic best linear unbiased prediction was used to predict genomic breeding values. Accuracy of genomic breeding values was evaluated in an across ram half-sib family cross-validation scheme as the correlation of predicted and measured phenotypes divided by the square root of heritability. The accuracy was moderate in most traits but has increased with the inclusion of more phenotypes. This indicates that prediction of novel traits will be a feasible option to increase genetic gain in sheep provided that the reference population is large enough.

Breeding the ideal heifer

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Genomic selection has the potential to double the rate of genetic gain in dairy cattle. This is primarily due to the improved ability to predict breeding values with molecular markers for young unproved bulls. The accuracy of genomic predictions is thought to be caused by close associations between markers and causal mutations affecting traits. However, it is possible that markers do not track the genes causing variation in economic traits completely. An alternative approach is to track segments of a chromosome from influential ancestors to their many descendants and estimate the contribution of the segment to their breeding value. We have used SNP markers to track chromosome segments from an influential Holstein sire and compare the effect of the segments on milk yield with that predicted by genome wide association studies and genomic EBVs.

The potential value of genomic technologies to the beef industry

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Australian Performance Beef Breeders' Association and Australian Limousin Breeders' Society

Genomics has the potential to increase the rate of genetic gain in beef cattle improvement programs through the incorporation of genomic predictions into current genetic evaluation procedures.

The greatest value of genomic predictions is for traits which are difficult or expensive to measure early in life such as female fertility, feed efficiency and tenderness

The promise of genomic technology has not been realized in the beef industry as quickly as expected because initial anticipation that 50 percent of genetic variation for economically important traits would be explained by six to ten SNPs with large effects have proved to be wrong. It is now clear that high density SNP tests are required to explain anywhere near 50 percent of the genetic variation for these traits.

Genomics technology is further advanced in the dairy industry because they have a much greater population of sires with high accuracy breeding values based on progeny testing. The challenge for the beef industry is to develop adequate resource populations which relate genomics predictions to phenotypic performance. It is hoped that denser marker panels will provide genomic predictions which will work across breeds.

The ability to impute genotypes for high density SNP panels from low density panels may allow the use of lower priced, SNP panels at the commercial level to predict phenotypic performance in feedlots and carcass traits at slaughter. Results of high density SNP panels for sires will increase the accuracy of predictions from these low density panels.

Testing strategies likely to be used in the beef industry will depend on the amount of genetic variation explained for each trait and the cost of the tests.

Getting value from genomics for the Merino industry – current challenges and future expectations

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Victorian Stud Merino Sheep Breeders Association

- The potential benefit of genomics selection at a very young age is enormous
- The practical application of genomic testing is currently the biggest challenge for widespread uptake
- The current cost for a 50K SNP test of \$150-\$250 is one major stumbling block
- The other current major handicap to genomics testing is that the lag time from sampling to results is too long
- To guarantee value from genomic technology, for merinos, the cost per test should be no more than \$20 and the turnaround time from sampling to results should be less than ten days.
- Concentrating genomic selection on traits that cannot be seen or felt, such as some carcass traits, innate staple strength, worm resistance and fertility, will deliver the most benefit to the merino industry.
- Stud merino operations typically have animal progeny numbers over one thousand or so, and to get the most benefit from genomics, all the progeny should be screened for various traits to indicate superior and inferior performers so that maximum genetic gain can be achieved in future breeding decisions.

Integration of genomic technologies into beef cattle and sheep genetic evaluations in Australia

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Genomic information has the potential to change the way beef cattle and sheep are selected and to substantially increase genetic gains. Ideally genomic data will be used in combination with pedigree and phenotypic data to increase the accuracy of estimated breeding values. The first example of this in Australia was the integration of markers for tenderness into beef cattle breeding values. Subsequently, the availability of high density SNP panels has made genomic selection possible, and created significant challenges for genetic evaluation with regard to both data management and statistical modelling. Discovery populations have been established in both industries, in which an extensive range of phenotypes have been collected and animals genotyped using 50K SNP panels. From this information genomic predictions of breeding value have been developed, albeit with varying levels of accuracy. These predictions have been incorporated into routine genetic evaluations using three approaches and results are now available to breeders. In the first, genomic predictions have been included in genetic evaluation models as additional traits. The challenges with this method have been the construction of consistent genetic covariance matrices, and a significant increase in computing time. The second approach has been to use a selection index procedure to blend genomic predictions with existing estimated breeding values. This method has been shown to produce very similar results, and has the advantage of being simple to implement and fast to operate. Thirdly, in sheep a single step analysis combining a genomic relationship matrix with a standard pedigree based relationship matrix has been used to estimate breeding values for carcass and eating quality traits. It is likely this procedure or one similar will be incorporated into routine evaluations in the near future. While the progress made in methods of integrating genomic information has been impressive in both beef and sheep evaluations in Australia, one of the major challenges for the future will be in managing much large volumes of genomic data as the number of animals genotyped and the density of markers increases.

Integration of genomic technologies into dairy genetic evaluations

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The Australian Dairy Herd Improvement Scheme (ADHIS) has run genetic evaluations for Australian and international dairy cattle to facilitate genetic gain in the dairy industry since 1983. In 2010, genomic information was incorporated into the genetic evaluations, with the release of genomic estimated breeding values (GEBVs) in 2010. The genomic estimated breeding values are predicted by blending a marker only breeding value (Direct Genetic Value or DGV) and the traditional Australian breeding value (ABV), according to the reliability of the two components. The estimation of DGVs is based on Ridge Regression BLUP on data from Australian daughters of bulls. The blending method takes into account the proportion of polygenic variation explained by the DGVs. In Holstein cattle the latter varies from 0.4 to 0.8 depending on the trait (0.8 for yield traits). In February 2011, a total of 2749 Holstein and 686 Jersey bulls had been genotyped, and the reference populations for yield traits consisted of 2247 and 609 animals for Holstein and Jersey respectively. For conformation the reference population was only about half this size reflecting the lower level of recording for this trait. For young Holstein bulls without daughters, on average the reliability of the GEBVs is at least twice that of the ABV. The increase is smaller in animals which have ABVs with higher reliabilities, such as proven bulls or well-recorded cows and in Jerseys where the reference set is considerably smaller.

Genomics – who gets the benefit? A commercial perspective

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Genomics represents the biggest change to the AI industry since BLUP. But unlike BLUP, genomics comes with a potentially disruptive aspect. There is no doubt that genomics will benefit dairy producers and the industry overall. For the AI industry however, the introduction of genomics poses significant challenges. Where genomic technology has been developed “in house” by breeding companies, a competitive advantage can be gained and a degree of control maintained. Where genomic technology is commercially available, the circumstances are different.

The promised efficiency gains through a reduction in bull numbers are hard to realise in an environment where competitors have access to the same technology, the same population and share a common breeding goal. Numbers of bulls tested (both genomically screened and progeny tested) becomes one of the few ways of establishing an advantage over competitors.

In a market place that is mature, the increased cost of running a breeding program incorporating genomics is difficult to recover. The market is struggling to pay a premium for genomically screened young bulls with no daughter information, and the intermediate priced genomic semen product is eroding sales in the premium, daughter proven end of the market.

Genomics poses a threat to the AI industry in its current form. Maybe that is a good thing, maybe not. It will ultimately be up to the marketplace to decide.

Future opportunities and needs in beef

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Genomic selection is rapidly changing dairy breeding but to date it has had little impact in beef cattle breeding. Unlike the dairy industry, the beef industry has relatively few sires with highly accurate EBVs and training of genomic predictions has generally relied on a few thousand animals with both phenotypes and genotypes. To date the accuracy of genomic predictions are generally less than 0.5. Therefore the immediate challenge for beef is to increase the accuracy of genomic predictions by greatly increasing the number of animals with phenotypes and genotypes. Particular focus should be given to traits that are difficult to record on the young animal or for new traits that may be required for future breeding objectives. Current results with 50K chip are showing low predictability across breeds. Therefore given the number of important beef breeds, the large effective population sizes and small breed datasets, genotyping with higher density SNP chips is likely to be required to generate accurate genomic predictions that are predictive across breeds. Genetic evaluation procedures are now available in beef that combine traditional pedigree and performance data with genomic predictions. This will allow greater rates of genetic gain through increased accuracies and reduced generation intervals. In the medium term as the availability of high density genotypes increases, the genetic evaluations systems can be modified to use the genomic information via a modified relationship matrix built using SNP genotypes. In the longer term, the challenge for breeding and production will be to harness the power of whole genome sequence data. For the beef industry there will be both challenges and opportunities in the future to restructure the breeding sector as the utility of genomics information increases. Strategic performance recording and genotyping, coupled with use of accelerated reproduction technologies, will be required to maximise the potential of the different technologies to effectively contribute to increasing rates of genetic gain in the beef industry.

Future requirements for sheep breeders to capture the full benefits of genomics

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The introduction of integrated genomic and genetic information into current breeding programs offers significant benefits to ram breeders in Australia. Specifically the ability to incorporate traits that are either expensive or hard to measure commercially at young ages with relative accuracies equivalent to measurement at later life will change the way that breeders select breeding animals. All these advantages if used successfully should improve the rate of genetic gain that breeders are able to achieve. However with these additions will come future challenges that will require different information and new tools to enable breeders to take full advantage.

Traits that are either expensive to hard to measure are usually traits that also are difficult to quantify in terms of economic value and commercial impact. Breeders will require better tools to estimate the appropriate economic weighting of such traits or there is a real risk that such traits will be overemphasised in the breeding objective because of either novelty or perception of value.

Selection at younger ages offers the ability to reduce the generation interval. However for many breeders there is a risk that selection of young animals may mask traits such a structure, visual traits and fitness (reproduction) that could have a major impact on the commercial viability of sheep. It will critical that the population of selected young animals are linked to a population of animals where traits that are expressed at later ages are measured to minimise potentially deleterious effects. The alternative is that further effort must be put into finding genomic predictions of the structural, fitness and visual traits which may require further investment as generally the numbers of phenotypes for these traits are limited.

Tools that assist in selecting the right animals will be a critical requirement by breeders as they face genomic integration with better accuracies. Not only is the question of which animal to measure (genotype) going to become more complex but more strategically which animals are selected as parents such that genetic diversity is maintained at a level to manage inbreeding and favourable allele frequencies. Mate selection tools such as TGRM already are capable of doing this; however such will have to have much higher adoption rates if industry is to successfully capture the most benefit from genomic integration.